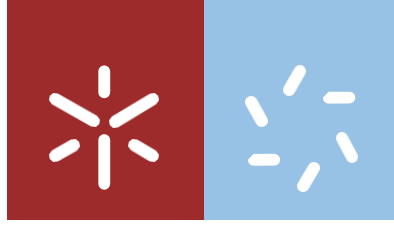


**Universidade do Minho**  
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Marta Sofia Ferreira Rocha

Environmental correlates of European rabbit  
(*Oryctolagus cuniculus*) activity



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Dissertação de Mestrado  
Mestrado em Ecologia

Trabalho efetuado sob a orientação da  
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Outubro de 2019

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## AGRADECIMENTOS

A realização desta dissertação de mestrado contou com importantes apoios e incentivos sem os quais não se teria tornado uma realidade. Desta forma, não poderia deixar de agradecer àqueles que contribuíram para a conclusão desta etapa.

Em primeiro lugar, quero agradecer aos meus orientadores, começando pelo Doutor Pedro Monterroso, por todo o conhecimento transmitido e carinho demonstrado. Também agradeço pela força de vontade que transmitiu. À minha orientadora, Professora Fernanda Cássio, pelo interesse demonstrado e por sempre ter sido prestável.

Em segundo, quero agradecer ao Nuno, por toda paciência que teve ao longo do ano e também pela pessoa amiga que foi, pois sem o seu contributo este trabalho não teria sido possível. Quero agradecer também à Ana que sempre se mostrou disponível para ajudar.

Ao Ricardo, que me acompanhou nos bons e maus momentos, pelo apoio e carinho demonstrado, e por me motivar a lutar pelos meus objetivos.

No geral aos meus amigos que me acompanharam e apoiaram neste processo.

Por fim, agradeço à minha família, em especial aos meus pais e irmã, sem os quais este trabalho não seria possível. Por todo o apoio incondicional que me deram e motivação em fazer sempre o meu melhor e lutar pelo que me faz feliz.

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## RESUMO

O coelho-europeu (*Oryctolagus cuniculus*) é endêmico da Península Ibérica, onde é considerado uma espécie-chave e uma espécie cinegética. As suas populações estão em declínio há décadas, com sérias implicações no funcionamento do ecossistema e na economia ibérica. Estratégias de recuperação foram implementadas, mas com sucesso limitado, enfatizando a necessidade de uma compreensão mais profunda da ecologia do coelho-europeu.

Utilizando armadilhas fotográficas em várias propriedades de caça no sul de Portugal, foram investigados os fatores ambientais relacionados com o nível de atividade diário do coelho europeu, e sua sobreposição de atividade e sincronização com a dos predadores mamíferos coexistentes.

Os coelhos reduziram seu nível de atividade em resposta à temperatura diária máxima, provavelmente para assegurar uma termorregulação eficaz. Os efeitos negativos da densidade no nível de atividade do coelho estão provavelmente relacionados a uma adaptação para maximizar a ingestão de alimento enquanto minimizam o risco de predação. Finalmente, os coelhos apresentaram alto nível de atividade associado a picos de atividade menos intensos nos habitats constituídos por matos, o que sugere uma estratégia para a redução da probabilidade individual de risco de predação. Por outro lado, nos montados, eles revelaram um menor nível de atividade diário. Isto está de acordo com a hipótese “risk allocation”, que postula que as presas que vivem num ambiente de risco moderam o seu nível de atividade, aumentando a atividade durante breves pulsos de segurança. Além disso, ao não responder à atividade do predador, mas à estrutura do habitat e ao tamanho do seu grupo, sugere que os coelhos europeus possam responder mais à percepção de risco do que ao próprio risco de predação.

Esses resultados fornecem novas ideias sobre as respostas de predadores de coelho, importantes para definir estratégias de conservação para sua recuperação.

## PALAVRAS-CHAVE

Atividade; estratégias de conservação; *Oryctolagus cuniculus*; Península Ibéria.



## ABSTRACT

The European rabbit (*Oryctolagus cuniculus*) is endemic of the Iberian Peninsula, where it is considered a keystone and an emblematic game species. Its populations have been declining for decades, with serious implications to ecosystem functioning and to Iberian economy. Recovery strategies have been implemented but with limited success, stressing the need for a deeper understanding of European rabbit ecology.

Using camera trapping on multiple game estates in south Portugal, I investigated the environmental factors related to European rabbit diel activity level, and its activity overlap and synchrony with that of coexisting mammalian predators.

Rabbits reduced their activity level as a response to maximum daily temperature, likely to ensure effective thermoregulation. The negative density-dependence effects on rabbit activity level is related probably to an adaptation to maximize the food intake while minimizing predation risk. Finally, European rabbits were found to have high activity level associated to less intense activity bursts in scrubland habitats, which suggest a strategy for the reduction of individual probability of predation risk. Conversely, in agroforestry, they revealed a lower diel activity level. This is in accordance with the risk allocation hypothesis, which postulates that prey living in a risky environment moderate their activity level, increasing activity during brief pulses of safety. Furthermore, by not responding to predator activity but rather to habitat structure and to their group size, suggests that European rabbits' may respond to the perception of risk more than to predation risk itself.

These results provide new insights into rabbit anti-predator responses, important to define conservation strategies for its recovery.

## KEY WORDS

Activity; conservation strategies; Iberian Peninsula; *Oryctolagus cuniculus*





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## LIST OF ABBREVIATIONS AND ACRONYMS

<b>AIC</b>	Akaike's Information Criterion
<b>BNV</b>	Benavente
<b>CT</b>	Camera trap
<b>COS</b>	Carta de Uso e Ocupação do Solo
<b>FAL</b>	Ferreira do Alentejo
<b>MRT</b>	Mértola
<b>NDVI</b>	Normalized Difference Vegetation Index
<b>RNAP</b>	Protected areas of Portugal
<b>QGIS</b>	Quantum GIS



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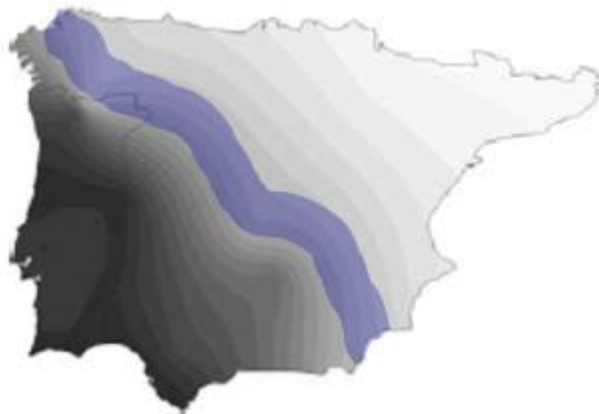
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# 1. INTRODUCTION

## 1.1 The European rabbit

The European rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758), is a species of the family Leporidae which occurs in both wild and domestic forms and is considered as a post-glacial endemism of the Iberian Peninsula (Ferrand, 2008; Rogers *et al.*, 1994). This species includes two subspecies: the smaller *Oryctolagus cuniculus algirus* is found in the southwestern Iberian Peninsula and on the Atlantic islands of the Azores, Madeira and Porto Santo; conversely, the larger *O. cuniculus cuniculus* occupies the northeast of the Iberian Peninsula and France and it is the subspecies that has been introduced throughout Europe and worldwide (Ferreira *et al.*, 2015; Lees and Bell, 2008). The distribution of the two subspecies overlaps along a contact zone that crosses the Iberian Peninsula in a Northwest-Southeast direction (Ferrand & Branco, 2007) (Figure 1).



**Figure 1.** Geographical distribution of the European rabbit subspecies in the Iberian Peninsula: *O. cuniculus algirus* (in dark grey), *O. cuniculus cuniculus* (in light grey) and hybrid zone (in blue) where hybrids and both species coexist. (Adapted from Ferrand, 2008)

### 1.1.1 Historical and recent population trends

From the late Pleistocene until Classical antiquity, European rabbits were present only on the Iberian Peninsula and in a small area in southern France (Monnerot *et al.*, 1994). Currently, this species is a widespread colonizer since *O. cuniculus cuniculus* has been successfully introduced in countries of all continents except in Antarctica (Lees & Bell, 2008). The spread of the European rabbit

resulted from exchanges between human societies from prehistory until the early Middle Ages (Masseti & Marinis, 2008).

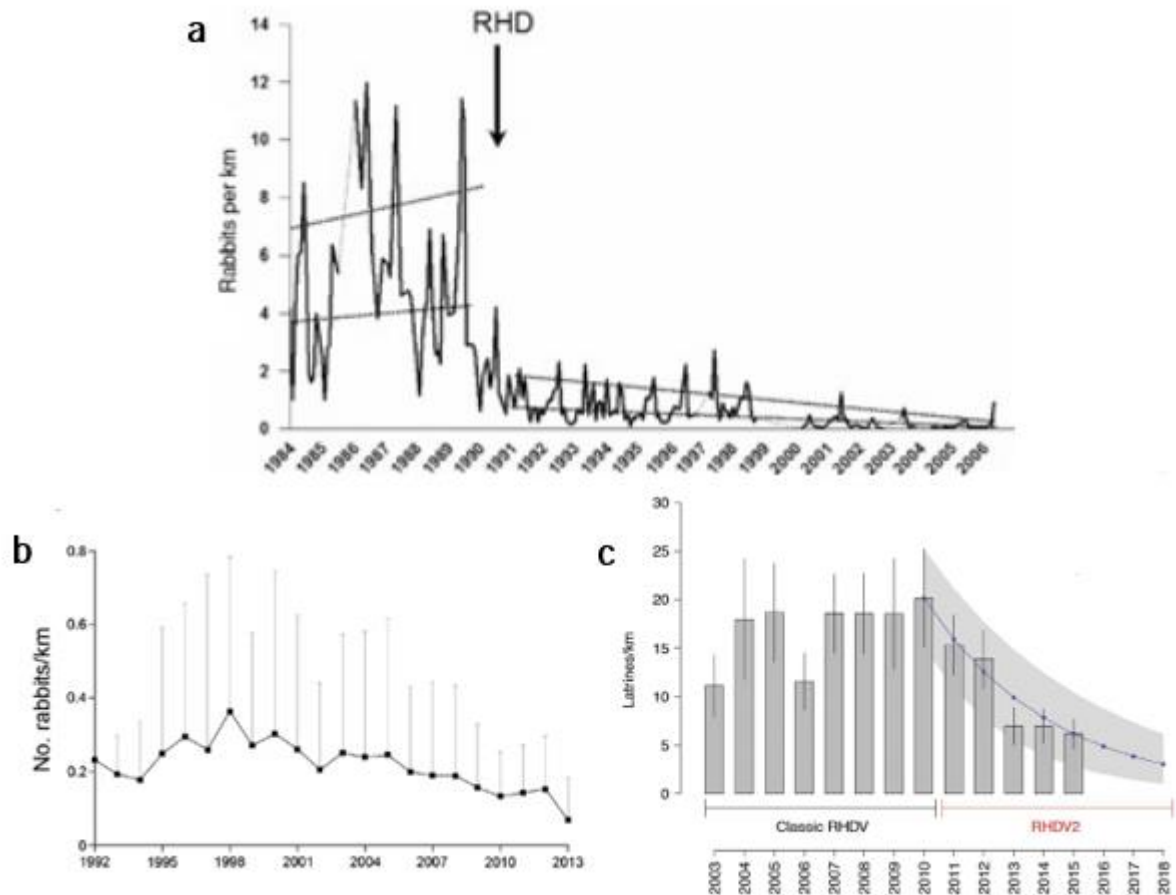
The European rabbit's current distribution range includes most of Europe, North Africa, parts of South America, Australia and New Zealand, as well as more than 800 islands, where it occupies a variety of different habitats (Flux 1994, Flux & Fullagar, 1992). This makes the *O. cuniculus* by far the most successful colonizing lagomorph (Hackländer *et al.*, 2008), and demonstrates its ecological plasticity and ability to change behavior to increase fitness (Gibb, 1993). This ability makes this species paradoxical, being a keystone species where it is indigenous, and an invasive species outside its native range, often with devastating effects on local biodiversity and ecosystems (Delibes-Mateos *et al.*, 2007; Lees and Bell, 2008). Notwithstanding, European rabbits are also regarded as an agricultural pest in a few areas in its native range (*i.e.* Iberian Peninsula) (Barrio *et al.*, 2010b).

The European rabbit has been massively declining since the mid-XX<sup>th</sup> century, due to habitat loss and fragmentation, and the arrival of two viral diseases: myxomatosis and rabbit hemorrhagic disease (RHD) (Ferreira & Delibes-Mateos, 2010).

The decline of rabbit populations in its native range was greatly accelerated by the arrival of myxomatosis during the 1950s (Muñoz, 1960). When populations were recovering from myxomatosis, another viral disease, RHD, greatly impacted rabbit populations again (Ferreira & Delibes-Mateos, 2010) (Figure 2a). RHD is caused by a calicivirus (RHDV or GI.1) and is a highly infectious, often fatal, viral disease for European rabbits (Abrantes *et al.*, 2012; Pendu *et al.*, 2017). It was first reported in the Iberian Peninsula in 1989 (Villafuerte *et al.*, 1995), causing initial mortalities of 55–75% (Villafuerte *et al.*, 1994), devastating most of the rabbit populations (Figure 2). Finally, in 2010, a new virus designated RHDV or GI.2 emerged with a distinct genetic and antigenic profile (Le Gall-Reculé *et al.*, 2011; Pendu *et al.*, 2017). It was first identified in France in 2010 (Le Gall-Reculé *et al.* 2011), and rapidly spread to the Iberian Peninsula (Abrantes *et al.*, 2013, Dalton *et al.*, 2012) causing important declines in natural populations of European rabbits, with an estimated annual decline of approximately 20% (Monterroso *et al.*, 2016a) (Figure 2). This virus also impacted rabbit populations in several European countries (Baily *et al.*, 20014; Le Gall-Reculé *et al.*, 2013; Westcott *et al.*, 2014) and outside Europe (Duarte *et al.*, 2015; Hall *et al.*, 2015; Martin-Alonso *et al.*, 2016).

Rabbit populations are currently at generalized low densities throughout the Iberian Peninsula (Delibes-Mateos *et al.*, 2009) and negative trends in rabbit numbers have been reported in Spain and Portugal (Delibes-Mateos *et al.*, 2014a; Ferreira & Delibes-Mateos, 2010; Monterroso *et al.*, 2016a)

(Figure 2). This species is listed as Near Threatened by the IUCN red list (Smith and Boyer, 2008), as abundance levels of their populations have declined in its native range (Ferreira & Delibes-Mateos, 2010).



**Figure 2.** European rabbit (*Oryctolagus cuniculus*) trends in Spain due to viral diseases. (a) Doñana National Park rabbit abundance estimated by kilometric abundance index (KAI) during a 23-year period (1984 – 2006) including the first outbreak of viral rabbit hemorrhagic disease (RHD) (arrow) (Moreno *et al.*, 2008) (b) Average rabbit abundance (+SD) of populations in Aragón (Delibes-Mateos *et al.*, 2014a) (c) Average rabbit abundance ( $\pm$  95% CI) in Sierra de Andújar estimated by latrines counts (bar plot). Blue lines (and shaded area) indicate the population projections (and 95% CI) for the period after the arrival of RHDV2 or GI.2. (Monterroso *et al.*, 2016a)

### 1.1.2 Ecological and social relevance

The European rabbit is a staple prey for more than 40 predator species (Delibes-Mateos *et al.*, 2008a). The diet of the Iberian lynx (*Lynx pardinus*) and of the Imperial eagle (*Aquila adalberti*) consist of 80-100% and 40-80% rabbit, respectively (Ferrer *et al.*, 2003, Palomares; 2001a). Therefore, the decline of *O. cuniculus* has been linked to the near extinction of these two globally endangered predators (Ferrer & Negro, 2004).

European rabbits also act as ecosystem engineers in Mediterranean ecosystems, by modifying vegetation, providing feeding resources, breeding sites and shelter for many species (Delibes-Mateos *et al.*, 2008a). They alter plant species composition and vegetation structure through grazing and seed dispersal, allowing the preservation of plant species diversity and the creation of open areas (Bravo *et al.* 2009, Delibes-Mateos *et al.* 2008a). Rabbits may play a similar important role in areas outside their native range (Lees & Bell 2008), such as in the coastal dunes in the Netherlands where they are important for its management because they slow down the rate of natural succession (Bankert *et al.* 2003). European rabbits are sedentary herbivores with a unique excavatory behavior among lagomorphs. They build structures such as burrows (or warrens) with associated mounds and scrapes (Gálvez *et al.*, 2008). Rabbits burrows provide breeding sites and shelter for other species (Delibes-Mateos *et al.*, 2008). Rabbit also build latrines, which are areas of pellet accumulation and soil perturbation (Cowan 1987) that increase plant diversity and biomass by inducing soil fertility (Willot *et al.*, 2000), and they also provide a food resource for invertebrates (Verdu & Galante 2004).

