

1 Title: Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human  
2 disturbance or habitat structure?

3 Abbreviated title: Drivers of red fox activity patterns

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17 **Abstract**

18 Daily activity patterns in mammals depend on food availability, reproductive stage,  
19 habitat selection, intraspecific interactions and predation risk, among other factors. Some  
20 mammals exhibit behavioral plasticity in activity patterns, which allows them to adapt to  
21 environmental changes. A good example of this can be found in the red fox *Vulpes vulpes*.  
22 This species is adapted to living in highly humanized environments, where it is often  
23 culled because it may affect human interests (e.g. through the consumption of game  
24 species or livestock). We assessed the potential main drivers of the daily activity patterns  
25 of the red fox in 12 Iberian Mediterranean areas through the use of camera traps. Among  
26 drivers, we considered main prey availability (wild rabbit *Oryctolagus cuniculus*), degree  
27 of human disturbance (e.g. distance to human settlements, and intensity of predator  
28 control) and habitat structure. Our results revealed a predominantly crepuscular and  
29 nocturnal activity of foxes with local variations. Although overall activity of fox  
30 increased with rabbit availability, the temporal overlap with prey activity was on average  
31 low, because foxes increased activity when rabbits decreased theirs (twilight-night). Red  
32 fox activity rhythms seemed to be determined by human presence where human  
33 disturbance is high. In addition, diurnal activity decreased in areas with higher levels of  
34 human disturbance (closer to human settlements and high predator control intensity) and  
35 increased in dense habitats. Our study shows that daily activity patterns of highly  
36 adaptable species are determined by several interacting drivers, resulting in complex  
37 behavioral patterns. This suggests that further studies should consider different factors  
38 simultaneously for a better understanding of daily activity patterns of wildlife in  
39 humanized landscapes.

40 **Key words:** camera trap, circadian rhythms, human disturbance, fox control,  
41 *Oryctolagus cuniculus*.

## 42 **Introduction**

43 Daily activity patterns have been defined as adaptive sequences of routines that meet the  
44 time structure of the environment, shaped by evolution and fine-tuned to the actual state  
45 of the environment (Halle, 2000). In mammals, daily activity is internally regulated by  
46 species-specific endogenous clocks (Kronfeld-Schor & Dayan, 2003), but also by  
47 external factors such as nutritional requirements (Masi, Cipolletta & Robbins, 2009),  
48 temporal habitat selection (Chavez & Gese, 2006), intraguild interactions (Di Bitetti *et*  
49 *al.*, 2010) or predation risk (Lima & Dill, 1990). Additionally, mammals, as well as other  
50 animals, show behavioral responses to environmental changes induced by human  
51 activities (Tuomainen & Candolin, 2011).

52 Similarly to other mammals, daily activity patterns in mammalian predators are mainly  
53 determined by both innate activity rhythms and prey availability. The latter has been  
54 defined as the combination of prey abundance and their accessibility; prey can be  
55 abundant but inaccessible to predators when not active or in inaccessible habitats  
56 (Ontiveros, Pleguezuelos & Caro, 2005). A high level of synchrony between predator and  
57 prey activity has thus been reported in some cases (Foster *et al.*, 2013; Monterroso, Alves  
58 & Ferreras, 2013). Additionally, daily activity patterns of mammalian predators may be  
59 influenced by other external factors like habitat structure or human disturbance.  
60 Mammalian predators frequently decrease their activity at daytime in open habitats  
61 (Chavez & Gese, 2006), where predator removal is conducted (Kitchen *et al.*, 2000) or  
62 where human activities such as hunting or outdoor recreational activities are common  
63 (Belotti *et al.*, 2012; Ordiz *et al.*, 2012).

64 We chose the red fox *Vulpes vulpes* as a model to study the flexibility of mammalian  
65 predator daily activity patterns due to its high ecological plasticity. The red fox is the  
66 most widely distributed mammalian carnivore of the world and it is found in many  
67 different habitats, where it can be abundant and feeds on a large variety of foods (Sillero-  
68 Zubiri *et al.*, 2004; Díaz-Ruiz *et al.*, 2013). Although the species is a generalist predator,  
69 in certain regions such as central-southern Spain, European wild rabbits *Oryctolagus*  
70 *cuniculus* are the fox main prey when abundant (Delibes-Mateos *et al.* 2008; Díaz-Ruiz  
71 *et al.*, 2013). Red foxes have adapted to living in highly human-dominated landscapes,  
72 where they take advantage of human subsidiary resources (Bino *et al.*, 2010). On the other  
73 hand, they are often persecuted by humans because they feed on game species and

74 livestock (Sillero-Zubiri *et al.*, 2004). In areas where predator control is carried out more  
75 intensively foxes are exposed to a higher ‘risk of predation’ by humans (Reynolds &  
76 Tapper, 1996). Thus, fox control could cause stronger fox behavioral responses to human  
77 presence in these areas: when hunting constitutes an important source of mortality, human  
78 presence itself may create a ‘landscape of fear’ and thereby provoke strong behavioral  
79 responses (Martin *et al.*, 2010; Ordiz *et al.*, 2012).

80 Daily rhythms of activity are among the least studied aspects of the ecology and biology  
81 of red foxes. Different studies have shown that red foxes are mainly nocturnal-  
82 crepuscular, a pattern that can be explained by factors such as season, habitat structure,  
83 prey and human activities (Blanco, 1986; Cavallini & Lovari, 1994; Baker *et al.*, 2007;  
84 Monterroso, Alves & Ferreras, 2013; Villar *et al.*, 2013). Notwithstanding, to our  
85 knowledge no study has examined the simultaneous influence of ecological (e.g. habitat  
86 and prey availability) and human-related factors on red fox activity.