For all above-mentioned reasons, rabbits are considered a keystone species in Iberian Mediterranean ecosystems and have the potential to increase biodiversity at different scales (Delibes-Mateos *et al.*, 2007).

Additionally, the European rabbit is one of most emblematic game species in the Iberian Peninsula (Angulo & Villafuerte, 2004). Over 70% and 87% of the land in Spain and Portugal, respectively, consist of hunting grounds used every year by more than 900,000 and 150,000 hunters, respectively, that preferentially hunt rabbits (Delibes-Mateos *et al.*, 2014b). Hunting activities play an important socio-economically role. In fact, agro-environmental estates may depend economically on hunting, when agricultural practices or cattle-rearing are non-efficient (Bernabeu, 2000).

### 1.1.3 Conservation strategies

Different management techniques have been employed to revert the decline of rabbit populations throughout the Iberian Peninsula, such as adjusting hunting pressure, predator control, rabbit vaccination, habitat management and restocking (Ferreira & Delibes-Mateos, 2010). However, rabbits arouse diverse ecological, social and economic interests, leading to management conflicts (Delibes-Mateos *et al.*, 2014b). On one hand, the European rabbit is one of the most important game species in the Iberian Peninsula (Angulo & Villafuerte 2004) and therefore hunters are interested in population growth, as well as conservationists since is a keystone species in Mediterranean ecosystems (Delibes-Mateos *et al.*, 2007). On the other hand, the species may cause significant agricultural damage and so farmers require the control of rabbit populations (Virgós *et al.*, 2007).

Conservation management actions for the European rabbit are aimed at minimizing the impact of high adult and juvenile mortality (caused by viral diseases, predation, *etc.*) and at incrementing population productivity (warren building, supplementary food, *etc.*) (Ferreira & Delibes-Mateos, 2010).

Game management is one of the most available tools for rabbit recovery in hunting reserves that involves the cooperation between stakeholders and game managers. It may include adjusting hunting pressure (hunting days, number of hunters, moratoriums), hunting bags (number of rabbits harvested) or predator control (Ferreira & Delibes-Mateos, 2010). However, predator control poses a serious threat to biodiversity since both target and non-target species are captured. Furthermore, most of the times there is no true knowledge on the real size of the predator population nor the extent of the damages in prey populations (Ferreira & Delibes-Mateos, 2010).

Some of the mitigation strategies for wild rabbit populations include local vaccination campaigns against both viral diseases in specific areas, and other alternatives such as the implementation of educational programs for hunters, reduction of hunting bounties, and vector control. However, the empirical evidence of vaccination campaigns effectiveness is negligible (Calvete *et al.* 2004) and overall there seems to be no relevant relation between this management tool and rabbit population change after the arrival of RHD to the Iberian Peninsula (Delibes-Mateos *et al.*, 2008b).

Conservation strategies of wild rabbit populations have usually been based on restocking operations and habitat management. However, restockings are frequently unsuccessful since they require several steps that are rarely undertaken (Calvete *et al.*, 1997).

Habitat management arises as a preferred technique for promoting population growth given its general reduced costs and simpler application, without bringing negative biological effects to native

populations (Faragó *et al.* 2001). Habitat management improves the carrying capacity of a given area, through increasing the availability of basic ecological resources (*e.g.* high-quality food, quantity and quality of breeding sites, and refuge cover from predators) (Villafuerte 1994), inducing a global positive impact on biodiversity by beneficiating not only target but also several other species (Faragó *et al.* 2001). Habitat management needs to be considered an important strategy in the light of climate change scenarios, since alterations in the temperature and rainfall patterns changes vegetation growth, which consequently affects rabbit breeding patterns (*i.e.*, breeding season length, rate of pregnancies and litter size) (Ferreira & Delibes-Mateos, 2010; Tablado, 2009).

One of the most urgent management measures to implement is a working platform congregating researchers, hunters and game managers, conservationists and further sectors involved in wild rabbit management for the definition of a global strategy that defends collective interests and serves the goal of conserving this lagomorph (Ferreira & Delibe-Mateos, 2010).

#### 1.1.4 Ecology

*Oryctolagus cuniculus* is an herbivore, that feeds on a diverse diet of grasses, leaves, buds, tree bark, and roots, but grass-forbs, cereals and browse preferably (Rogers *et al.*, 1994). This lagomorph is able to adapt its feeding strategy to the quantity and quality of resources available: in winter they fed mainly on herbs and in managed areas they fed mainly on grasses (Ferreira and Alves, 2009, Martins *et al.* 2002).

Rabbits' auspicious habitats include a combination of herbaceous vegetation, that provide adequate food resources, and vegetation cover or warrens, that offer protection against predators (Palomares & Delibes, 1997). Given these general ecological conditions, rabbits can occur over a wide variety of habitat configurations, ranging from areas dominated by scrubland interspersed with small herbaceous patches, to crops or open grasslands, where protection is provided primarily by warrens (Lombardi *et al.*, 2003). In the Iberian Peninsula, they preferentially inhabit grasslands/scrublands mosaics, or oak agroforestry systems known as "dehesas" (Spain) or "montados" (Portugal), where livestock - cattle, sheep and goats - graze under extensive sparse forests (Ferreira & Delibes-Mateos, 2010; Lees & Bell, 2008). These habitats provide intermediate levels of both resources: suitable food and protective cover, and adequate soil conditions for burrowing (Lombardi *et al.*, 2003). Rabbit

habitat use may be influenced by individuals' age and by seasonal variations in resources, given that adults are extremely constrained by green food whereas juveniles are typically limited by refuge availability (Rueda *et al.*, 2008). European rabbits tend to avoid cold and wet ecotypes and rarely occur above 1500 m (Lees & Bell 2008).

In Iberia *O. cuniculus* breeds from November to June, corresponding to winter and spring, when favorable climate and food availability exist (Gonçalves *et al.*, 2002).

European rabbits are territorial animals and they can be solitary or gregarious when conditions are limited (Cowan, 1987). They build burrow systems (or warrens) that can reach high densities and may have a large extension (radius of more than 15 m) (Lange & Graham, 1983). Warrens have associated structures such as mounds, scrapes, latrines, and paths that result from their activities (*e.g.* excavating, trampling, pellet deposition, browsing). Latrines are defined areas of pellet accumulation and soil perturbation, used as territorial beacons (Cowan, 1987).

Rabbits are very alert mammals. Their vigilance focuses on the detection of predators and conspecific competitors (Monclús & Rödel, 2009).

European rabbits have a unique social behavior, being the only leporid species known to form stable social groups (Cowan & Bell 1986). They exhibit intraspecific communication through scent marking known as 'chinning' (Mykytowycz, 1968), to assess the territorial, sexual, and social status of conspecifics (Barrio *et al.*, 2010b).

European rabbits breeding groups are typically composed by a dominant buck that shares a territory with several females and subordinate males around a multientranced burrow system (Divincenti & Rehrig, 2016). The degree of sociality varies according to subspecies, population density, habitat and substrate types, which in turn influences group structure and mating systems (Lees & Bell, 2008). In fact, group size is influenced by climate (thermal limits, rainfall, vegetation quality and quantity), terrain (suitable soil type for their major food species and substrate for warren construction), predation pressure (density and diversity of predators), and more recently, introduced pathogens (Divincenti & Rehrig, 2016; Lees & Bell, 2008). For example, in habitats where cover is limited, rabbits tend to aggregate around burrows. Conversely, they become more scattered in habitats where cover is readily available (Lombardi *et al.*, 2003) and in light soils in which warrens can be constructed easily (Divincenti & Rehrig, 2016).

In larger groups, individuals tend to reduce their vigilance, which can be explained by the dilution effect, *i. e.*, the presence of companions in a group dilutes individual risk when predators attack

(Becauchamp, 2002; Dehn, 1990; Lima, 1990), and/or the shared vigilance and collective detection (Lima, 1995). Social groups allow each individual to devote less time to vigilance, as more individuals means more eyes scanning for predators (Lima, 1995) and allocated more time to other activities such as foraging (Becauchamp, 2002). Therefore, sociality in rabbits may be an adaptation to maximize food intake while minimizing predation risk (Villafuerte & Moreno 1997).

Moreover, group living can arise other benefits, such as cooperative construction and maintenance of the group warren, thermoregulation and desirable changes in the quality of food produced by group foraging effects (Lees & Bell, 2008).

#### 1.1.5 Activity

Research on animal activity usually aims at quantifying how the species distribute their activity budget over the day (Frey *et al.*, 2017). It is an important dimension of animal behavior and ecology as it provides valuable information about species' natural history and its ecological niche (Frey *et al.*, 2017). According to the predation risk allocation hypothesis, prey species tend to adapt their activity strategies to avoid being active in high-risk periods, and by focusing its feeding effort in low-risk situations (Lima & Bednekoff, 1999).

European rabbits are generally described as crepuscular-nocturnal (Gibb, 1993; Villafuerte *et al.*, 1993; Díez *et al.*, 2005). Rabbits spend much of the daytime underground inside their burrows, and emerge at dusk, to feed, patrol and mark their territories throughout the night, return to their burrows at dawn (Jilge & Hudson, 2001).

In Mediterranean areas, rabbits have been described as exhibiting a daily bimodal pattern that peaked around sunrise and sunset which was higher at sunrise than at dusk (Díez *et al.*, 2005; Villafuerte *et al.*, 1993), especially in the non-breeding season (Monterroso *et al.*, 2013). This activity circadian pattern seems to result from a combination of antipredatory, reproductive and thermoregulatory strategies (Moreno *et al.*, 1996; Villafuerte & Moreno, 1997; Villafuerte *et al.*, 1993). In fact, the crepuscular period is probably the most favorable for survival, since predation risk is low both by diurnal (*e. g.* avian raptors) and nocturnal predators (*e. g.* mammalian carnivores) (García-Canseco, 1997).

In Iberian Peninsula, Villafuerte *et al.* (1993) concluded that activity controlling mechanisms are correlated mainly with temperature, but it also can be affected by sunlight, moonlight, rain, and wind.



Temperature appears to highly influence the activity of rabbits since their circadian pattern could be modified by thermoregulatory requirements. Hence, rabbits are more active in mild temperatures avoiding extreme temperatures. For example, rabbit activity in the winter decreases at dawn despite the favorable light conditions, and increases at night due to higher temperatures at night than at dawn (Villafuerte *et al.*, 1993). Increased activity was found with moonlit night (Villafuerte *et al.*, 1993), which is contradictory to studies on non-native areas (*e.g.* Kolb 1992; Twigg *et al.* 1998; Van Strien *et al.* 2011). Rainy nights and stronger winds seem to reduce rabbit's activity in both native and non-native areas (*e.g.* Fletcher *et al.* 1999, Villafuerte *et al.* 1993; Ballinger and Morgan, 2002). Regardless, other studies found no effect of rainy nights and stronger winds (Wallage-Drees, 1989; Twigg *et al.* 1998).

European rabbit has demonstrated its ecological flexibility and ability to adapt behavior to predator pressure and food availability (Moreno *et al.*, 1996; Lombardi *et al.*, 2003). In fact, different aspects of rabbit biology such as activity rhythms, spatial and social behavior and reproductive parameters vary with predation pressure (Lombardi *et al.*, 2007).

Most research about European rabbit ecology has been performed at local level, which limits the extrapolation of results to other ecological contexts (Ferreira 2012). Behavior was never investigated as a correlate of environmental features, although their understanding is essential for the development of appropriate population and habitat management strategies (Martins *et al.*, 2003). It is important to study behavior of rabbits and activity patterns on habitats under different environmental conditions in order to capture variability and understand its driving factors. Additionally, animal behavior can undermine the suitability of direct and indirect methods to assess rabbit population sizes (*e.g.* influence significantly the accuracy and precision of density estimates derived from distance sampling) (Hounsome *et al.*, 2005), having implications on rabbit population surveys. Estimates of the size of rabbit populations are fundamental to many aspects of conservation biology and wildlife management (Barrio *et al.*, 2010a). Therefore, it is important to understand the rabbit behavior and activity patterns to improve these methodologies.

## 1.2 Methods to study activity

### 1.2.1 Camera trapping

Camera traps (CTs) are noninvasive survey devices that record animals as they pass, typically triggered by a passive infrared motion sensor (Rowcliffe *et al.*, 2011). Camera traps vary in how they detect animals (using passive or active infrared sensors), how they illuminate at night and other important features (Swann *et al.*, 2011). Camera trap performance is affected by weather, particularly extreme heat and cold, due to the sensitivity of the passive infrared (PIR) sensors. PIR sensors tend to be less reliable as the temperature differential between the moving object and ambient levels decrease whereas it responds to changes in infrared energy, or heat, emitted by background temperature and a passing object (Meek *et al.*, 2012).

CTs are non-invasive when photographs are captured using invisible IR flashes and do not rely on animal capture, therefore they do not affect animal behavior. The equipment is relatively cheap and easy to deploy, which results in lower cost and labor effort (Bridges & Noss, 2011). In addition, it allows a permanent record of robust data (*e. g.* date, location, behavior, species and indirectly activity, movement path, travel speed, day range) (Kays *et al.*, 2011). Furthermore, it can provide datasets on elusive, rare, and protected species and it also enables the discovery of new species (*e.g.* Rovero *et al.*, 2008).

CT, like any other technique, has associated shortcomings. Particularly the problem of imperfect detection, where individuals or species present within a sampling area may not always be detected either by not triggering the CT or by not entering the detection zone (Burton *et al.* 2015). The probability of detection can be affected by many factors including a camera's detection zone, sensitivity and specific placement, habitat characteristics or attractants at a camera; ambient and animal temperatures, timing, and duration of sampling; and animal density and behavior in the landscape (Rowcliffe *et al.*, 2011).

Camera trapping has become popular in ecology and conservation due to its versatility usage that allows the investigation of species' distribution, abundance/density, behavior, activity curves and community structure (Meek *et al.*, 2014; Rovero *et al.*, 2013). However, camera trapping studies had been less used to examine species' behavior and interactions, and their associated consequences for community structure (*e.g.* activity patterns, diet), once they mainly focused on the spatial and

numerical aspects of species and population ecology (*e.g.* relative abundance, presence–absence, population density, occupancy) (Burton *et al.*, 2015; Frey *et al.*, 2017).

CTs have been used for providing information on patterns of activity (Bridges & Noss, 2011), and new analytical methods are emerging that enable scientists to quantify aspects of behavior from camera trap data (Oliveira-Santos *et al.*, 2013; Ridout & Linkie, 2009). Nevertheless, reliable accounting for movement behaviors of unmarked individuals is still difficult, particularly when considering potential complexities of movement dynamics, such as behaviors dependent on habitat or density (Burton *et al.*, 2015). To quantify behavior and activity is important to consider the camera trap event, which refers to the detection of an animal, on a single occasion in a location. A camera trap event can be defined by a successive images or sequences of consecutive images, *i.e.*, video or pseudo video) initiated by a trigger. Whilst the optimal independence interval between camera trapping events has never been empirically tested from camera traps, it typically ranges from 10 to 60 min, although 1–5 min has been used for small mammals (Meek *et al.*, 2014).

Camera trap data allows to report animal activity as diel activity level - the proportion of time that animals spend active during the day (Rowcliffe *et al.*, 2014), and density of detections - the number of detections per unit time (Rowcliffe *et al.*, 2008).

### 1.2.2 Direct observation

Direct observation may be made on transects or fixed positions (*e.g.* towers) with the aid of optical devices, such as binoculars.

Activity can be quantified as an index of activity (IA) by dividing the number of rabbits observed at this count by the highest number of rabbits observed at any count of the same sampling period (minimum number of rabbits present at this month) if rabbit abundance does not vary within the days of each monthly sampling period (Villafuerte *et al.*, 1993).

To study rabbit behavior two different sampling techniques can be used: focal sampling (continuous recording), to register frequencies of different behaviors; and scan sampling, to register the spatial data (Monclús *et al.*, 2006).

However, visual observations are conditioned by the experience and concealment of the observer, and detection of the rabbits (Lashley *et al.*, 2018), as they spend most of the day hidden in warrens (Gonzales-Redondo, 2009). Another limitation arises due to the observation of the entire day being

impractical, which restricts the sampling period. Regarding observations by transects, the insufficient area to walk or drive transects, and the appropriate terrain surface are limiting factors (Gonzales-Redondo, 2009).

### 1.2.3 Radio tracking

Radio tracking is a technique that requires the capture and tagging of the animals with posture-activity sensors (Lombardi *et al.*, 2003). Radiotags enable the collection of precise and frequent animal locations, that can be retrieved remotely and in near real time, allowing more accurate monitoring of animal activity in the wild (Millspaugh & Marzluff *et al.*, 2001). Radio tracking has been used to infer activity from speed of movement (Palomares & Delibes 1993), or from variance in signal strength (Kays *et al.* 2011, Suselbeek *et al.* 2014). Tilt switches connected with telemetry devices have also been used to infer activity (Knowlton *et al.* 1968), and more recently, multiaxial accelerometers have been used to provide detailed remote records of behavioral patterns (Nathan *et al.* 2012, Shepard *et al.* 2008). Radiotags increasingly are being used to estimate activity curves to evaluate a variety of hypotheses on a wide variety of species (*e.g.* Athreya *et al.* 2014, Bonnot *et al.* 2016, Ensing *et al.*, 2014, Pagon *et al.*, 2013, Selebatso *et al.*, 2017).

Notwithstanding, tagging animals is an invasive, expensive, labor intensive, and in some cases unfeasible sampling technique (*e.g.* elusive or rare animals, endangered species) (Lashley *et al.* 2018). For the above-mentioned reasons, another limitation of radio tracking is the low sample size (*i. e.* number of individuals). Moreover, multiple relocations per minute would be required to accurately measure movement distances (Rowcliffe *et al.* 2011), which is an important measure to calculate activity patterns from radiotag data (Lashley *et al.* 2018).

### 1.3 Statement of the problem and objective of the study

As previously stated, the European rabbit is endemic of the Iberian Peninsula, where they have been declining for decades (Delibes-Mateos *et al.*, 2014a; Ferreira & Delibes-Mateos, 2010; Monterroso *et al.*, 2016a) due to habitat loss and fragmentation, and viral diseases (Ferreira & Delibes-Mateos, 2010). This had serious implications to ecosystem functioning and to Iberian economy, given its importance as a keystone and game species (Angulo & Villafuerte, 2004; Delibes-Mateos *et al.*, 2007). Hence, recovery strategies have been implemented, but with limited success, stressing the need for a deeper understanding of European rabbit ecology.

Most research about European rabbit ecology has been performed at local level, which limits extrapolation to other ecological contexts (Ferreira, 2012). In Mediterranean areas of Iberia, research has been done on the effects of vegetation type, weather or light conditions on rabbit counts (*e.g.* Soriguer & Rogers, 1981; B eltran, 1991; Villafuerte *et al.*, 1993). However, behavior was never investigated as a function of environmental features, although its understanding is essential for the development of appropriate population and habitat management strategies (Martins *et al.*, 2003). In fact, rabbit behavior can undermine the suitability of direct and indirect methods to assess population sizes (Hounsome *et al.*, 2005), with implications on rabbit population surveys. Estimates of the size of rabbit populations are fundamental to many aspects of conservation biology and wildlife management (Barrio *et al.*, 2010a). Therefore, it is important to understand the rabbit behavior and activity patterns on different habitats and different environmental conditions to understand its driving factors, but also to develop appropriate population and habitat management strategies.

This project aims to evaluate the levels and rhythms of diel activity of the European rabbit and to investigate how abiotic (temperature, precipitation, habitat) and biotic (primary productivity, rabbit density, activity of predators) environmental variables may influence such parameters in its Portuguese native range. For this effect, camera trapping was used on five game estates in south Portugal to assess the European rabbit diel activity level and its activity overlap and synchrony with that of coexisting mammalian predators. The activity level indicates the proportion of day active during the day (Rowcliffe *et al.*, 2014), whereas the activity coefficient of overlap indicates the probability of two species: European rabbits and its predator species, being active at a given period of the day (Ridout & Linkie, 2009), and the synchrony of activity peaks, the time interval between European rabbits and its predators, when each species population register major activity.

## 2. MATERIALS AND METHODS

### 2.1 Study area

This study was conducted in five turistic hunting states in Portugal. Three of these areas are located in the county of Mértola (reintroduction area for the Iberian lynx in Portugal (MRT1, MRT2 and MRT3)), one is located in the county of Ferreira do Alentejo (FAL1) and the other in the county of Benavente (BNV1) (Figure 3).

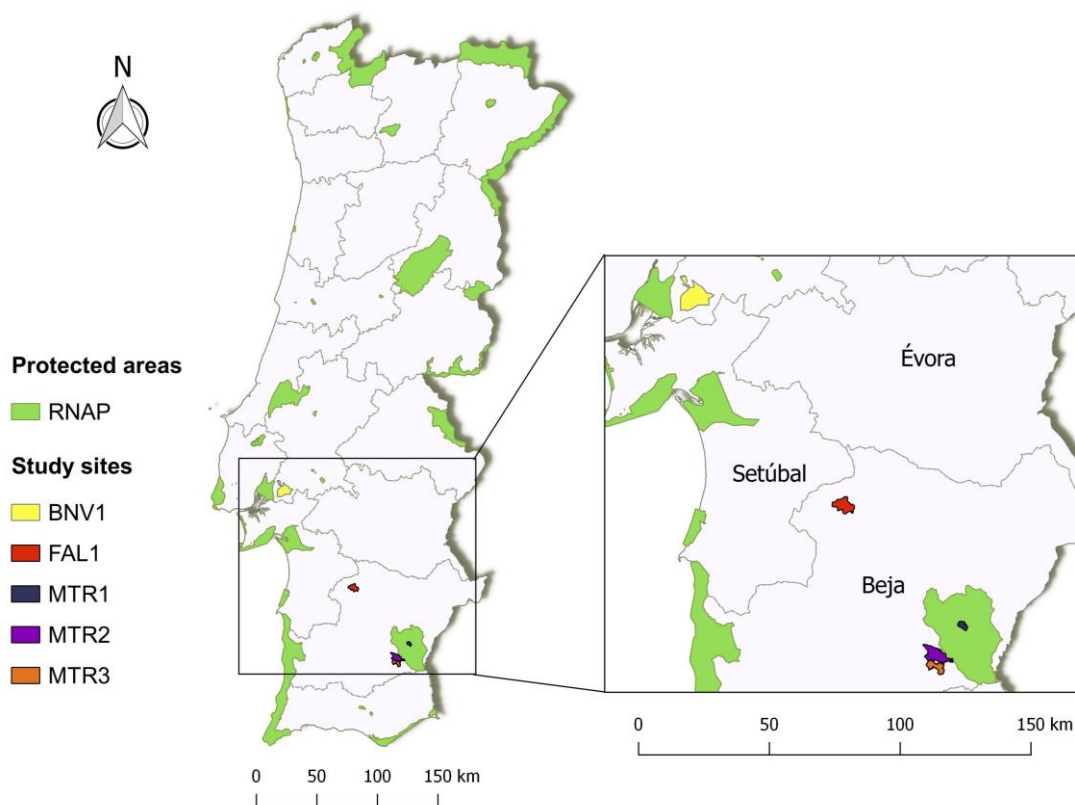
All study areas are located in the Mediterranean region of the Iberian Peninsula and it's characterized by a Mediterranean pluviseasonal continental bioclimate, with hot dry summers and rainy mild winters (Rivas-Martínez *et al.*, 2004). Siliceous soils (mostly schists or granites) dominate the region, where an ancient endemic flora such as *Cytisus grandiflorus*, *Cytisus striatus* var. *eriocarpus*, *Festuca duriotagana*, *Genista hirsuta hirsuta*, *Gladiolus reuteri*, *Hyacinthoides hispanica*, *Lavandula luisieri*, *Paeonia broteroi*, *Silene coutinhoi*, *Quercion broteroi*, *Genistion floridae*, *Ericion umbellatae*, and *Osmundo-Alnion* may be found (Costa *et al.*, 1998).

Ferreira do Alentejo's landscape is characterized by holm oak (*Quercus rotundifolia*) and cork oak (*Quercus suber*) agroforestry and *Quercus suber* forest. The natural wildlife found here includes European rabbits, European polecat (*Mustela putorius*), wild boars (*Sus scrofa*), beech marten (*Martes foina*), European Badger (*Meles meles*), red fox (*Vulpes vulpes*), Egyptian mongoose (*Herpestes ichneumon*), common genet (*Genetta genetta*).

Benavente is a study area essentially dominated by cork oak forest and holm oak agroforestry, where the soil is mostly sandy or loam, with poor superficial drainage, difficult infiltration and periodic flooding. Approximately 150 bird species and 24 mammal species have been reported there, such as booted eagle (*Hieraaetus pennatus*), common buzzard (*Buteo buteo*), European honey buzzard (*Pernis apivorus*), northern goshawk (*Accipiter gentilis*), Bonelli's eagle (*Hieraaetus fasciatus*), Eurasian hobby (*Falco subbuteo*), European nightjar (*Caprimulgus europaeus*), red-necked nightjar (*Caprimulgus ruficollis*), European polecat, wild cat (*Felis silvestris*) and Cabrera's vole (*Microtus cabrerae*) (Companhia das Lezírias, 2016).

Mértola study sites occur in different landscapes but are part of the same ecosystem (reintroduction area for the Iberian lynx). MTR1 is situated in a protected area of Portugal - the Guadiana Valley Natural Park (Figure 3) and it is essentially dominated by holm oak agroforestry and forests, but also *Eucalyptus globulus* forest. MTR2 is dominated by scrubland and MTR3 is characterized by stone pine (*Pinus pinea*)

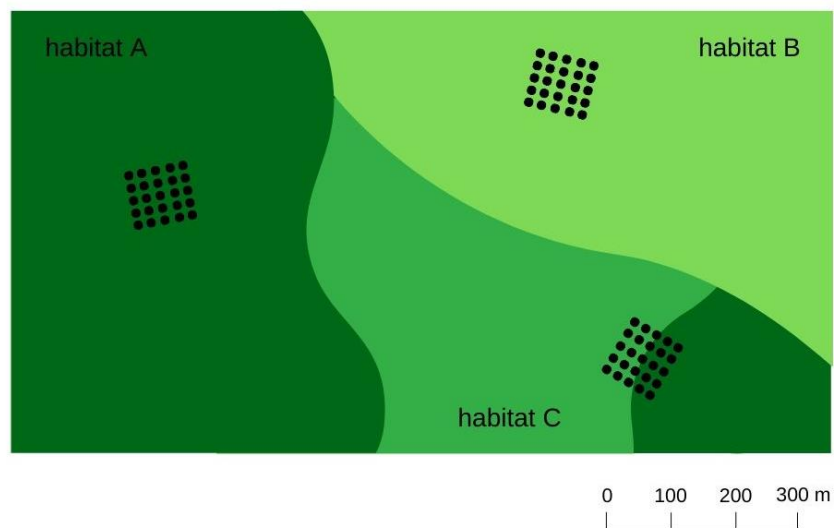
forest. The natural wildlife found here include variate animal classes. Birds is one of the most visible group including prey birds, such as the Bonelli's eagle (*Hieraaetus fasciatus*), the golden eagle (*Aquila chrysaetos*) and the Eurasian eagle owl (*Bubo bubo*). There are 35 species of mammals inventoried, standing out for its conservation status the Eurasian otter (*Lutra lutra*), the wildcat (*Felis silvestris*), the garden dormouse (*Elyomis quercinus*). There are also conditions that promoted the reintroduction of Iberian lynx (*Lynx pardinus*) (ICNF, 2017).



**Figure 3.** Protected areas of Portugal (RNAP) and study sites: Benavente (BNV1), Ferreira do Alentejo (FAL1) and Mértola (MRT1, MRT2 and MRT3).

In each study area three independent study sites (grids, sampling unit) were selected within a surface area of 20 ha, identified by the owner as hosting a reasonably abundant population of European rabbits. This resulted on a total of 30 sampling units.

Each sampling grid covers an 2 ha surface (100 m x 100 m) and it's located between 300 to 500 m apart to avoid recording the same individuals across sites (Sarmiento, 2012) (Figure 4). The grids were selected according to the following criteria: high European rabbit abundance, feasibility and low flooding susceptibility.



**Figure 4.** Scheme of the geographical distribution of the sampling units within a study site. Each sampling grid covers 2 ha surface and it's located between 300 to 500 m apart.

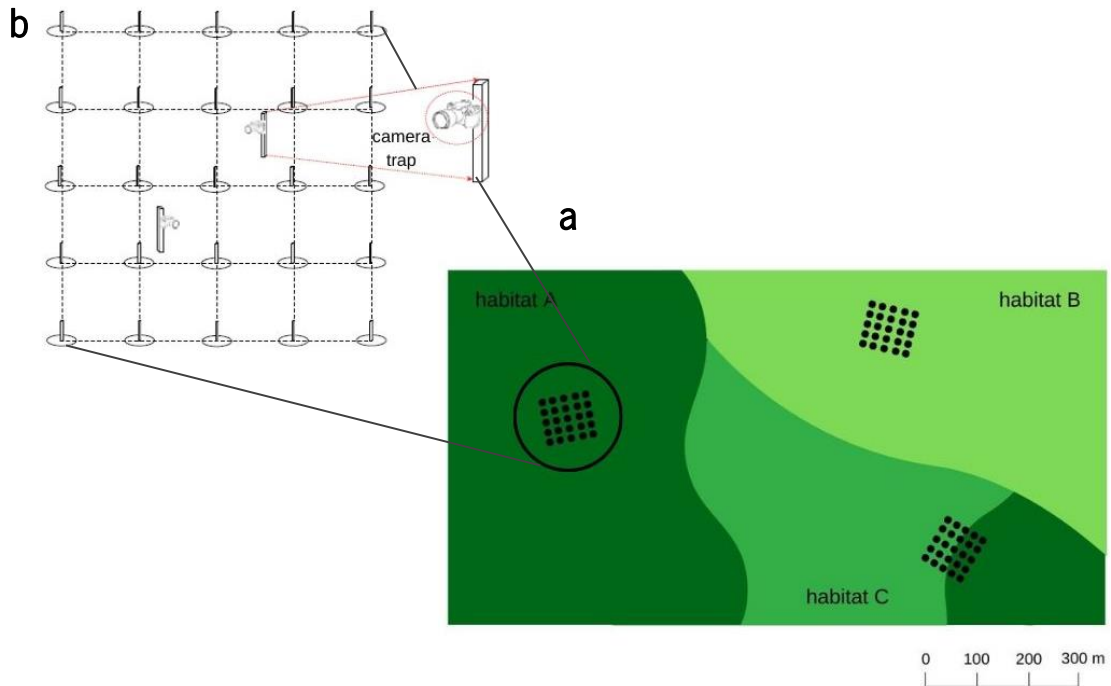
## 2.2 Methods

### 2.2.1 Field sampling

Data collection was carried out between November 2014 and November 2016 in the project “SOS Coelho: Bases para a recuperação de uma espécie chave nos ecossistemas Ibéricos”, developed by the Research Centre in Biodiversity and Genetic Resources (CIBIO/InBIO), University of Porto, and funded through for the Fund for Conservation of Nature and Biodiversity. Field sampling was based on camera trapping and on European rabbit pellet counts.