87 We evaluated the plasticity of red fox daily activity in environments with varying levels  
88 of prey availability, habitat structure and human disturbance (e.g. fox control and distance  
89 to human settlements) in Mediterranean areas of central Spain, where fox control is a  
90 widespread game management tool (Delibes-Mateos *et al.*, 2013; Díaz-Ruiz & Ferreras,  
91 2013). According to previous studies on mammal predator activity we expected that foxes  
92 would adapt their activity pattern to that of their preferred prey at least where this is highly  
93 available, but that this behavioral pattern could be disrupted by other factors, such as  
94 habitat composition or human disturbance. To assess this, we first tested whether the daily  
95 activity patterns of the red fox were related to the daily activity of its preferred prey  
96 (European wild rabbit) in central Spain (Delibes-Mateos *et al.* 2008). Secondly, we tested  
97 the relationships between the daily activity of red foxes and prey availability, human  
98 disturbance and habitat structure simultaneously.

## 99 **Material and Methods**

### 100 *Study area*

101 The study was conducted in 12 localities within central Spain (Fig. 1), with  
102 Mediterranean-continental climate (Rivas-Martínez, Penas & Díaz, 2004). The landscape  
103 was heterogeneous and dominated by cereal croplands and permanent crops such as olive  
104 groves and vineyards and natural pastures, mixed with Mediterranean scrubland (mainly

105 *Cistus* spp. and holm oak *Quercus ilex* forests). Other less abundant habitats included  
106 riparian habitats, ‘dehesas’ (pastureland with savannah-like open tree layer, mainly  
107 dominated by Mediterranean evergreen oaks) and tree plantations (*Pinus* spp., *Eucalyptus*  
108 spp. and *Populus* spp.). Villages and scattered dwellings were interspersed in the  
109 landscape. Surface and habitat composition varied among localities (see Table 1 for a  
110 detailed description).

111 Agriculture and livestock were the main economic activities in all localities, which were  
112 hunting estates too, with the exception of two protected areas where hunting was not  
113 allowed (numbers 5 and 11 in Fig. 1). Hunting estates were managed to improve small  
114 game populations, mainly by the provision of supplementary food and water, and predator  
115 control. Direct shooting and live trapping with cage traps and neck snares are the methods  
116 most used for legal fox culling (Delibes-Mateos *et al.*, 2013, Díaz-Ruiz & Ferreras, 2013).  
117 In central Spain, there is a high variation in the use of these management measures among  
118 hunting estates (Arroyo *et al.*, 2012). In addition, estates usually employ diverse  
119 management tools simultaneously and their intensity of use is generally correlated; more  
120 intensively managed estates employ more game keepers per km<sup>2</sup>, and have higher hunting  
121 pressure (e.g. more hunting days per year) and larger bags (Arroyo *et al.*, 2012). In our  
122 study the intensity of fox control also varied largely among hunting estates (Table 1), thus  
123 reflecting differences in general game management intensity.

#### 124 *Camera trap surveys*

125 Camera trap surveys were carried out between 2010 and 2013. One sampling survey was  
126 developed in each study area between mid-May and mid-August (Table 1) outside the  
127 regular hunting season. We used two similar models of infrared-triggered digital cameras:  
128 Leaf River IR5 (LeafRiver Outdoor Products, USA) were used only in 2010 surveys (35  
129 cameras), and HCO ScoutGuard (HCO Outdoor Products, USA) in the remaining  
130 surveys (179 cameras). Cameras were uniformly spaced in each locality following a grid-  
131 sampling scheme according to field features; the average distance between neighbouring  
132 cameras was ~1.2 km, boosting independence between them (Monterroso, Alves &  
133 Ferreras, 2013; 2014). Between 14 and 20 camera traps were deployed in each study  
134 locality, proportionally to locality surface (Table 1). Cameras were mounted on trees  
135 approximately 0.5m off the ground and set to record time and date when triggered.  
136 Cameras operated 24 h a day for an average period of  $28.4 \pm 0.4$  days (mean  $\pm$  SE). We

137 programmed cameras with the minimum time delay between consecutive photos to ensure  
138 species identification of each event.

139 In order to increase the detection probability of red fox, we set the sensitivity of the  
140 infrared sensor at the highest level, and used a combination of Valerian scent and Iberian  
141 lynx *Lynx pardinus* urine, which is an effective attractant for the red fox (Monterroso,  
142 Alves & Ferreras, 2011). Lures were put in two independent perforated plastic vials (3-4  
143 ml) secured to a metal rod, set at 2-3 m from each camera trap, and replenished every two  
144 weeks. Consecutive images of the same species within 30 min interval were considered  
145 as the same event and those separated by a longer interval as independent events (O'Brien,  
146 Kinniard & Wibisono 2003; Davis, Kelly & Stauffer, 2011). To assess the ability of  
147 camera-trapping to detect foxes and rabbits we estimated weekly detection probability  
148 conditioned to their presence in our study area using single season-species occupancy  
149 models (see MacKenzie et al. 2006). Models were built taking into account a habitat  
150 covariate (i.e. open or dense, a description of how habitats were classified in these two  
151 categories is provided below) that may affect both species detection and occupancy  
152 probabilities (MacKenzie et al. 2006).

153 In an independent study, we tested whether rabbit detection in the cameras was affected  
154 by the use of lures. We gathered data during field trials performed in 2013 with the same  
155 methodology (n=37 cameras during ~one month) in a near-by area with similar landscape  
156 features as in our study areas (i.e. Mediterranean habitats; Monfragüe National Park).  
157 Single season-species occupancy models showed that the probability of weekly rabbit  
158 detection conditioned to its presence did not change significantly between lured cameras  
159 (average detectability  $\pm$  SE:  $0.174 \pm 0.105$ ) and non-lured ones ( $0.03 \pm 0.078$ ) (author's  
160 unpublished data), so the use of these scent attractants does not reduce rabbit detectability.

#### 161 *Relationship between fox and rabbit activity patterns*

162 We studied the activity patterns of red foxes and rabbits to estimate the probability of  
163 both species concurring in a time period. Probability density functions of activity for both  
164 species were estimated non-parametrically for each locality from their detection records  
165 using kernel density estimates (Ridout & Linkie, 2009). Density functions were only  
166 estimated for species in localities with >10 records. We also estimated for each locality  
167 the coefficient of overlap  $\Delta_1$  for small sample sizes (Ridout & Linkie 2009, Linkie &  
168 Ridout 2011) between both species.  $\Delta_1$  ranges from 0 (no overlap) to 1 (complete

169 overlap). The precision of this estimator was obtained through confidence intervals as  
170 percentile intervals from 500 bootstrap samples (Linkie & Ridout, 2011). These analyses  
171 were performed in R 3.0.1 (R Core Development Team 2013), using an adaptation of the  
172 scripts developed by Linkie & Ridout (2011)  
173 (<http://www.kent.ac.uk/ims/personal/msr/overlap.html>).

174 *Relationship between fox activity, rabbit availability, human disturbance and habitat*  
175 *structure*

176 Records of red fox activity were assigned to one of three time periods defined according  
177 to light levels: i) twilight (one hour prior to sunrise and one hour after sunset, as a semi-  
178 darkness period; Mills, 2008); ii) diurnal; and iii) nocturnal periods, taking into account  
179 the time of sunset and sunrise in each study site during the sampling period.

180 We calculated a rabbit availability index for each camera station as the number of  
181 independent detections (regardless of time period) of rabbits per 100 trap days  
182 (Monterroso, Alves & Ferreras, 2014).

183 Distance to human settlement was used as a proxy of human disturbance (Ordeñana *et*  
184 *al.*, 2010). We calculated the distance (in kilometres) to the nearest human settlement  
185 from each camera using a Geographic Information System (QGIS 1.8.0; QGIS  
186 Development Team 2013).

187 Fox control intensity was gathered through face-to-face interviews with game managers  
188 of each hunting estate, conducted in February before field sampling. We asked managers  
189 about the number of foxes removed in the previous hunting season (Table 1). We  
190 estimated intensity of fox control as the number of foxes removed per km<sup>2</sup> and year  
191 (fox·year<sup>-1</sup>·km<sup>-2</sup>). As explained above, we used this variable as another index of human  
192 disturbance because high levels of predator extraction are generally associated with more  
193 game keepers and more intensive management activities (Arroyo *et al.*, 2012).

194 We grouped habitat types in: dense (including scrubland, forests and riparian habitats)  
195 and open habitats (including ‘dehesas’, pasturelands and croplands). Habitat types  
196 surrounding each camera trap were identified from CORINE land-cover 2006 and  
197 updated satellite orthophotos (Instituto Geográfico Nacional, <<http://www.ign.es/>>) and  
198 checked during fieldwork. Using QGIS 1.8.0, we calculated the percentage of each habitat  
199 type (i.e. open versus dense) within a buffer of 200 m radius around each camera trap

200 (Ordeñana *et al.*, 2010). Either open or dense habitat was assigned to each camera trap  
201 according to the prevailing category (>50%) within the buffer. Overall, 124 cameras were  
202 assigned to open habitat and 90 to dense habitat.

203 Generalized Linear Mixed Models (GLMM) were employed to assess red fox activity as  
204 a function of time period (day, twilight and night), rabbit availability, human disturbance  
205 (fox control intensity and distance to human settlement) and habitat type. The response  
206 variable was the number of independent red fox detections for each camera in a given  
207 time period. It was fitted to a Poisson distribution through a log link function. We included  
208 as an offset in the models the trapping effort in each camera for each period and locality,  
209 calculated as No. camera-days  $\times$  period duration in hours, to standardize activity measures  
210 in each period per time unit. Camera trap identity was included as a random effect nested  
211 within study locality, to account for the non-independence of observations according to  
212 these factors. Fixed explanatory effects included: time period and habitat as categorical  
213 variables; distance to human settlement, intensity of fox control and overall rabbit  
214 availability as continuous variables; and all two-way interactions between time period  
215 and other variables. Analyses were carried out with R 3.0.1 with lme4 package (Bates &  
216 Maechler, 2010). We compared all possible combinations of these independent effects,  
217 as all of those models were biologically plausible, by using the dredge function (package  
218 MuMIn; Bartoń, 2012). We selected the models with delta  $\Delta AIC_c < 2$ , and if no single  
219 model accounted for >90% of the total model weights we calculated model-averaged  
220 parameter estimates for the variables included in those models (Burnham & Anderson,  
221 2002). We assessed whether models were affected by overdispersion, accepting  
222 dispersion parameter levels between 0.5 and 1.5 (Zuur *et al.*, 2009). We also checked for  
223 potential collinearity and redundancy of the explanatory variables by analysing the  
224 Variable Inflation Factor (VIF). All the predictor variables had VIF <1.26, so they were  
225 considered not collinear nor redundant and included in the analysis (Belsley, Kuh &  
226 Welsch, 1980).

## 227 **Results**

### 228 *Red fox daily activity patterns and overlap with rabbit activity*

229 During a total effort of 6128 trap-days (mean  $\pm$  SE: 511 $\pm$ 27 trapping days $\cdot$ locality<sup>-1</sup>; Table  
230 1) (all means are presented  $\pm$  SE), we obtained 610 independent detections of red foxes  
231 (51 $\pm$ 14 detections $\cdot$ locality<sup>-1</sup>) and 1190 of rabbits (99 $\pm$ 37 detections $\cdot$ locality<sup>-1</sup>; Table 2).