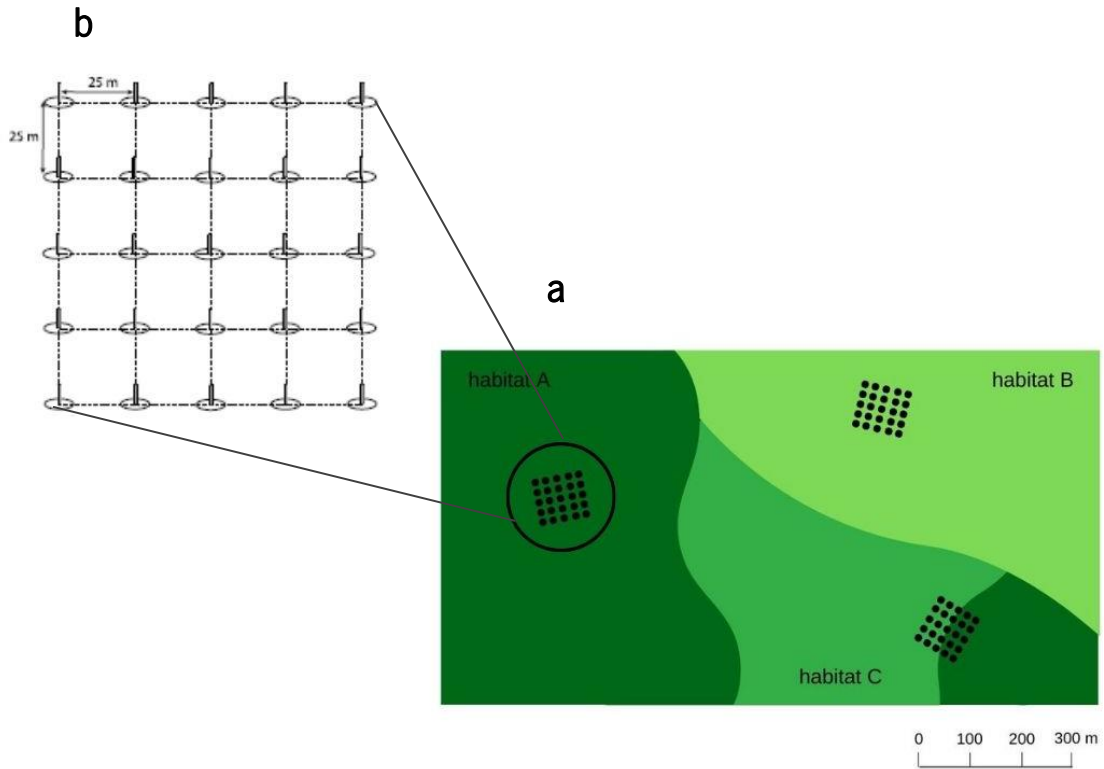
Camera trap data was collected to estimate rabbit's and predator's activity through animal time-of-detection (Ridout & Linkie, 2009). Camera trapping data collection occurred between March 2015 and November 2016, covering both dry and rainy seasons. Two camera trapping stations were installed per sampling grid (Figure 5), and their location was selected to maximize detection of the European rabbit. No attractants were used to avoid influencing animals' activity. Two camera models with thermal and movement sensors were used: model HCO ScoutGuard SG550V and SG570V (HCO OutDoor Products, Norcross, Georgia, USA), with triggering speed of 1.3 s. Cameras were mounted on trees at a height of 0.5-1.0 meters off the ground (Figure 5), programmed at the highest sensibility setting, minimum latency speed (<1 min), and to shoot a burst of 3 pictures when activated, in order to maximize the number of records per individual. All cameras were checked monthly, for batteries' and memory cards replacement, and for troubleshooting.





**Figure 5.** Scheme of the distribution of camera traps stations within the sampling grid. Geographical distribution of (a) the sampling units within a study site (b) the camera traps stations within the sampling grids. The location of the camera trapping stations within each sampling grid was defined to maximize the detection of the European rabbit. (Adapted from Monterroso *et al.*, 2016b)

Pellet counts with clearance were carried out between January 2015 and June 2016, and were used to estimate European rabbits' density as it is considered a reliable indirect method (Palomares, 2001b). Each sampling grid consisted of twenty-five (5 x 5) 1 m<sup>2</sup> counting plots centered at a wooden, spaced 25 m apart covering the grid total area (Figure 6). For each month, all pellets within the defined plots were counted and removed (Fernández-de-Simón *et al.*, 2011) to ensure that only fresh pellets were deposited between sampling campaigns (Figure 7). Monthly rabbit density was estimated considering the average daily rate of rabbit defecation (Gonzalez-Redondo, 2009). The detailed sampling protocol for pellet counts can be found in Appendix A. The vegetation was also removed in each counting point for better and easier counting (Figure 7).



**Figure 6.** Scheme of the distribution of the counting grids within the study area. (a) Geographical distribution of the counting grids, covering 1 ha surface, within a study site. (b) Each sampling grid consists of twenty-five (5 x 5) counting points of 1 m<sup>2</sup>. Each counting point, centered at a wooden stake, is spaced 25 m apart. (Adapted from Monterroso *et al.*, 2016b)



**Figure 7.** Photographs of a pellet counting unit, where the circle corresponds to a circular area of 1 m<sup>2</sup>, with exemplification of vegetation removal and removal of European rabbit pellet for counting.

## 2.2.2 Variables

### 2.2.2.1 Response variables

Camera trapping data were organized in a species record table with information about date, time, number of records and number of individuals for each detection record. The optimal independence interval of a camera trap event was considered to be >30 min, hence whenever multiple photographs of the same species were taken within a 30 min interval, they were considered as a single capture event, unless animals were clearly individually distinguishable (Linkie & Ridout, 2011; Monterroso *et al.* 2013). This data was grouped into individual sampling units (sampling grid x month) for statistical analysis.

Activity level, activity coefficient of overlap and activity peak synchrony were the selected variables to study activity patterns and rhythms of the European rabbit (Ridout & Linkie 2009). These variables were calculated using the package *activity* (Rowcliffe, 2019) in R software (R Core Team 2019). The method involves using time-of-detection data from camera trapping data, fitting a flexible circular distribution (kernel density function), and calculating overall proportion of time active from this distribution (Ridout & Linkie, 2009; Linkie & Ridout, 2011). The time of the observations was converted to radians (in the range 0 to 2pi). Only sampling units with over 30 European rabbit detection records were used in the analysis, to ensure reliability in the estimation of their activity patterns. A minimum sample size of 10 was used as a threshold for carnivores because the low number of predator detections (Monterroso *et al.*, 2014). The predators included the following species: Iberian lynx, wild cat, domestic cat (*Felis catus*), domestic dog (*Canis familiaris*), Egyptian mongoose, wild boar, common genet, beach marten, European Badger, European polecat and red fox. The wild boar was included as a predator since it has been reported as predator/competitor of rabbits (Cabezas-Díaz *et al.*, 2011).

A circular kernel probability density function was estimated for each sampling unit using the “fitact” function. Confidence intervals were obtained from a bootstrapping procedure with 500 iterations. Activity level estimates, defined the proportion of time that rabbits spend active during the day (Rowcliffe *et al.*, 2014), were derived from the circular kernel probability density function.

Activity overlap was estimated using the “ovl5” function applied to kernel probability density functions resulted by “fitact” of both predators and rabbits. This function calculates Dhat5 overlap index between the rabbit and predators kernel distributions for each sampling unit, which translates

into the degree of similarity between the two kernel density curves. Therefore, the coefficient of activity overlap indicates the probability that the two species – European rabbits and its predator – are simultaneously active (Ridout & Linkie, 2009).

The activity peak synchrony was obtained by estimating the difference between the time of the day when European rabbit and its predators are estimated to have the highest activity (i.e. daily maxima). Lower values of this metric indicate that species tend to reach their period of maximum diel activity at the same time, hence were considered as more synchronized. Conversely, large time differences between activity peaks indicate asynchronous activity.

#### 2.2.2.2 Explanatory variables

The environmental predictors selected for modelling were: temperature (maximum, minimum and range), precipitation, primary productivity, habitat, predator activity, and rabbit density. The hypothesis, expected response, and sources of the eight variables are presented in Table 1. These potential environmental predictors of European rabbit activity patterns were selected according to the literature.

**Table 1.** Activity expected response with respective hypothesis and source according to the environmental variables.

Variable (units)	Hypothesis	Expected response	Source
<b>Minimum temperature</b> (°C)	Temperature compromises the rabbits' thermoregulation (Villafuerte <i>et al.</i> , 1993)	Rabbits should decrease their diel activity when temperatures are high.	CHELSAcruts
<b>Maximum temperature</b> (°C)	Temperature compromises the rabbits' thermoregulation: they spend more energy when temperature isn't according with their body temperature (Villafuerte <i>et al.</i> , 1993)	Rabbits should decrease their diel activity when temperatures are high.	CHELSAcruts
<b>Temperature range</b> (°C)	Temperature range may compromise the rabbits' thermoregulation, influencing their activity (Villafuerte <i>et al.</i> , 1993)	Rabbits should avoid being active with extreme temperature range: decreasing their diel activity when temperature range is higher.	calculations based on CHELSAcruts data
<b>Precipitation</b> (mm)	Intense rainfall compromises rabbit thermoregulation (Villafuerte <i>et al.</i> , 1997; Rodel, 2000).	Intense precipitation should decrease the daily time that rabbits spend active, <i>i. e.</i> , rabbit activity level.	CHELSAcruts
<b>Primary productivity</b>	High-quality food availability is related to the reproductive period (Gonçalves <i>et al.</i> , 2002)	High-quality food availability is associated with the breeding period and therefore rabbits need to be more active for social activities and have higher feeding requirements.	Copernicus Global Land Service
<b>Habitat type</b>	Habitat type determines food and refuge availability that influences their diel activity and feeding effort (Moreno <i>et al.</i> , 1996; Lombardi <i>et al.</i> , 2003)	Higher diurnal activity in habitat that provides cover - scrubland, and higher nocturnal activity in open habitat - grasslands.	Direção-Geral do Território
<b>Predator Activity</b> (individuals/effort)	Prey species adapt their activity to avoid high-risk periods, according to predation risk (Lima and Bednekoff, 1999; Villafuerte & Moreno, 1997)	Low activity peak in brief or infrequent high-risk predation periods, and high activity peak and more intense feeding effort in long or frequent high-risk periods	estimates using camera trapping data
<b>Rabbit density</b> (individuals/ha)	Rabbit groups allows to reduce predation risk while maximizing the foraging activity (Lima, 1995)	High density should reduce rabbit diel activity by maximize the time allocated into feeding.	estimates based on pellet counts data

Precipitation and maximum and minimum temperatures were extracted from the freely available 'CHELSAcruts' (High resolution temperature and precipitation timeseries for the 20th century) dataset (Karger et al., 2017). This climate data is based on the delta change method by B-spline interpolation of anomalies of the 'CRU TS 4.01' dataset that are interpolated between all 'CRU TS' grid cells and are then added (for temperature variables) or multiplied (in case of precipitation) to high resolution climate data from 'CHELSA V1.2' (Karger *et al.*, 2017). This method has the assumption that climate only varies on the scale of the coarser ('CRU TS') dataset, and the spatial pattern (from 'CHELSA') is consistent over time, therefore having a lower accuracy. The resulting data consists of monthly precipitation sums and mean monthly maximum and minimum temperatures for the years 2015-2016 (sampling period) with a spatial resolution of 30 arc seconds, which approximates 1 km × 1 km.

Temperature range per month was calculated using R by the difference of maximum and minimum temperature data downloaded.

Normalized Difference Vegetation Index (NDVI) is one of the most commonly used vegetation indices in ecological studies (Pettoirelli *et al.*, 2005). NDVI was used as a surrogate of vegetation productivity, since it quantifies vegetation by measuring the difference between near-infrared (which vegetation strongly reflects) and red light (which vegetation absorbs). NDVI was downloaded from the Copernicus Global Land Service (Copernicus Service information, 2018) and was calculated by the following equation:

$$\text{NDVI} = (\text{REFnir} - \text{REFred}) / (\text{REFnir} + \text{REFred})$$

where REFnir and REFred are the spectral reflectances measured in the near infrared and red wavebands respectively. The resulting data consisted of a 10-daily period NDVI for the years 2015-2016 with a grid resolution of 1/336°, which approximates 300 m × 300 m.

Portugal's land cover data – Carta de Uso e Ocupação do Solo (COS) of 2015 – was extracted from Direção-Geral do Território (Direção-Geral do Território, 2018). COS is a digital cartography of polygons, which represent units of homogeneous land use/occupation with a spatial resolution of 1 ha characterized in 48 classes. For this study, the original dataset was reclassified into 5 ecologically relevant classes for the European rabbit: stone pine forest, eucalyptus forest, quercus (holm or cork oak) forest, scrubland, and agroforestry (Moreno *et al.* 1996, Lombardi *et al.*, 2003, Virgos *et al.*, 2003, Calvete *et al.* 2004, Ferreira & Alves, 2009). The latter includes agroforestry of holm or cork

oak, or a combination of both species. Land cover of the sampling grids can be found on Appendix (Table S1).

These geographical files were manipulated using QGIS 1.28.16 (QGIS Development Team, 2016). To obtain the values for each sampling unit, camera sampling points were extracted from the raster files using the “Point sampling tool” plugin (Jurgiel, 2008). Cameras on the same grid were considered as replicates.

Encounter rate, a surrogate of predator activity, was estimated from predators’ camera trapping records. The predators included were previous mentioned in 2.2.1. The encounter rate was calculated with the number of recorded predator individuals (carnivores and boars) during independent events divided by camera trapping effort for each sampling grid per month. Camera trapping effort is the number of trap days each camera trap site was operational (Meek *et al.* 2014), and was calculated with *camtrapR* package (Jürgen Niedballa *et al.*, 2016) by summing the days (24 h period) each camera trap site was operational.

The European rabbit density per sampling unit, was calculated through pellet counts using the average daily rate of wild rabbit defecation (Palomares, 2001b; Monterroso *et al.*, 2016b). The density was estimated by the following equation:

$$\hat{D} = \sum_{i=1}^n C \times A^{-1} \times \Delta t^{-1} \times DR^{-1} / n$$

Where  $\hat{D}$  is the mean density of wild rabbit per sampling unit, in number of individuals per ha;  $C$  is the pellet count present in a counting area of a fixed grid point;  $A$  is the fixed-point counting area;  $\Delta t$  is the period of time, in days, between cleaning and counting;  $DR$  is the daily wild rabbit defecation rate (estimated by Gonzalez-Redondo (2009)), and  $n$  is the number of counting units actually counted.

### 2.2.3 Statistical analysis

All statistical analysis was conducted in R software version 3.6.0 (R Core Team, 2019).

Initially, a nonparametric Spearman’ correlation analysis was performed using *psych* package (Revelle 2018) to analyze multicollinearity among continuous predictors. Variables were considered multicollinear when  $\rho > 0.70$ .

The activity level and activity overlap were logit-transformed for data resize. All continuous predictors were scaled to “z-scores” - standard deviation scores, which translates into the number of standard deviations from the mean (Shiffler, 1988). This allows the predictors are in appropriate scales for modelling.

With the aim of selecting the best family of models to implement several different candidate models were tested for each response variable (activity level, overlap and peak synchrony). All models were near-full effects models and included the following fixed effects covariates: temperature range, precipitation, NDVI, encounter rate, COS and density. The tested models were:

- Fixed-effects Linear Model, fitted using the ‘lm’ function (Chambers, 1992);
- Linear Mixed-effects Model with study area as random factor, fitted using the *lme4* package (Bates *et al.*, 2015);
- Linear Mixed-effects Model with Nested Design with ‘sampling grid’ nested in ‘study area’ as random factors, fitted using the *lme4* package.

Model selection was determined by the Akaike’s Information Criterion (AIC), which weights the likelihood of the model and the total number of parameters, identifying the most parsimonious model (smallest AIC). For this was used *MuMIn* package (Barton, 2019).

After selecting the family of models most appropriate for the data at hand, I generated a set of models including all covariate combinations, with the constraint that correlated covariates could not be included in the same model, since predictors with strong linear relationship may bias the model averaging. An additional constrain imposed on model generation was a maximum 1:10 ratio between the number of estimated parameters (covariate coefficients) and sample size, as a good rule of thumb is to have 10-15 observations per term in multiple linear regression. This model set was produced using the ‘dredge’ function from the *MuMIn* package (Barton, 2019).

Inferences were based on model averaging, which is a multimodel inference technique that improves the predictive ability by combining predictions from a set of models. For this, it was used ‘model.avg’ function of *MuMIn* package for conditional averaging, *i. e.*, only averages over the models where the parameter appears. Model averaging was only applied to models with  $\Delta_{AIC} < 7$ , since these models have substantial support of being the best models (Anderson and Burnham, 2002).

Finally, predicted values for each response variable were estimated using the ‘predict’ function of *MuMIn* package, which generates predicted values based on model-averaged estimates of the



transformed data with standard errors. All predicted values were backtransformed to the real scale and their 95% confidence intervals calculated.

### 3. RESULTS

#### 3.1 General results

Sampling effort totaled 11,990 trap days from 30 camera trapping stations. MRT1 was the area with highest number of camera trapping days (Table 2).

Ten out of a total of 266 grid-month combinations were excluded from the analysis due to camera trapping operability problems.

**Table 2.** Camera trapping effort at the 3 sampling grids in the study areas: Ferreira do Alentejo – FAL1, Benavente – BNV1, and Mértola – MRT1, MRT2 and MRT3. Camera trapping days per month are presented as average  $\pm$  SD.

	FAL1			BNV1			MRT1			MRT2			MRT3		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Camera trapping days	554	692	640	598	636	687	1,062	1,004	876	777	881	797	871	999	916
Camera trapping days per month	13 $\pm$ 2	16 $\pm$ 2	15 $\pm$ 2	14 $\pm$ 2	15 $\pm$ 2	16 $\pm$ 2	25 $\pm$ 2	24 $\pm$ 2	21 $\pm$ 2	19 $\pm$ 2	21 $\pm$ 2	19 $\pm$ 2	21 $\pm$ 2	24 $\pm$ 2	22 $\pm$ 2

A total of 42,912 camera trapping detections were obtained, of which 31,090 were considered independent. These included 22,937 European rabbit records, and 1,436 records of its predators: Iberian lynx (n=4), domestic cat (n=89), European wildcat (n=48), domestic dog (n=313), Egyptian mongoose (n=423), wild boar (n=201), common genet (n=11), stone marten (n=14), Eurasian Badger (n=21), European polecat (n=2), red fox (n=270), and unidentified (NI) carnivores (n=40) (Table 3).

The European rabbit was detected in all study areas, but predator community composition varied between study areas. The stone marten was only detected at FAL1, MRT2 and MRT3; the Iberian lynx was only detected at Mértola (MRT1 and MRT2); common genet was only detected at BNV1 and MRT1; the European wildcat was detected on BNV1, MRT1, MRT2 and MRT3, the Eurasian Badger was only detected at FAL1, BNV1 and MRT2, and the European polecat was only detected at FAL1 and MRT1; while the domestic dog, domestic cat, Egyptian mongoose, wild boar, and red fox were detected in all study areas (Table 3).

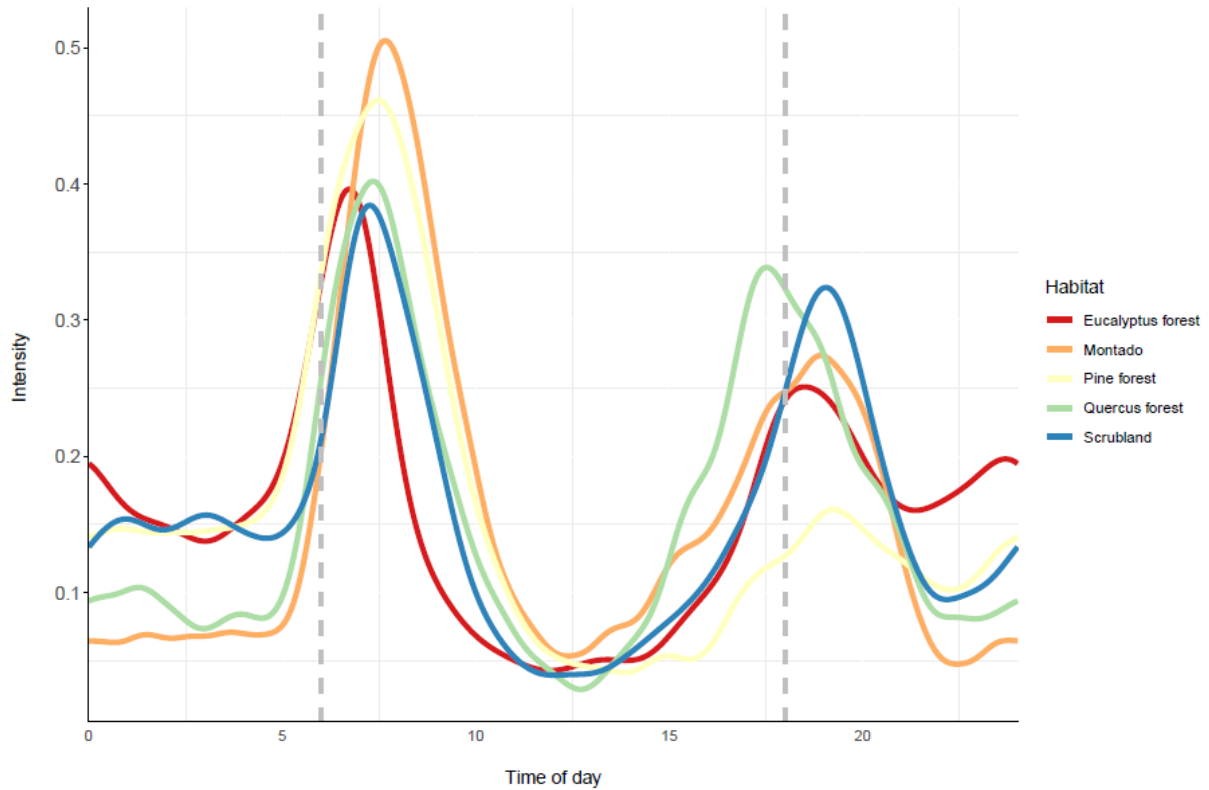
Overall, European rabbits were more frequently detected between March and July, and between August and November. FAL1 was the study site with more European rabbit records (6,796 records) (Table 3). MTR2 had the highest number of records ever register per month in September 2015 (1,124 records), followed by September 2016 (1,110 records).

European rabbits revealed different population density levels, which varied between 1 and 90 individuals ha<sup>-1</sup>. Population density was higher between March and July, and lower between August and March. Overall, the sampling area with the highest abundance was MTR1 (31 ± 1 individuals ha<sup>-1</sup>), and the lowest was MTR3 (10 ± 1 individuals ha<sup>-1</sup>). Conversely, the sampling unit with the highest abundance was the sampling grid number 1 in BNV1 (39 ± 6 individuals ha<sup>-1</sup>) and the lowest was the sampling grid number 2 in BNV1 (6 ± 2 individuals ha<sup>-1</sup>).

**Table 3.** Number of independent European rabbit and predator camera-trapping detections for each sampling grid in the in the study areas of Ferreira do Alentejo - FAL1, Benavente - BNV1, and Mértola - MRT1, MRT2 and MRT3.

Species	FAL1			BNV1			MRT1			MRT2			MRT3		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<i>Oryctolagus cuniculus</i>	966	3,765	2,065	2,120	491	242	942	1,722	756	1,906	4,543	391	1,137	1,042	849
<i>Canis familiaris</i>	2	4	2	3	1	3	3	4	2	14	244	4	24	1	2
<i>Felis catus</i>	0	1	1	0	1	3	9	5	12	20	17	7	5	4	4
<i>Felis silvestris</i>	0	0	0	0	0	1	0	3	5	2	6	0	11	13	7
<i>Herpestes ichneumon</i>	13	23	31	108	77	41	6	15	0	50	16	14	6	18	5
<i>Martes foina</i>	1	0	2	0	0	0	0	0	0	1	4	0	6	0	0
<i>Sus scrofa</i>	14	14	12	1	5	8	4	5	9	2	80	1	17	7	22
<i>Vulpes vulpes</i>	5	89	13	27	11	10	13	5	18	22	14	17	13	7	6
<i>Meles meles</i>	3	3	2	4	8	0	0	1	0	0	0	0	0	0	0
<i>Mustela putorius</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Genetta genetta</i>	0	0	0	0	9	0	1	1	0	0	0	0	0	0	0
<i>Lynx pardinus</i>	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0
NI carnivores	0	0	0	0	0	0	3	7	4	2	10	1	6	7	0

Rabbit activity was recorded at all hours of the day. Overall, rabbits revealed a bimodal activity pattern with a major activity peak occurring at sunrise and a second, but less pronounced peak at sunset (Figure 8).



**Figure 8.** European rabbit diel activity on the five habitat types: eucalyptus forest, agroforestry, pine forest, quercus forest and scrubland resulting from camera trapping. Grey vertical lines represent 06h00 and 18h00.

According to the Spearman correlation test the correlated covariates were: maximum temperature with minimum temperature; precipitation with temperature range; maximum temperature with temperature range; maximum temperature with NDVI; and minimum temperature with NDVI. Maximum temperature and minimum temperature had the highest value among these pairwise comparisons ( $\rho > 0.9$ ). Minimum and maximum temperature were correlated with food quality (NDV) (Table 4).

**Table 4.** Spearman correlation coefficient among the continuous covariates: precipitation, maximum temperature - Max. T, minimum temperature - Min. T, temperature range - Temp. range, Predator Activity, Normalized Difference Vegetation Index – NDVI, and rabbit density.

	Precipitation	Temp. range	Min. T	Max. T	Predator Act.	NDVI	Density
Precipitation		-0.79	-0.52	-0.65	-0.10	0.46	-0.20
Temp. range	-0.79		0.47	0.72	-0.01	-0.50	0.37
Min. T	-0.52	0.47		0.93	0.14	-0.77	0.20
Max. T	-0.65	0.72	0.93		0.11	-0.80	0.31
Predator Act.	-0.10	-0.01	0.14	0.11		0.05	0.17
NDVI	0.46	-0.50	-0.77	-0.80	0.05		-0.21
Density	-0.20	0.37	0.20	0.31	0.17	-0.21	

### 3.2 Activity level

The activity level data consisted of 167 estimates that ranged from 0.12 (2.94 h) to 0.74 (17.75 h) of the day active, and averaged  $0.35 \pm 0.13$  ( $8.31 \pm 3.06$  h; mean  $\pm$  SD).

The first selection procedure provided highest support for the linear model family, which ranked highest according to the AIC ranking criterion (Table 5). Moreover, the variance explained by the random factors “sampling grid” and “study area” was lower than the residual variance, further supporting that including these covariates did not increase model performance.

**Table 5.** Models’ selection table for activity level. All models included the following fixed-effects covariates: temperature range, precipitation, NDVI, predator activity, habitat and rabbit density. ‘Study area’ was included as random factor in the Linear Mixed-effects model, and ‘sampling grid’ nested in ‘study area’ as random factors in the Nested Design Linear Mixed-Effects models. Number of model parameters - df, log-likelihood - logLik, the Akaike’s Information Criterion – AICc,  $\Delta_{AIC}$  - delta and weight.

Model	df	logLik	AICc	delta	weight
Linear Model	11	-124.933	273.6	0.00	1.0
Linear Mixed Effects Model - Nested Design	13	-135.541	299.5	25.89	0.0
Linear Mixed Effects Model	12	-136.821	299.7	26.10	0.0

The model explaining European rabbit activity level with the highest support included rabbit density, habitat and maximum temperature as covariates. Temperature range, maximum and minimum temperature, precipitation, encounter rate, habitat and density were all included in the top-supported model set (i.e. within  $\Delta AIC < 7$ ). Models including NDVI did not have substantial support ( $\Delta AIC > 7$ ) (Table 6, Appendix - Table S2)

**Table 6.** Set of models for European rabbits' activity level with  $\Delta AIC < 7$ . These models resulted from dredging, excluding models containing correlated covariates. The covariates considered in the models are: density, predator activity -ER, precipitation - Prec., temperature range – Temp. range, maximum temperature – Max. Temp., and minimum temperature – Min. Temp.. Additional information about each model: number of model parameters - df), log-likelihood - logLik, the value of the information criterion used – AICc,  $\Delta AIC$  - delta and 'Akaike weight' – weight.

Model	df	logLik	AICc	delta	weight
Habitat; Density; Max.Temp.	8	-122.55	262.01	0.00	0.28
Habitat; ER; Max.Temp.	9	-122.26	263.66	1.65	0.12
Habitat; Density; Temp. Range; Min.Temp.	9	-122.29	263.72	1.71	0.12
Habitat; Density; Prec.; Max.Temp.	9	-122.43	264.00	1.99	0.10
Habitat; Max.Temp.	7	-125.04	264.79	2.79	0.07
Habitat; Density; ER; Temp.Range; Min.Temp.	10	-122.05	265.51	3.51	0.05
Habitat; Density; ER; Prec.; Max. Temp.	10	-122.17	265.74	3.73	0.04
Habitat; Temp. Range; Min. Temp.	8	-124.42	265.75	3.74	0.04
Habitat; Density; Min. Temp.	8	-124.62	266.15	4.14	0.04
Habitat; Prec.; Max. Temp.	8	-124.99	266.89	4.88	0.02
Habitat; ER; Max. Temp	8	-125.04	266.99	4.98	0.02
Habitat; Density; ER; Min. Temp.	9	-124.27	267.68	5.67	0.02
Habitat; Density; Prec.; Min. Temp.	9	-124.38	267.90	5.89	0.01
Habitat; ER; Temp. Range; Min. Temp.	9	-124.42	267.98	5.97	0.01

Model averaging revealed that rabbit density, maximum temperature, minimum temperature, temperature range, and agroforestry, eucalyptus forest and scrubland had a significant effect on rabbit activity level ( $z < 0.05$ ) (Table 7). Conversely, no statistically significant effect was detected for precipitation, predator activity, *Quercus* and *Pinus* forests ( $z > 0.05$ ) (Table 7).

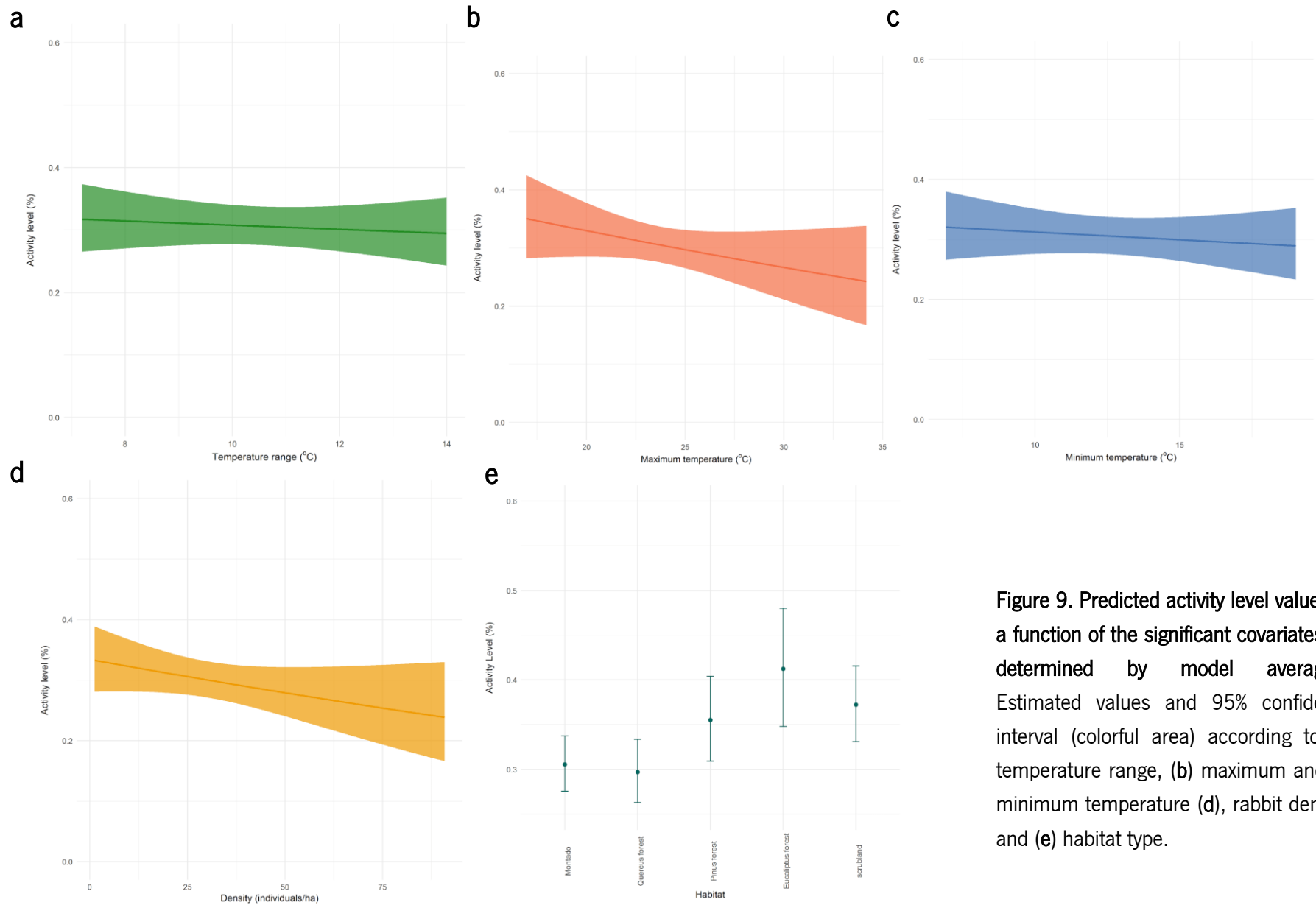
Maximum temperature, minimum temperature, temperature range and density negatively affected the activity level, but maximum temperature was the strongest predictor ( $\beta=-0.23$ ; SE=0.05) (Table 7; Figure 9a-d).

European rabbits exhibited a lower activity level in agroforestry habitats when compared to eucalyptus forest and scrubland, where it displayed an higher activity level (Table 7, Figure 9e).

**Table 7.** Model averaging of activity level of conditional average as delta  $\Delta_{AIC} < 7$  confidence set.  $\hat{\beta}$  – parameter estimate, SE – standard error, CI<sub>95</sub> - 95% confidence.