232 Mean weekly detection probability was overall similar for both species (red fox:  
233  $0.35 \pm 0.07$ ; rabbit:  $0.33 \pm 0.08$ ), but varied among study localities (Table 2).

234 Red foxes were detected in all localities (Table 2). Fox activity density functions varied  
235 slightly among localities but, as a rule, two major activity peaks occurred, one after sunset  
236 and another before sunrise (Fig. 2a).

237 Rabbits were detected in most localities (Table 2). Rabbit activity density functions were  
238 similar among localities, revealing a strong bimodal pattern, with a major activity peak  
239 occurring after sunrise and throughout the morning and a second peak before sunset (Fig.  
240 2b).

241 The coefficient of activity overlap between red fox and rabbit was estimated in nine  
242 localities with enough detections of both species (Table 2), and varied widely among  
243 them, ranging from 0.24 to 0.60 (mean =  $0.40 \pm 0.04$ ; Table 2 and Fig. 3). Activity overlap  
244 in a given locality was not correlated with mean rabbit availability in that locality  
245 (Pearson's correlation =  $-0.45$ ,  $p=0.2$ ).

246 *Rabbit availability, human disturbance and habitat structure as factors explaining red*  
247 *fox activity patterns*

248 Five of the evaluated models showed  $\Delta AIC_c < 2$ , involving a total weight of 0.70 (Table  
249 3). None of these models were affected by overdispersion (dispersion parameter levels:  
250 0.67-0.69). All these models included all the fixed variables, except fox control, which  
251 was not included in two of the selected models (Table 3). Interactions between time period  
252 and the remaining fixed variables were also included in the selected models (Table 3).  
253 The most important variables explaining fox activity were time period, rabbit availability,  
254 distance to human settlement and habitat type, and the interactions between time period  
255 and both rabbit availability and habitat type (Table 4). Fox control and other interactions  
256 between variables contributed less to explain the variability in daily activity of foxes  
257 (relative importance  $< 0.6$ ; Table 4).

258 Model-averaged parameter estimates revealed that red fox activity was in general lowest  
259 during daytime, and increased with rabbit availability except during daytime (Table 4;  
260 Fig. 4a). Daytime activity of red foxes increased in dense habitats (Day\*Dense habitat  
261 interaction, Table 4, Fig. 4). Overall red fox activity increased with increasing distance to  
262 human settlements (Table 4; Fig. 4b), although that trend was less marked during daytime

263 (Day\*Distance interaction, Table 4; Fig. 4b). Overall fox activity did not change strongly  
264 with fox control, but diurnal activity decreased where fox control was more intense  
265 (Day\*Fox control interaction, Table 4; Fig. 4c).

## 266 **Discussion**

267 Our results indicate that the red fox is mainly crepuscular and nocturnal in our study areas  
268 (Fig. 2a and Table 4). This is in agreement with previous studies across red fox worldwide  
269 distribution (Blanco 1986; Sunquist, 1989; Phillips & Catling, 1991; Cavallini & Lovari,  
270 1994) and supports that the red fox is ‘facultative nocturnal’ (Monterroso, Alves &  
271 Ferreras, 2014).

272 Unlike foxes, rabbits presented two main activity peaks in the diurnal time period in our  
273 study areas (Fig. 2b). This means that the mean activity overlap between red fox and  
274 rabbit (0.40) was low compared with that described for other mammalian predator-prey  
275 examples (0.60: Foster *et al.*, 2013; Monterroso, Alves & Ferreras, 2013). Therefore, our  
276 results initially disagree with the hypothesis that predators adapt their activity to that of  
277 their main prey species (Foster *et al.*, 2013). This partial lack of activity synchrony  
278 between predator and its main prey has been previously reported by Arias-Del Razo *et al.*  
279 (2011) and Monterroso, Alves & Ferreras (2013), who interpreted this as an adaptation  
280 of prey to reduce predation risk. These low overlaps between rabbit and fox activity  
281 patterns may suggest that rabbit activity is not the most important factor explaining  
282 variations in red fox activity patterns and suggest the implication of other factors.

283 In fact, the overlap between rabbit and fox activity was highest during twilight (Table 4  
284 and Fig.3), the time period when rabbits are accessible for foxes. Similarly, our findings  
285 show that the overall activity of red foxes increased where rabbits were more available  
286 (Table 4 and Fig.4a), reflecting the importance of rabbits in fox diet in central Spain  
287 (Delibes-Mateos *et al.* 2008). However, this increase only occurred during twilight and  
288 night time periods, i.e. excluding the period when rabbits were most active and accessible  
289 (Table 4 and Fig.3). This suggests that fox activity during daytime is probably constrained  
290 by factors unrelated to prey abundance, and also explains the lack of relationship between  
291 the coefficient of overlap and rabbit availability at the locality level. Thus, our results  
292 could indicate that red foxes do not need a high synchrony with rabbits where the latter  
293 are abundant, and/or that prey-predator patterns may be altered by human disturbance, as  
294 it has been also suggested for wolves *Canis lupus* and moose *Alces alces* in Scandinavia

295 (Eriksen *et al.*, 2009, 2011) or for African lions *Panthera leo* and wild prey/livestock in  
296 Botswana (Valeix *et al.* 2012).