Covariates	$\hat{\beta}$ (SE)	CI <sub>95</sub>	Probability (z value)
<b>Habitat type</b>			
Agroforestry	-0.82 (0.07)	[-0.97 -0.67]	0.00
Quercus forest	-0.04 (0.11)	[-0.26 0.18]	0.73
Pinus forest	0.22 (0.14)	[-0.04 0.49]	0.10
Eucalyptus forest	0.47 (0.16)	[0.16 0.77]	0.00
Scrubland	0.30 (0.12)	[0.07 0.53]	0.01
Rabbit density	-0.11 (0.05)	[-0.21 -0.01]	0.03
Maximum Temperature	-0.23 (0.05)	[-0.32 -0.13]	0.00
Minimum Temperature	-0.16 (0.05)	[-0.26 -0.05]	0.00
Temperature Range	-0.11 (0.05)	[-0.22 -0.01]	0.03
Encounter Rate	0.03 (0.05)	[-0.06 0.12]	0.54
Precipitation	-0.02 (0.05)	[-0.12 0.09]	0.73





**Figure 9.** Predicted activity level values as a function of the significant covariates, as determined by model averaging. Estimated values and 95% confidence interval (colorful area) according to (a) temperature range, (b) maximum and (c) minimum temperature (d), rabbit density, and (e) habitat type.

### 3.3 Activity overlap

I obtained 39 estimates of activity overlap between European rabbits and its' predators. The coefficient of overlap ranged from 0.02 to 0.72, and averaged  $0.40 \pm 0.19$  (mean  $\pm$  SE).

The first selection procedure supported the selection of the linear model family, which ranked highest according to the AIC ranking criterion (Table 8). Moreover, the variance explained by the random factors "sampling grid" and "study area" was lower than the residual variance, further supporting that including these covariates did not increase model performance.

**Table 8.** Models' selection table for activity overlap. All models included the following fixed-effects covariates: temperature range, precipitation, NDVI, predator activity, habitat and rabbit density. 'Study area' was included as random factor in the Linear Mized-effects model, and 'sampling grid' nested in 'study area' as random factors in the Nested Design Linear Mixed-Effects models. Number of model parameters - df, log-likelihood - logLik, the Akaike's Information Criterion – AICc,  $\Delta_{AIC}$  - delta and weight.

Model	df	logLik	AICc	delta	weight
Linear Model	10	-51.648	131.2	0.00	0.977
Linear Mixed Effects Model	11	-53.642	139.1	7.91	0.019
Linear Mixed Effects Model - Nested Design	12	-53.092	142.2	11.03	0.004

The coefficient of overlap was not estimated in sampling units placed at eucalyptus forests because of insufficient predator records, therefore this variable was excluded for model averaging.

The model explaining European rabbit - predators activity overlap with the highest support included habitat type as the sole covariate (Table 9). All the covariates with the exception of eucalyptus forest were included in the top-supported model set (i.e. within  $\Delta_{AIC} < 7$  – Appendix (Table S3)).

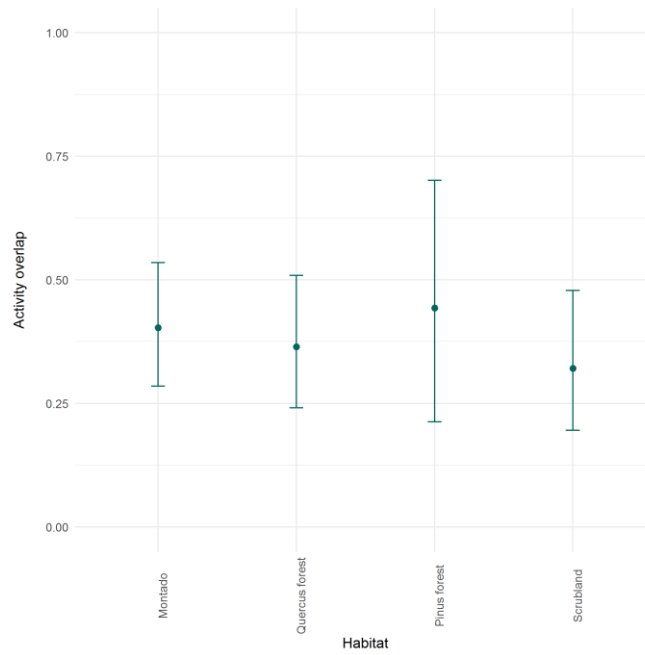
**Table 9.** Set of models for activity overlap with  $\Delta_{AIC} < 4$ . These models resulted from dredging, excluding models containing correlated covariates. The covariates considered in the models are: density, predator activity -ER, precipitation - Prec., temperature range – Temp. range, maximum temperature – Max. Temp., and minimum temperature – Min. Temp.. Additional information about each model: number of model parameters - df), log-likelihood - logLik, the value of the information criterion used – AICc,  $\Delta_{AIC}$  - delta and ‘Akaike weight’ – weight.

Model	df	logLik	AICc	delta	weight
Habitat	5	-53.27	118.37	0	0.06
NULL	2	-57.09	118.51	0.14	0.06
Habitat; Density	6	-52.3	119.22	0.85	0.04
NDVI	3	-56.32	119.33	0.96	0.04
Density; Max. Temp.	4	-55.1	119.38	1.01	0.04
Min. Temp.	3	-56.42	119.54	1.17	0.03
Max. Temp.	3	-56.44	119.57	1.2	0.03
Habitat; Density; Max. Temp.	7	-51.04	119.68	1.32	0.03
Habitat; Density; Max. Temp.	7	-51.06	119.73	1.36	0.03
Density; Max. Temp.	4	-55.29	119.75	1.38	0.03
Density; NDVI	4	-55.45	120.07	1.7	0.03
Density	3	-56.7	120.08	1.72	0.03
Temp. range	3	-56.82	120.32	1.95	0.02
Habitat; Min. Temp.	6	-52.9	120.42	2.05	0.02
ER	3	-56.93	120.56	2.19	0.02
Habitat; ER	6	-53.02	120.66	2.29	0.02
Habitat; Max. Temp.	6	-53.04	120.7	2.33	0.02
Prec.	3	-57.08	120.85	2.48	0.02
Temp. range; Density	4	-55.87	120.91	2.54	0.02
ER; Min. Temp	4	-55.89	120.96	2.59	0.02
ER; Max. Temp	4	-55.9	120.97	2.6	0.02
Habitat; Prec.	6	-53.23	121.08	2.71	0.02
ER; NDVI	4	-55.97	121.12	2.75	0.01
Habitat; NDVI	6	-53.26	121.14	2.77	0.01
Habitat; Temp. range	6	-53.27	121.16	2.8	0.01
Habitat; Temp. range; Density	7	-51.82	121.25	2.89	0.01

Model averaging revealed that activity overlap between European rabbits and its predators were equivalent in all habitat types, with the exception of scrublands where overlap was significantly lower (Table 10, Figure 10).

**Table 10.** Model averaging of activity overlap of conditional average as delta  $\Delta_{AIC} < 7$  confidence set.  $\hat{\beta}$  – parameter estimate, SE – standard error,  $CI_{95}$  - 95% confidence. Covariates are in “zscore” scale.

Covariates	$\hat{\beta}$ (SE)	$CI_{95}$	Probability (z value)
<b>Habitat type</b>			
Agroforestry	-0.39	[-0.93 0.15]	0.16
Quercus forest	-0.40	[-1.43 0.63]	0.44
Pinus forest	0.40	[-0.98 1.77]	0.57
Scrubland	-0.88	[-1.64 -0.11]	0.03
Rabbit density	0.27	[-0.14 0.68]	0.19
NDVI	0.19	[-0.21 0.60]	0.35
Maximum Temperature	-0.26	[-0.68 0.15]	0.21
Minimum Temperature	-0.24	[-0.63 0.15]	0.23
Temperature Range	-0.11	[-0.54 0.32]	0.63
Encounter Rate	0.11	[-0.28 0.50]	0.57
Precipitation	-0.04	[-0.45 0.38]	0.86



**Figure 10.** Activity coefficient overlap estimated values and confidence interval (error bar) according to habitat type, fitted by average linear models of conditional average.

### 3.4 Activity peak synchrony

Activity peak synchrony data consisted on 39 estimates, and ranged between 0.47 h and 11.86 h ( $5.54 \pm 3.51$  h, mean  $\pm$  se).

Like for the previous response variables, the linear model family had the highest support (Table 11), as it ranked first according to the AIC model selection procedure and because the variance explained by random factors was lower than the residual variance.

**Table 11.** Models' selection table for activity peak synchrony. All models included the following fixed-effects covariates: temperature range, precipitation, NDVI, predator activity, habitat and rabbit density. 'Study area' was included as random factor in the Linear Mixed-effects model, and 'sampling grid' nested in 'study area' as random factors in the Nested Design Linear Mixed-Effects models. Number of model parameters - df, log-likelihood - logLik, the Akaike's Information Criterion - AICc,  $\Delta_{AIC}$  - delta and weight.

Model	df	logLik	AICc	delta	weight
Linear Model	10	-93.279	218.3	0.00	0.89
Linear Mixed Effects Model	11	-93.279	222.6	4.22	0.11
Linear Mixed Effects Model - Nested Design	12	-100.436	228.7	10.39	0.01

Among all models for activity peak synchrony, the null model was the one that had the strongest support, indicating that the considered covariates had low predictive power and a weak relationship with the response variable (Table 12).

**Table 12.** Set of models for activity peak synchrony with  $\Delta_{AIC} < 4$ . These models resulted from dredging, excluding models containing correlated covariates. The covariates considered in the models are: density, predator activity -ER, precipitation - Prec., temperature range – Temp. range, maximum temperature – Max. Temp., and minimum temperature – Min. Temp.. Additional information about each model: number of model parameters - df), log-likelihood - logLik, the value of the information criterion used – AICc,  $\Delta_{AIC}$  - delta and 'Akaike weight' – weight.

Model	df	logLik	AICc	delta	weight
NULL	2	-103.74	211.81	0	0.1
Density	3	-102.65	211.99	0.18	0.09
Temp. range; Density	4	-101.78	212.74	0.93	0.06
Density; Prec.	4	-101.8	212.78	0.97	0.06
ER	3	-103.43	213.54	1.73	0.04
Temp. Min.	3	-103.46	213.6	1.79	0.04
Prec	3	-103.59	213.86	2.05	0.03
Temp. range	3	-103.62	213.93	2.12	0.03
NDVI	3	-103.65	213.99	2.18	0.03
Temp. Max.	3	-103.66	214.01	2.2	0.03
Density; Temp. Max.	4	-102.6	214.37	2.56	0.03
Density; Temp. Min.	4	-102.64	214.45	2.64	0.03
Density; ER	4	-102.65	214.48	2.66	0.03
Density; NDVI	4	-102.65	214.48	2.67	0.03
Temp. range; Density; Temp. Min.	5	-101.37	214.57	2.75	0.02
Temp. range; Temp. Min.	4	-102.86	214.89	3.08	0.02
Temp. range; Density; NDVI	5	-101.57	214.95	3.14	0.02
Density; Prec.; Temp. Min.	5	-101.6	215.01	3.2	0.02
Prec.; Temp. Min.	4	-102.98	215.14	3.32	0.02
Density; Prec.; Temp. Max.	5	-101.73	215.28	3.46	0.02
ER; Prec.	4	-103.07	215.31	3.5	0.02
Density; NDVI; Prec.	5	-101.75	215.32	3.5	0.02
Density; ER; Prec.	5	-101.77	215.36	3.55	0.02
Temp. range. Density; ER	5	-101.77	215.37	3.55	0.02
Temp. range; ER	4	-103.16	215.5	3.69	0.02
Prec.; Temp. Max.	4	-103.18	215.53	3.72	0.01
ER; Temp. Min.	4	-103.3	215.77	3.96	0.01

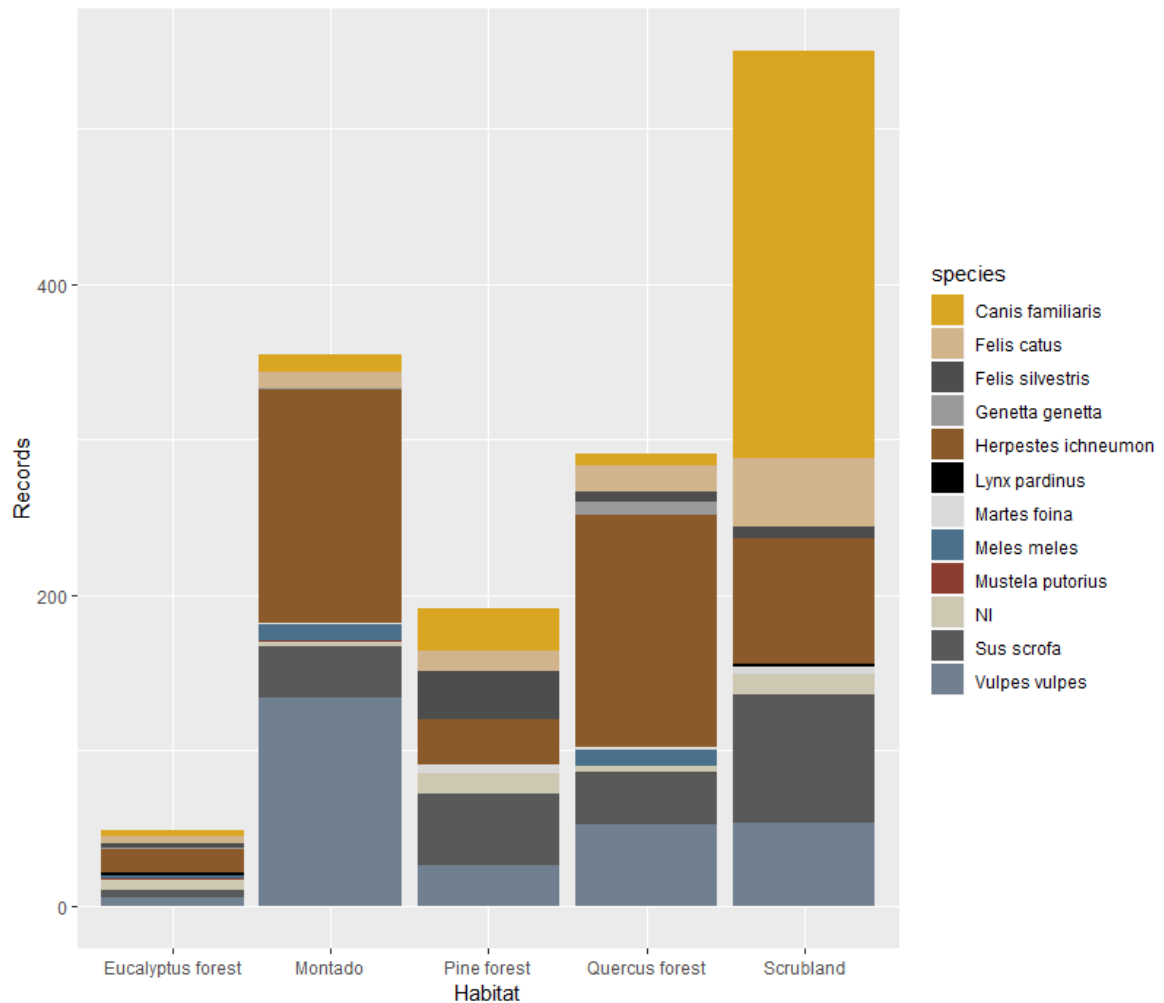
## 4. DISCUSSION

### 4.1 General discussion

Overall, European rabbits revealed a bimodal diel activity pattern with higher activity density at sunrise than at sunset, consistent with the patterns described in other Mediterranean study areas (Díez *et al.*, 2005; Monterroso *et al.*, 2013; Villafuerte *et al.* 1993). This activity pattern centered on the crepuscular period seems to be the better anti-predator strategy to avoid both diurnal (*e. g.* avian raptors) and nocturnal predators (*e. g.* mammalian carnivores) (García-Canseco, 1997; Halle 2000; Monterroso *et al.*, 2013).