297 In our study, red fox activity decreased in areas closer to human settlements, particularly  
298 during twilight and night (Table 4 and Fig. 4b), when foxes are overall more active.  
299 Several studies have shown that human disturbance caused by activities such as  
300 agriculture, stockbreeding or outdoor leisure activities, which frequently take place in our  
301 study areas, affect the activity of mammal predators. For example, Matthews *et al.* (2006)  
302 and Belloti *et al.* (2012) demonstrated that tourist activities altered the activity patterns  
303 of black bears *Ursus americanus* and Eurasian lynxes *Lynx lynx*, respectively, or road  
304 traffic in the case of red foxes (Baker *et al.* 2007). The effect of human disturbance on  
305 predator behavior is especially evident when hunting is an important source of mortality  
306 in a given species. In such case, human presence alone may create strong behavioral  
307 responses through fear (Martin *et al.*, 2010), which is in accordance with our results.

308 Culling by humans has been globally identified as an important cause of mortality in the  
309 red fox (Sillero-Zubiri *et al.*, 2004). From this point of view, an effect of predator control  
310 on the activity pattern of the target species could be expected. For example, in areas where  
311 predators are removed, canids decrease their activity, especially during the daytime  
312 period (Kitchen, Gese & Schauster, 2000; Rasmussen & Macdonald, 2011; but see  
313 Monteverde & Piudo, 2011). In this line, in our study red fox decreased even more its  
314 activity during daytime (Table 4 and Fig.4c) in areas with more intense fox control (thus  
315 with higher human activity and direct mortality risk). The lack of an overall behavioral  
316 response of foxes to predator control intensity, together with the high influence of human  
317 presence on fox activity (Table 4 and Fig.4b and c), could indicate that “fear to humans”  
318 could be an intrinsic behavior in foxes, accentuated by the historical persecution of this  
319 canid by humans in our study area (Vargas, 2002).

320 The circadian variations in habitat use by hunted species in human-modified landscapes  
321 are possibly a response to human presence (Chavez & Gese, 2006; Martin *et al.*, 2010).  
322 Therefore, anti-predator behavior in terms of avoidance of human disturbance may  
323 explain the observed increase in fox diurnal activity in dense habitats (Table 4), which  
324 would be safer for this canid. In agreement with this, several studies have reported that  
325 red foxes in rural areas select habitats dominated by dense vegetation during daytime even

326 with human presence (Cavallini & Lovary, 1994; Reynolds & Tapper, 1995; Janko *et al.*,  
327 2012; but see Sunquist, 1989).

328 Our results show that the red fox presents a high degree of behavioral plasticity adjusting  
329 its daily activity rhythms to different ecological scenarios. In this sense, rabbit availability  
330 seems to drive fox activity in a scenario of low human disturbance, and foxes actively  
331 track rabbits at twilight and night time. However, where foxes are close to urbanized areas  
332 or culled, human disturbance may determine the activity of red foxes, which is strongly  
333 reduced during daytime, despite the higher accessibility of rabbits then. Our findings  
334 show how wildlife adapts to different environmental conditions, including human  
335 disturbance, contributing reliable information about an adaptive species such as the red  
336 fox. Thus further studies should consider different factors simultaneously for a better  
337 understanding of daily activity patterns of wildlife in humanized landscapes.

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499 **Figure 1** Location of the study localities (1-12) in the Iberian Peninsula.

500

501 **Figure 2** Overall Kernel densities of red fox (a) and rabbit (b) activity in study localities  
502 (mean: solid line; range: dashed lines). Vertical dashed lines represent approximate  
503 sunrise and sunset times.

504

505 **Figure 3** Overlap between red fox (dashed line) and rabbit (solid line) activity,  
506 determined by camera trapping. The numbers shown in brackets correspond to the study  
507 sites ID, as in Fig. 1. Vertical dashed lines represent approximate sunrise and sunset times  
508 during the study period in study localities.

509

510 **Figure 4** Model-averaged relationships between red fox activity (expressed as  
511 detections·100 trapping-hour<sup>-1</sup>) and: a) Rabbit availability (rabbits·100 trapping-day<sup>-1</sup>),  
512 b) Distance to human settlements (km), and c) Fox control (fox·year<sup>-1</sup>·km<sup>-2</sup>) during the  
513 three periods of the daily cycle (day, twilight and night) at two different habitat types  
514 (dense and open). For plotting the results, data were back-transformed.

515

516

517 **Table 1** Description of study localities (\* in the ‘Map ID’ indicates protected areas; the rest were hunting estates). The predominant landscape  
518 (agriculture or scrubland) is indicated along with the habitat types present in each area: Oa: open areas, Scr: scrubland, Wc: woody crops, Rip:  
519 riparian, Fo: forest, Dh: dehesa. The start and end dates of each survey are shown in the sampling year column. ‘Cameras’ indicate the number of  
520 camera traps used in each locality. ‘Effort’ (survey effort) is expressed as camera-days, or the sum of days each camera was active in the field in  
521 each locality. Descriptive statistics of independent variables for each study locality are also shown: ‘Rabbit availability’ is expressed as the number  
522 of independent detections of rabbits per 100 trap days; ‘Distance’ is the distance in km to the nearest human settlement; ‘Red fox control’ refers to  
523 the number of foxes culled per square km and year; ‘Habitat’ represents the number of cameras assigned to open or dense predominant habitat,  
524 respectively.