Notwithstanding, rabbits were expected to exhibit a more diurnal activity particularly on scrublands. The risk of encountering mammalian predators is higher in closed habitats such as scrublands because these predators are specialized for hunting in such habitat types (Murray *et al.*, 1995), and because carnivore presence is difficult to detect in thick vegetation (Villafuerte & Moreno, 1997). However, rabbits could compensate by being more active during daytime (Bakker *et al.*, 2005), as this habitat provides refuge against diurnal raptors and mammalian carnivores are mostly nocturnal (Monterroso *et al.*, 2013; Murray *et al.*, 1995). This strategy was observed in other studies, where rabbits exhibited higher diurnal activity in covered habitat (scrublands) and higher nocturnal activity in open habitats (Lombardi *et al.*, 2003; Lombardi *et al.*, 2007; Martins *et al.*, 2003; Moreno *et al.*, 1996, Navarro-Castilla *et al.*, 2018), demonstrating the European rabbit adaptability in changing activity patterns according to habitat type. Nevertheless, this variation in diel activity pattern according to habitat was not observed in our case. Other factors may be modifying rabbits' activity in scrubland, such as disturbance by hunting activities (Barrio *et al.*, 2011; Poole 2003). In fact, dog records were higher in scrublands than in any other habitat type (Figure 11), which can be associated with hunting activities. Furthermore, human disturbance and hunting activity during the day, coupled with the occurrence of higher proportion of diurnal carnivores (Figure 11), may be determining the diel activity pattern observed.





**Figure 11.** Number of independent predator records (n=1436) according to habitat type, with respective predator species, being NI- unidentified species of carnivores.

Higher rabbit density was record between March and July, coinciding with the final months of breeding season (Gonçalves *et al.*, 2002; Villafuerte *et al.*,1997). This can be explained by the recruitment of juvenile individuals, that at this stage already incorporate the population.

#### 4.2 Activity level

Temperature range, maximum and minimum temperature negatively affected rabbits' activity level, with maximum daily temperature producing the strongest effect. High temperatures affect rabbit's thermoregulation (Villafuerte *et al.*, 1993). Hence, they tend to avoid being active during extreme heat periods. Furthermore, temperature can also affect the rabbit's reproduction (Tablado *et al.*, 2009). High temperatures (summer) are associated with the end of breeding season in Mediterranean climates, due

to the inhibition of reproductive status (fertility) of European rabbits and the lower availability of green food (Myers, 1971; Gonçalves *et al.*, 2002; Kotsiotis *et al.*, 2018). Therefore, the negative effect of temperature in activity level may also be explained by reproduction: with the end of breeding season, rabbits are less active for social activities and consequently they have less energy requirements. This explains the negative effect of minimum temperature, although rabbits were expected to minimize the diel active time with cold temperatures for efficient thermoregulation (Villafuerte *et al.*, 1993).

Rabbit density was negatively related to their activity level. These results are coherent with a cooperative social system leading to food intake facilitation through decrease in vigilance time. When in larger groups, the individual feeding requirement tends to be more easily achieved because less time needs to be devoted to vigilance (Becauchamp, 2002; Lima 1995; Villafuerte & Moreno, 1997). The decrease in vigilance with larger rabbit group size can be explained by the dilution effect (Becauchamp, 2002; Dehn, 1990; Lima, 1990), and / or shared vigilance and collective detection, as more individuals means more eyes scanning for predators (Lima, 1995). The dilution effect is the presence of companions in a group dilutes individual risk when predators attack (Becauchamp, 2002; Dehn, 1990; Lima, 1990). The many-eyes hypothesis relies on the shared vigilance and collective detection. This hypothesis suggests that as group size increases, there are progressively more eyes scanning the environment for predators and thus an individual can devote less time to vigilance (and more time to feeding). shared vigilance and collective detection, as more individuals means more eyes scanning for predators (Lima, 1995).

Habitat type determines food and refuge availability that influences their diel activity (Moreno *et al.*, 1996; Lombardi *et al.*, 2003). Differences in vegetation structure and cover also imply differences in exposure of rabbits to predators. European rabbits exhibited the highest activity level in the eucalyptus forest and scrubland when compared to the reference habitat (agroforestry). The high activity level on the eucalyptus forest may be related to the inferior food availability of this habitat and to the reduced predator activity. Thus, rabbits need spend more time foraging to achieve their feeding requirements and they have less predator pressure, since the predation risk is low (Lima & Bednekoff, 1999). However, it is important to emphasize that eucalyptus forest was associated with worst model performance as a result of few data. In fact, this habitat was barely represented being associated to/with only one sampling grid (Appendix, Table S1).

As previously stated, rabbits have higher protection from diurnal raptors on scrublands, whereas they are more susceptible to mammalian carnivores, which are mostly nocturnal (Villafuerte *et al.* 1993;

Díez *et al.*, 2005; Monterroso *et al.*, 2013;). However, these habitats in the studied areas had predator communities with a higher proportion of diurnal carnivores - Egyptian mongooses and domestic dogs (Monterroso *et al.*, 2014) – which provide 62.1% of all predator records in scrublands. Hence, hunting activity during the day, coupled with the occurrence of both nocturnal and diurnal carnivores in this area, may reflect into a constant high perceived predation risk throughout the day. According to the predation risk allocation hypothesis (Lima & Bednekoff, 1999), if high-risk periods are frequent or lengthy, the prey will show less pronounced antipredator behavior, since it has little choice but to feed under high risk (Monterroso *et al.*, 2013). In this case, the probability of any individual rabbit being killed by predation may be lower when activity is span for a longer period of the day, instead of being concentrated in time (Halle 2000), as hypothesized to be the situation of murids in the Iberian Peninsula (Monterroso *et al.*, 2013). This would explain the increasing of European rabbits' activity level in this habitat, contrary to what was expected.

European rabbits showed a lower activity level in agroforestry habitats. This is concordance with the risk allocation hypothesis (Lima & Bednekoff, 1999), which postulates that prey living in a dangerous environment moderate the activity level, increasing their activity during brief pulses of safety (Sih & McCarthy, 2002). By exhibiting a clearly bimodal activity pattern with peaks on sunrise and sunset (Diez *et al.*, 2005; Monterroso *et al.*, 2013 Villafuerte *et al.*, 1993), they minimize the diel active time.

Contrary to what was expected, European rabbits' activity level did not correlate with predator activity. Previously described antipredator strategies by European rabbits rely mainly on avoiding risky areas and reducing their activity (Navarro-Castilla *et al.*, 2018; Villafuerte *et al.*, 1997). However, our results suggest that, by not responding to predator activity but rather to habitat structure and to their own density, perception of risk by European rabbits may be more important in shaping their activity level than to predation risk itself (Brown *et al.*, 1999; Preisser *et al.*, 2005; Villafuerte & Moreno, 1997). Predators can affect prey directly through mortality, but also indirectly via predation risk (Lima & Dill, 1990; Preisser *et al.*, 2005). Prey responds to fear of predation, *i. e.*, perceived predation risk, by adapting their anti-predator strategies, through what has been described as “the ecology of fear” (Brown *et al.* 1999; Ripple & Beschta, 2004). This may include reducing active time, increasing vigilance, and foraging in group (Lima & Dill, 1990). Previous studies had suggested that European rabbits can locally adapt their spatial and temporal strategies as a response to perceived predation risk (Moreno *et al.*, 1996; Villafuerte & Moreno, 1997). In fact, both group size and habitat structure may influence the predation risk, that ultimately will model activity level.

Seasonal variations in food resources has been reported to have an important role in the reproduction period (Tablado *et al.*, 2009). In particular, the availability of green food seems to be correlated with the breeding season (Soriguer & Rogers 1981; Gonçalves *et al.*, 2002). Therefore, the availability of high-quality food was expected to be associated to the reproductive period and consequently increase the activity level, since in the period rabbits need to be more active for social activities and thus, they have less energy requirements. However, no relation was found between NDVI, a proxy for vegetation quality, and activity level. The majority of habitats considered in this study included evergreen trees such as holm oak, cork oak, stone pine and eucalyptus, where only a fraction of the radiation reflected is originated from the ground layer (Borowik *et al.*, 2013). Therefore, such overshadowing of the understory layer, where plants ingested by rabbits are located, could provide a misrepresentation of rabbits' feeding resources. This fact could be related to the weak association between NDVI and rabbit activity level, and suggests that this metric may not be the most reliable in this context.

European rabbits were expected to display a negative relation between their activity level and precipitation, since high rainfall compromises thermoregulation (Villafuerte *et al.*, 1993; Rodel, 2000). However, the opposite is also a possibility: precipitation influence positively their activity level. In Mediterranean climates, rainfall is associated with the beginning of European rabbit's breeding period due to the increase of food availability, through favoring the germination and growth of plants (Soriguer & Rogers 1981; Gonçalves *et al.*, 2002). In this period, rabbits have more energy requirements (Villafuerte *et al.*, 1997) and they need to be more active for social activities, namely, to find and defend partners, and to the structuring of the social hierarchy. Nonetheless, this study failed to detect any correlation between precipitation and rabbit activity level. Precipitation has been reported to affect negatively rabbit activity in areas outside their native range (Ballinger & Morgan, 2000; Fletcher *et al.*, 1999; Rowley, 1957), however there is little evidence for any kind of effect of precipitation on its native area (*e.g.* Villafuerte *et al.*, 1993).

### 4.3 Activity overlap

According to optimal foraging theory, an animal should display a foraging pattern that maximizes its caloric intake per time unit (MacArthur & Pianka, 1966; Pyke *et al.*, 1977). In the Mediterranean region, the European rabbit is considered the most profitable the preferred prey because of its high energetic

value (Delibes-Mateos *et al.*, 2008a; Malo *et al.*, 2004). Therefore, it was expectable that predators would track rabbits' activity, increasing the overlap in their activity patterns (Monterroso *et al.*, 2013). However, our results revealed that scrublands was the only habitat type informative about activity overlap. All other tested covariates were uninformative with respect the overlap between European rabbits' and its predators' activity pattern. In scrublands, European rabbits were able to reduce the likelihood of encounters with predators when compared to agroforestry (the reference habitat type). This may be related to the cover provided by this habitat, but also the adjust of rabbits' diel activity.

Conversely, although not meaningfully, rabbits showed activity overlap with its predators on agroforestry areas, probably because of the higher frequency of nocturnal and crepuscular predators, such as red foxes, in these habitats. However, it should be noted that raptors were not take into consideration for this estimation, as camera trapping fails to detect avian predators' activity. The risk of predation by raptors during daytime is tangible (García-Canseco, 1997), so rabbits must balance the relative risk of being active during day and night (Moreno *et al.*, 1996). In addition, although in a smaller quantity, there were also detected other diurnal predators (*e.g.* Egyptian mongooses). Therefore, the balance of the "total" risk can benefit the nocturnal activity (Monterroso *et al.*, 2013).

#### 4.4 Activity peak synchrony

As previous stated, the European rabbit is the preferred prey for most carnivore species in the Mediterranean region because of its high energetic value (Delibes-Mateos *et al.*, 2008a; Malo *et al.*, 2004). Therefore, I expected that its predators would try to synchronize their activity with that of rabbits'. Consequently, predator activity was expected to be principal predictor of the synchrony of overlap. Overall, there I found a relative lack of synchrony in the activity patterns of predators and European rabbits, with peak timings differing by *ca.* 5h. Predator-prey activity relationships consist of an arm-race where prey continuously try to avoid high predators, whereas predators try to track their prey to maximize foraging (Blumstein, 2008). This lack of synchrony I found might suggest a more effective strategy of European rabbits in avoiding predators, than that of predators in tracking rabbits. However, my models revealed that none of the environmental covariates could explain the patterns of activity peak synchrony observed. This may be related to the fact that predator's peaks differ among species and they were calculated together as a result of few data from predators.

#### 4.5 Integration of activity level, activity overlap and activity peak synchrony

Overall, my results revealed that European rabbits revealed a bimodal diel activity pattern (Díez *et al.*, 2005; Monterroso *et al.*, 2013; Villafuerte *et al.*, 1993), which was consistent across the different habitats. Despite this general pattern, I found that, without meaningfully changing their activity pattern, rabbits are able to readjust the time length they are active in a day according to habitat type: increasing activity level in habitat with higher cover and reducing the activity level in open habitats. I hypothesize that such strategy aims at reducing the likelihood of predation given the longer periods of predation risk in this habitat (Halle, 2000). This assertion was further corroborated by the activity overlap results: by reducing their diel activity level, rabbits managed to reduce the activity overlap with that of their predators. Furthermore, despite some inevitable overlap between the diel rhythms of predators and rabbits, their activity was not synchronized (Monterroso *et al.*, 2013).

Predators only track prey activity up to a point when the combination of predation success and the energetic intake is sufficient to fulfil its biological needs (Monterroso *et al.*, 2013). It is possible that the level of synchronization and overlap with rabbits may be enough for predators to meet their energy requirements either by successfully preying rabbits or other alternative prey. As suggest by Monterroso *et al.*, 2013, the strategy that most benefits predators may be chasing alternative prey.

In summary, we were able to detect changes in the activity rhythms at a microspatial scale, reflecting the adaptability of European rabbits.

#### 4.6 Limitations of the approach

Overall, European rabbits' CT data allowed an effective reconstruction of European rabbit activity patterns. However, the accuracy of activity curves may have been affected by imperfect detection (Lashley *et al.*, 2018; Rowcliffe *et al.*, 2014), as individuals present within the sampling area might not always have been detected either by not triggering the CT or by not entering the detection zone (Burton *et al.*, 2015). Additionally, this methodology does not allow distinguishing individuals, therefore activity analysis was centered in the population, ignoring the individual intrinsic behavior variation on the population. Inter-individual heterogeneity may arise from distinct personality and by individuals' perceived of their environment (e.g. individual-specific landscape of fear; Mc Arthur *et al.*, 2014). This variability might bias population-level estimates of activity in unpredictable ways.

In this study, the detection rate of predators ( $0.14 \pm 0.18$  detection/trapping-day; mean  $\pm$  SD) was low, thus, the activity of predators might have been underestimated. One important limitation of this study was that predation risk by avian predators was not considered, as camera trapping did not allow their detection. These factors may have clouded the full understanding of predation risk variability across study sites, and could have been at partly responsible for the uninformative nature of some of the covariates considered. In particular, the role of predator activity on the rabbits' activity level as a driver of the "landscape of fear" may have been depreciated. Furthermore, domestic carnivores were frequently detected over the course of the sampling campaigns in Mértola, specially at MTR2, which may be interfering with the wildlife existing here and thus, my results may not be extrapolated to context of purely wildlife-composed communities.

In summary, several important implications might have not totally grasped by this study, but require serious empirical consideration, such as more accurate metrics to measure food quality and methods that have into consideration all classes of predators, including raptors.

#### 4.7 Implications for management and conservation

The rabbit plays an important role in Iberian ecosystems, as a keystone and an emblematic game species (Delibes-Mateos *et al.*, 2014b). In fact, some seriously threatened predator species such as the Spanish Imperial Eagle and the Iberian lynx rely heavily on rabbit abundance for survival.

The present study provides insights into how habitat structure and population density may affect the activity of European rabbits and can be used as a tool in local habitat management aimed at restoring rabbit populations in Mediterranean environments. The activity of rabbits seems to be influenced essentially by anti-predator strategies that are shaped processes leading a "landscape of fear" and "time-scape of fear". The risk of predation however, is perceived according to habitat structure and group size. This suggests that management actions for rabbits' population recovery should focus on improving habitat, combining favorable characteristics, including dense scrubland combined with grassland, that aim to minimize the predation risk (Ferreira *et al.*, 2013). Furthermore, effective ecological restoration may depend on reestablishing "landscapes of fear" because fear may be as or more important than direct predation (Manning *et al.*, 2009, Suraci *et al.*, 2016).

In the Iberian Peninsula rabbits seem to be recovering better in areas where several management activities have been carried out simultaneously and regularly (Delibes-Mateos *et al.* 2008). In particular,

improved rabbit recovery has been observed in hunting estates where both mammalian predator control and habitat management are frequently applied (Angulo 2003; Delibes-Mateos et al. 2008).



## 5. CONCLUSION

This work highlighted the importance of temperature (range, maximum and minimum), density and habitat for European rabbit's activity, as hypothesized in other studies for Mediterranean zones of Iberian Peninsula (Monterroso *et al.*, 2013; Moreno *et al.*, 1996; Villafuerte *et al.*, 1993; Villafuerte & Moreno, 1997, Palomares *et al.*, 2001). Notwithstanding it was difficult to discern the driving factors of activity given the complexity and correlation of environmental variables.

Rabbits reduced their activity level as a response to maximum daily temperature, likely to ensure effective thermoregulation. The negative density-dependence effects on rabbit activity level is related probably to an adaptation to maximize the food intake while minimizing predation risk. Finally, European rabbits were found to have high activity level associated to less intense activity bursts in scrubland habitats, which suggest a strategy for the reduction of individual probability of predation risk. Conversely, in agroforestry, they revealed a lower diel activity level with the risk allocation hypothesis, which postulates that prey living in a risky environment moderate their activity level, increasing activity during brief pulses of safety. Furthermore, by not responding to predator activity but rather to habitat structure and to their group size, European rabbits' may respond to the perception of risk more than to predation risk itself.