Study site (Map ID)	Area (km <sup>2</sup> )	Landscape (habitat types)	Sampling year (start/end)	Cameras	Effort	Rabbit availability (mean±SE)	Distance (km) (mean±SE)	Red fox control (foxes km <sup>-2</sup> year <sup>-1</sup> )	Habitat (open/dense)
1	20	Agricultural (Oa, Scr, Rip, Wc)	2010 (Jul/Aug)	20	620	7.74 ± 2.15	2.67 ± 1.05	0.08	16/4
2	16	Scrubland (Oa, Scr, Rip)	2010 (Jul/Aug)	15	424	30.15 ± 16.77	3.51 ± 0.94	1.98	3/12
3	50	Agricultural (Oa, Scr, Rip, Wc)	2011 (Jun/Jul)	16	493	66.53 ± 43.79	3.74 ± 1.85	0.89	13/3
4	36	Agricultural (Oa, Scr, Rip, Wc)	2011 (Jun/Jul)	17	485	36.03 ± 16.89	2.58 ± 1.44	0.43	16/1
5*	21	Scrubland (Oa, Scr, Rip, Dh, Fo)	2011 (Jul/Aug)	19	682	15.61 ± 7.61	6.56 ± 1.96	0	4/15
6	16	Scrubland (Oa, Scr, Rip, Wc)	2011 (Jul/Aug)	20	645	2.73 ± 2.57	5.86 ± 1.34	1.30	4/16
7	21	Agricultural (Oa, Scr, Rip, Dh)	2012 (Jul/Aug)	20	495	-	3.25 ± 1.27	0	16/4

8	20	Agricultural (Oa, Scr, Rip, Wc)	2012 (Jul/Aug)	20	503	2.61 ± 1.35	3.88 ± 1.30	4.00	19/1
9	9	Scrubland (Oa, Scr, Rip, Dh, Fo)	2012 (May/Jun)	15	417	-	9.21 ± 0.64	0.10	6/9
10	9	Agricultural (Oa, Scr, Rip)	2012 (May/Jun)	14	372	106.07 ± 64.01	5.18 ± 0.71	2.70	13/1
11*	26	Scrubland (Oa, Scr, Rip)	2012 (May/Jun)	20	529	2.23 ± 1.43	8.83 ± 1.40	0	9/11
12	16	Scrubland (Oa, Scr, Rip, Dh, Fo)	2013 (May/Jun)	18	463	2.31 ± 2.31	9.30 ± 1.40	0.70	5/13

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525

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**Table 2** Number of independent detections of red fox and rabbit and coefficient of overlap ( $\Delta_1$ ) of daily activity patterns of red fox and rabbit in each locality. CI95% is the 95% bootstrap confidence interval. Weekly detection probabilities ( $P$ ) conditioned to presence for both species are also shown (estimated using occupancy models).

<b>Study site (Map ID)</b>	<b>N° Red fox detections</b>	<b>N° Rabbit detections</b>	$\Delta_1$	<b>CI 95%</b>	<b><i>P</i> red fox</b>	<b><i>P</i> rabbit</b>
1	17	48	0.48	(0.33-0.67)	0.10	0.34
2	4	101	-	-	0.04	0.51
3	35	343	0.33	(0.31-0.52)	0.39	0.80
4	77	176	0.43	(0.36-0.56)	0.57	0.63
5	38	108	0.6	(0.39-0.66)	0.30	0.36
6	22	18	0.49	(0.36-0.72)	0.14	0.09
7	17	0	-	-	0.21	0.00
8	39	12	0.46	(0.29-0.63)	0.37	0.19
9	89	0	-	-	0.55	0.00
10	48	357	0.26	(0.15-0.32)	0.33	0.80
11	180	16	0.24	(0.25-0.49)	0.84	0.14
12	44	11	0.35	(0.11-0.56)	0.41	0.08

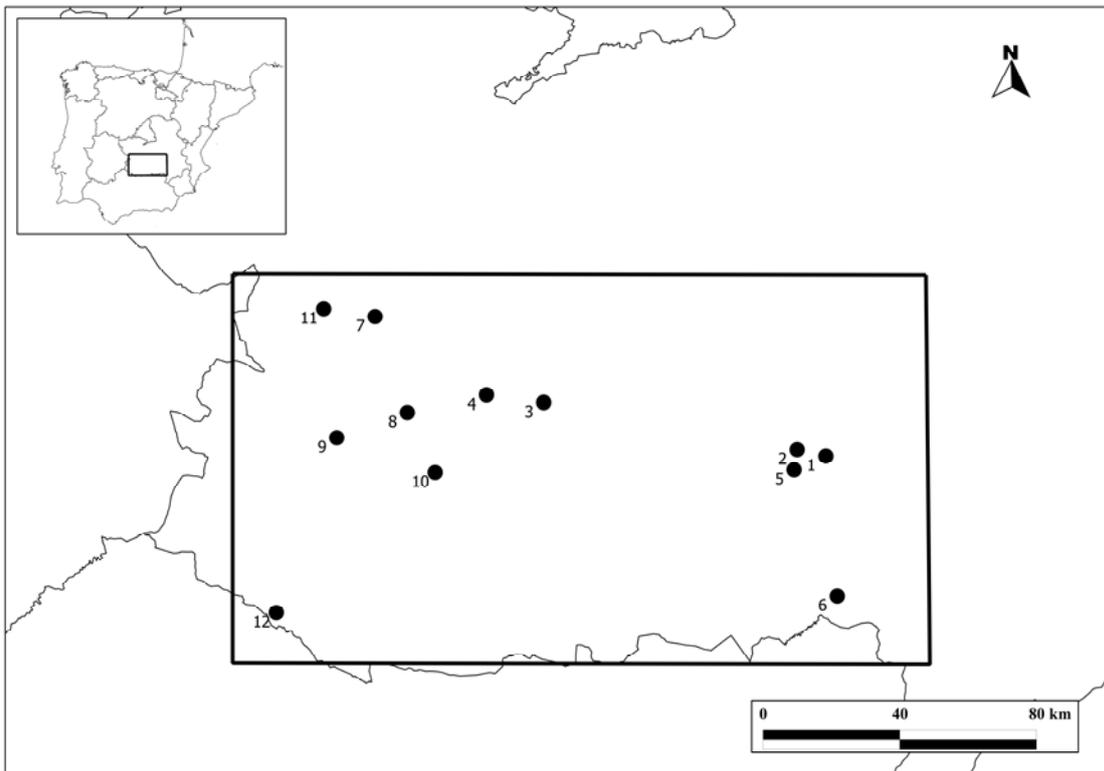
**Table 3** Models explaining red fox activity (number of independent red fox detections for each camera in a given period). We present data for those models with  $\Delta\text{AIC}_c < 2$ , as well as the full and null models. Variables are, *Time*: timer period (day, night and twilight), *Hbt*: habitat type (dense or open), *Dst*: distance to human settlement, *Rab*: rabbit availability, *Fc*: fox control. Interactions between variables are represented by \*.

<b>Model</b>	<b>df</b>	<b>logLik</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>w</b>
<i>Time+Hbt+Dst+Rab+Time*(Hbt+Rab)</i>	12	-421.74	867.99	0	0.20
<i>Time+Hbt+Dst+Rab+Time*(Dst+Hbt+Rab)</i>	14	-419.73	868.13	0.14	0.18
<i>Time+Fc+Hbt+Dst+Rab+Time*(Fc+Hbt+Dst+Rab)</i>	17	-416.82	868.63	0.64	0.14
<i>Time+Fc+Hbt+Dst+Rab+Time*(Hbt+Rab)</i>	13	-421.43	869.44	1.46	0.09
<i>Time+Fc+Hbt+Dst+Rab+Time*(Hbt+Dst+Rab)</i>	15	-419.42	869.61	1.63	0.09
Full model	18	-416.79	870.70	2.69	0.05
Null model	3	-604.63	1215.30	347.31	0.00

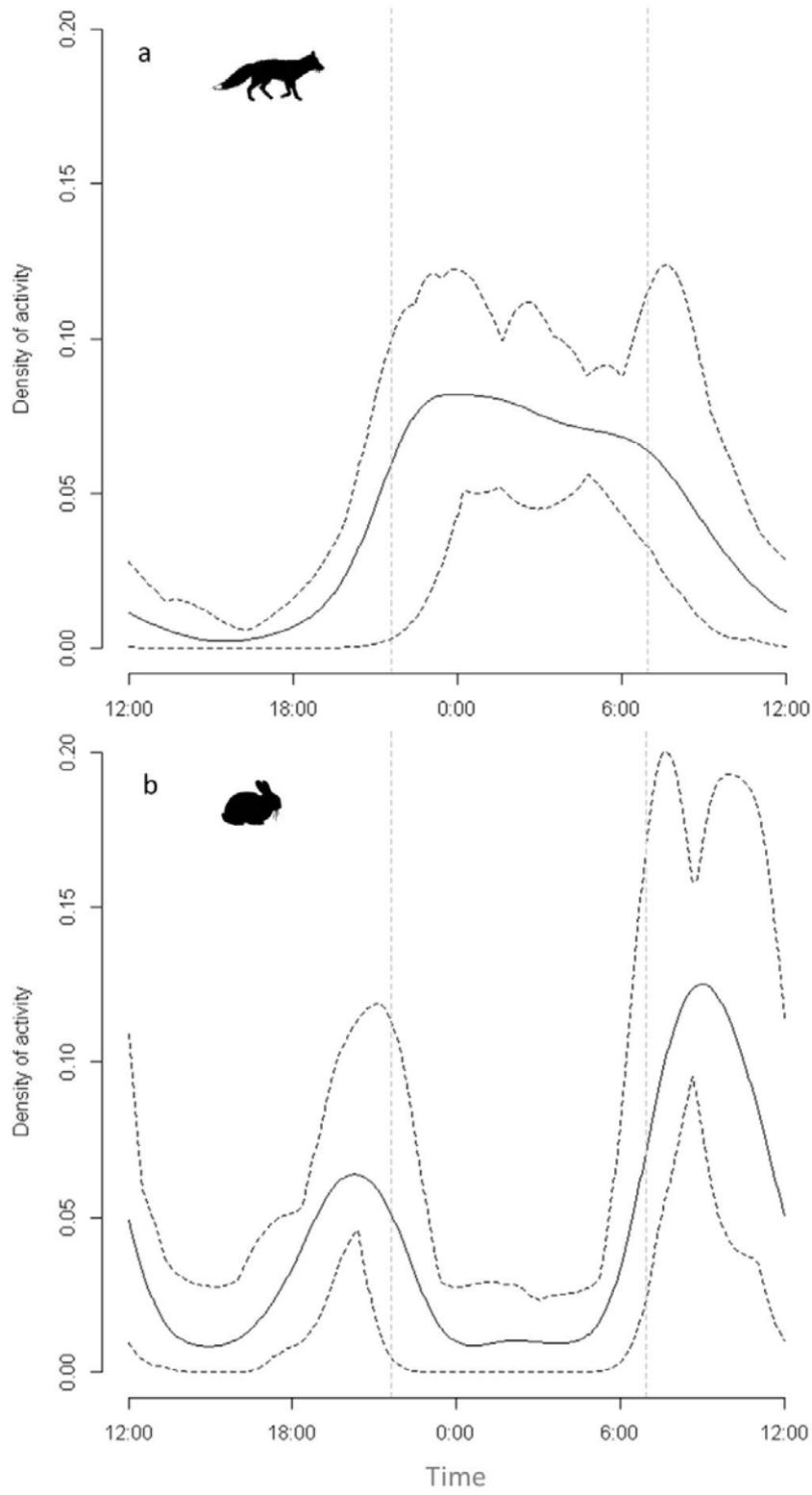
**Table 4** Model averaged coefficients and standard errors of the variables included in the five best models explaining the red fox activity (number of independent red fox detections for each camera in a given period). ‘RI’ is the relative variable importance from model average, ‘Time’ is the time period (day, night or twilight), ‘Distance’ is the distance to human settlement, and ‘Rabbit’ is the availability of rabbits.

<b>Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>RI</b>	<b>P value</b>
<b>Intercept</b>	-3.576	0.455	7.860	-	<b>&lt;0.001</b>
Time: Twilight	0.031	0.264	0.119	1	0.905
<b>Time: Day</b>	-1.469	0.347	4.232	1	<b>&lt;0.001</b>
Fox Control	-13.1	19.2	0.686	0.46	0.492
Habitat: Dense	-0.046	0.253	0.181	1	0.856
<b>Distance</b>	0.159	0.062	2.736	1	<b>0.009</b>
<b>Rabbit</b>	0.004	0.001	3.870	1	<b>&lt;0.001</b>
Twilight*Fox Control	3.923	11.06	0.369	0.20	0.712
Twilight*Dense habitat	0.192	0.237	0.811	1	0.417
Twilight*Distance	-0.001	0.043	0.036	0.59	0.971
<b>Twilight*Rabbit</b>	0.001	4·10 <sup>-04</sup>	2.037	1	<b>0.041</b>
<b>Day*Fox Control</b>	-22.9	11.5	1.979	0.20	<b>0.047</b>
<b>Day*Dense habitat</b>	0.910	0.223	4.082	1	<b>&lt;0.001</b>
<b>Day*Distance</b>	-0.076	0.037	2.043	0.59	<b>0.041</b>
<b>Day*Rabbit</b>	-0.002	0.001	2.273	1	<b>0.023</b>

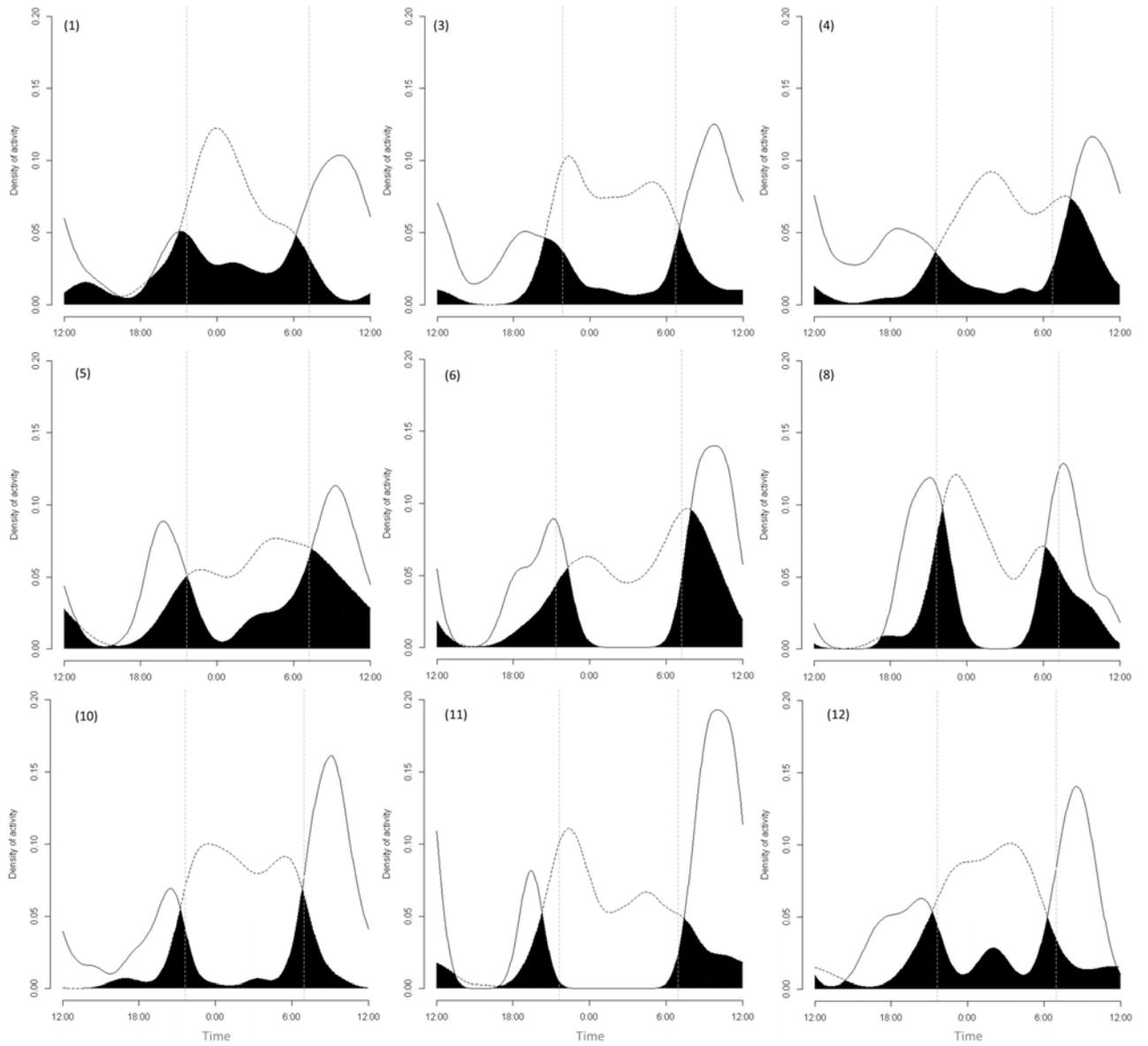
**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**