With this study I was able to detect changes in the activity rhythms in a microspatial scale, reflecting the adaptability of European rabbits. These results provide new insights into rabbit activity and anti-predator responses, important to define conservation strategies for the recovery of rabbit populations in Mediterranean environments.

## 6. FUTURE PERSPECTIVES

The structure and behavior of predators-prey occur mainly at two dimensions: spatial and temporal (Lima & Bednekoff 1999; Lima 2002). We focused on the temporal axis of prey adaptations to predator. This study provides new insights into temporal variation in predation risk and foraging, and consequently the activity level and rhythms of the European rabbit.

It is important not only to understand how temporal variation may affect rabbit activity and anti-predator responses, but also in a spatial scale. Hence, further research should focus on the evaluation of the spatial variation of these temporal strategies in relation to microhabitat, since behavior of both predator and prey species may change over a small spatial scale, as a consequence of as predation risk and prey vulnerability adjustment (Fenn & MacDonald 1995; Lima & Bednekoff 1999).

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## APPENDIX

**Table S1.** Habitat type corresponding to the sampling grids on each sampling area.

Habitat	Sampling grids
Quercus agroforestry	BNV1 – Grid 1
	FAL1 – Grid 1
	FAL1 – Grid 2
	MRT1 – Grid1
Scrubland	MRT2 – Grid 1
	MRT2 – Grid 2
	MRT2 – Grid 3
Quercus forest	BNV1 – Grid 2
	BNV1 – Grid 3
	FAL1 – Grid 3
	MRT1 – Grid 3
Pine forest	MRT3 – Grid 1
	MRT3 – Grid 2
	MRT3 – Grid 3
Eucalyptus forest	MRT1 – Grid 2

**Table S2.** Set of models for European rabbits' activity level. These models resulted from dredging, excluding models containing correlated covariates. The covariates considered in the models are: density, predator activity -ER, precipitation - Prec., temperature range – Temp. range, maximum temperature – Max. Temp., and minimum temperature – Min. Temp.. Additional information about each model: number of model parameters - df), log-likelihood - logLik, the value of the information criterion used – AICc,  $\Delta$ AIC - delta and 'Akaike weight' – weight.

Model	df	logLik	AICc	delta	weight
Habitat; Density; Max.Temp.	8	·122.55	262.01	0.00	0.28
Habitat; ER; Max.Temp.	9	·122.26	263.66	1.65	0.12
Habitat; Density; Temp. Range; Min.Temp.	9	·122.29	263.72	1.71	0.12
Habitat; Density; Prec.; Max.Temp.	9	·122.43	264.00	1.99	0.10
Habitat; Max.Temp.	7	·125.04	264.79	2.79	0.07
Habitat; Density; ER; Temp.Range; Min.Temp.	10	·122.05	265.51	3.51	0.05
Habitat; Density; ER; Prec.; Max. Temp.	10	·122.17	265.74	3.73	0.04
Habitat; Temp. Range; Min. Temp.	8	·124.42	265.75	3.74	0.04
Habitat; Density; Min. Temp.	8	·124.62	266.15	4.14	0.04
Habitat; Prec.; Max. Temp.	8	·124.99	266.89	4.88	0.02
Habitat; ER; Max. Temp	8	·125.04	266.99	4.98	0.02
Habitat; Density; ER; Min. Temp.	9	·124.27	267.68	5.67	0.02
Habitat; Density; Prec.; Min. Temp.	9	·124.38	267.90	5.89	0.01
Habitat; ER; Temp. Range; Min. Temp.	9	·124.42	267.98	5.97	0.01
Habitat; Density; ER; Prec; Min.Temp.	10	·123.97	269.35	7.34	0.01
Habitat, Density, Temp.Range	9	·125.27	269.69	7.68	0.01
Habitat, Density, Temp.Range	8	·126.63	270.17	8.16	0.00
Density, Max.Temp.	4	·131.47	271.18	9.18	0.00
Habitat, Min.Range	7	·128.34	271.38	9.37	0.00
Habitat, Density, ER, Temp.Range	10	·125.26	271.92	9.91	0.00
Habitat, Temp.Range	8	·127.70	272.32	10.31	0.00
Habitat, Density, ER, Temp.Range	9	·126.61	272.37	10.36	0.00
Habitat, Prec, Min.Temp.	8	·127.73	272.38	10.37	0.00

**Table S2. (continuation)**

Density, Prec, Max.Temp.	5	.131.29	272.96	10.95	0.00
Density, ER, Max.Temp.	5	.131.34	273.05	11.05	0.00
Density, Temp.Range, Min.Temp	5	.131.37	273.12	11.11	0.00
Habitat, Temp.Range	7	.129.30	273.31	11.30	0.00
Habitat, ER, Min.Temp	8	.128.34	273.59	11.58	0.00
Habitat, ER, Temp.Range	9	.127.58	274.31	12.30	0.00
Density, Min.Range	4	.133.11	274.48	12.47	0.00
Habitat, ER, Prec, Min.Temp.	9	.127.72	274.59	12.58	0.00
Max.Temp.	3	.134.34	274.82	12.81	0.00
Density, ER, Prec, Max.Temp	6	.131.19	274.90	12.89	0.00
Habitat, Density	8	.129.00	274.91	12.90	0.00
Density, ER, Temp.Range, Min.Temp.	6	.131.27	275.07	13.06	0.00
Habitat, Density, Prec	9	.127.98	275.11	13.10	0.00
Habitat, ER, Temp.Range	8	.129.17	275.25	13.24	0.00
Temp.Range, Min.Temp.	4	.133.93	276.10	14.09	0.00
Density, ER, Min.Temp.	5	.132.90	276.17	14.16	0.00
Density, Prec, Min.Temp.	5	.132.96	276.28	14.27	0.00
Prec, Max.Temp	4	.134.21	276.67	14.66	0.00
Er, Max.Temp.	4	.134.31	276.87	14.86	0.00
Habitat, Density, ER	9	.128.99	277.12	15.11	0.00
Habitat, Density, ER, Prec	10	.127.91	277.23	15.22	0.00
Density, ER, Prec, Min.Temp.	6	.132.71	277.95	15.94	0.00
ER, Temp.Range, Min.Temp	5	.133.88	278.14	16.13	0.00
ER, Prec, Max.Temp.	5	.134.17	278.72	16.71	0.00
Habitat, Density, Prec	8	.131.67	280.25	18.25	0.00
Min.Temp.	3	.137.15	280.45	18.44	0.00
Habitat, Prec	8	.131.80	280.51	18.50	0.00
Density, Temp.Range	4	.136.17	280.59	18.58	0.00

**Table S2. (continuation)**

Prec, Min.Temp.	4	.136.77	281.78	19.77	0.00
Habitat	7	.133.66	282.02	20.02	0.00
Habitat, Density, ER, Prec	9	.131.54	282.22	20.21	0.00
ER, Min.Temp	4	.137.13	282.50	20.49	0.00
Habitat, ER, Prec	9	.131.70	282.54	20.53	0.00
Density, Temp.Range	5	.136.14	282.65	20.64	0.00
Density, ER, Temp.Range	5	.136.17	282.71	20.70	0.00
Habitat, ER	8	.133.33	283.57	21.56	0.00
Temp.Range	3	.138.84	283.83	21.82	0.00
ER, Prec, Min.Temp.	5	.136.76	283.89	21.88	0.00
Habitat, Density	7	.134.68	284.06	22.05	0.00
Density, ER, Temp.Range	6	.136.14	284.80	22.79	0.00
ER, Temp.Range	4	.138.54	285.33	23.32	0.00
Temp.Range	4	.138.81	285.88	23.87	0.00
Habitat, Density, ER	8	.134.66	286.23	24.22	0.00
ER, Temp.Range	5	.138.51	287.40	25.39	0.00
Habitat, Prec.	7	.136.87	288.45	26.44	0.00
Density, Prec.	4	.140.59	289.43	27.42	0.00
Density, Prec.	5	.139.69	289.75	27.74	0.00
Habitat, ER, Prec.	8	.136.78	290.47	28.46	0.00
Density	4	.141.43	291.10	29.09	0.00
Density, ER, Prec.	5	.140.52	291.41	29.40	0.00
Density, ER, Prec.	6	.139.64	291.81	29.80	0.00
Density, ER	5	.141.43	293.22	31.22	0.00
Density	3	.143.71	293.57	31.56	0.00
Density, ER	4	.143.70	295.65	33.64	0.00
Prec.	4	.144.36	296.97	34.96	0.00
Habitat	6	.142.38	297.28	35.27	0.00



Table S2. (continuation)

Prec.	3	.145.69	297.53	35.53	0.00
Habitat, ER	7	.141.77	298.24	36.23	0.00
ER, Prec.	5	.144.16	298.69	36.68	0.00
ER, Prec.	4	.145.52	299.29	37.28	0.00
NULL	3	.146.98	300.11	38.10	0.00
ER	4	.146.48	301.22	39.21	0.00
NULL	2	.150.53	305.13	43.12	0.00
ER	3	.149.95	306.05	44.04	0.00

**Table S3.** Set of 85 models for overlap activity. These models resulted from dredging, excluding models containing correlated covariates. The covariates considered in the models are: density, predator activity - ER, precipitation - Prec., temperature range – Temp. range, maximum temperature – Max. Temp., and minimum temperature – Min. Temp.. Additional information about each model: number of model parameters - df), log-likelihood - logLik, the value of the information criterion used – AICc,  $\Delta$ AIC - delta and 'Akaike weight' – weight.

Model	df	logLik	AICc	delta	weight
Habitat	5	-53.27	118.37	0	0.06
	2	-57.09	118.51	0.14	0.06
Habitat; Density	6	-52.3	119.22	0.85	0.04
NDVI	3	-56.32	119.33	0.96	0.04
Density; Max. Temp.	4	-55.1	119.38	1.01	0.04
Min. Temp.	3	-56.42	119.54	1.17	0.03
Max. Temp.	3	-56.44	119.57	1.2	0.03
Habitat; Density; Max. Temp.	7	-51.04	119.68	1.32	0.03
Habitat; Density; Max. Temp.	7	-51.06	119.73	1.36	0.03
Density; Max. Temp.	4	-55.29	119.75	1.38	0.03
Density; NDVI	4	-55.45	120.07	1.7	0.03
Density	3	-56.7	120.08	1.72	0.03
Temp. range	3	-56.82	120.32	1.95	0.02
Habitat; Min. Temp.	6	-52.9	120.42	2.05	0.02
ER	3	-56.93	120.56	2.19	0.02
Habitat; ER	6	-53.02	120.66	2.29	0.02
Habitat; Max. Temp.	6	-53.04	120.7	2.33	0.02
Prec.	3	-57.08	120.85	2.48	0.02
Temp. range; Density	4	-55.87	120.91	2.54	0.02
ER; Min. Temp	4	-55.89	120.96	2.59	0.02
ER; Max. Temp	4	-55.9	120.97	2.6	0.02
Habitat; Prec.	6	-53.23	121.08	2.71	0.02

**Table S3. (continuation)**

ER; NDVI	4	-55.97	121.12	2.75	0.01
Habitat; NDVI	6	-53.26	121.14	2.77	0.01
Habitat; Temp. range	6	-53.27	121.16	2.8	0.01
Habitat; Temp. range; Density	7	-51.82	121.25	2.89	0.01
Prec.; Max. Temp.	4	-56.19	121.56	3.19	0.01
Habitat; Density; NDVI	7	-52.03	121.68	3.31	0.01
NDVI; Prec.	4	-56.28	121.73	3.36	0.01
Temp. range; NDVI	4	-56.31	121.8	3.44	0.01
Density; Prec.; Max. Temp.	5	-55.01	121.84	3.47	0.01
Density; ER; Max. Temp.	5	-55.01	121.84	3.47	0.01
Prec.; Min. Temp.	4	-56.34	121.85	3.48	0.01
Temp. range; Min. Temp.	4	-56.42	122.01	3.64	0.01
Temp. range; Density; Min. Temp.	5	-55.1	122.02	3.66	0.01
Habitat; Density; Prec.	7	-52.24	122.09	3.72	0.01
Temp. range; ER	4	-56.5	122.18	3.82	0.01
Density; ER; Min. Temp.	5	-55.19	122.19	3.83	0.01
Habitat; ER; Min. Temp	7	-52.29	122.2	3.83	0.01
Habitat; Density; ER	7	-52.3	122.21	3.84	0.01
Tem. Range; Density; NDVI	5	-55.22	122.25	3.88	0.01
Density; Prec.	4	-56.56	122.29	3.92	0.01
Density; Prec.; Min. Temp.	5	-55.29	122.39	4.02	0.01
Density; ER	4	-56.69	122.56	4.19	0.01
Habitat; ER; Max. Temp	7	-52.49	122.58	4.22	0.01
Habitat; Density; Prec.; Max. Temp.	8	-50.9	122.6	4.23	0.01
Density; ER; NDVI	5	-55.42	122.65	4.28	0.01
Density; NDVI; Prec.	5	-55.43	122.68	4.31	0.01
Habitat; Density; ER; Max. Temp.	8	-50.99	122.78	4.41	0.01
Habitat; Density; ER; Min. Temp.	8	-51	122.8	4.43	0.01

**Table S3. (continuation)**

Habitat; Min. Temp.	7	-52.6	122.82	4.45	0.01
Habitat; Tem. Range; Density; Min.Temp.	8	-51.01	122.83	4.46	0.01
Habitat; Prec.; Max. Temp.	7	-52.63	122.86	4.5	0.01
Habitat; Density; Prec.; Min. Temp.	8	-51.04	122.88	4.52	0.01
ER; Prec.	4	-56.89	122.95	4.58	0.01
Habitat; Temp. range; Min. Temp.	7	-52.78	123.18	4.81	0.01
ER; Prec.; Max. Temp	5	-55.73	123.28	4.91	0.01
Temp. range; Density; ER	5	-55.85	123.51	5.14	0
Habitat; ER; NDVI	7	-52.95	123.52	5.15	0
Habitat; Temp. range; ER	7	-52.97	123.54	5.18	0
Temp. range; ER; Min. Temp	5	-55.87	123.55	5.18	0
ER; Prec.; Min. Temp	5	-55.87	123.55	5.18	0
Habitat; ER; Prec	7	-53.01	123.64	5.27	0
Temp. range; ER; NDVI	5	-55.92	123.66	5.29	0
ER; NDVI; Prec.	5	-55.97	123.75	5.38	0
Habitat; NDVI; Prec.	7	-53.19	123.99	5.62	0
Habitat; Temp. range; NDVI	7	-53.26	124.13	5.76	0
Habitat; Temp. range; Density; NDVI	8	-51.74	124.29	5.92	0
Habitat; Temp. range; Density; ER	8	-51.82	124.44	6.07	0
Density; ER; Prec.; Max. Temp	6	-54.93	124.49	6.12	0
Temp. range; Density; ER; Min. Temp	6	-55.01	124.65	6.28	0
Habitat; Density; NDVI; Prec.	8	-52.01	124.82	6.45	0
Habitat; Density; ER; NDVI	8	-52.03	124.86	6.49	0
Density; ER; Prec.	5	-56.54	124.89	6.52	0
Tem. range; Density; ER; NDVI	6	-55.18	124.99	6.62	0
Density; ER; Prec.; Min. Temp	6	-55.19	125	6.63	0
Habitat; ER; Prec.; Min. Temp	8	-52.13	125.06	6.7	0
Habitat; ER; Prec.; Max. Temp	8	-52.18	125.16	6.79	0

**Table S3. (continuation)**

Habitat; Tem. range; ER; Min. Temp.	8	-52.23	125.26	6.89	0
Habitat; Density; ER; Prec.	8	-52.24	125.27	6.91	0
Density; ER; NDVI; Prec.	6	-55.4	125.42	7.05	0
Habitat; Temp. range; ER; NDVI	8	-52.94	126.67	8.31	0
Habitat; ER; NDVI; Prec.	8	-52.94	126.68	8.31	0

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## Ficha de Contagem de Excrementos

Zona de caça (se aplicável): \_\_\_\_\_ Grelha: \_\_\_\_\_

Observador(es): \_\_\_\_\_ Data: \_\_\_\_/\_\_\_\_/\_\_\_\_

Chuva nos últimos 3 dias: Sim  Não

Condições atmosféricas:

Pouco/Inebulado  Muito/Inebulado  Nevoeiro   
 Sem/Chuva  Chuva/fraca  Chuva/forte

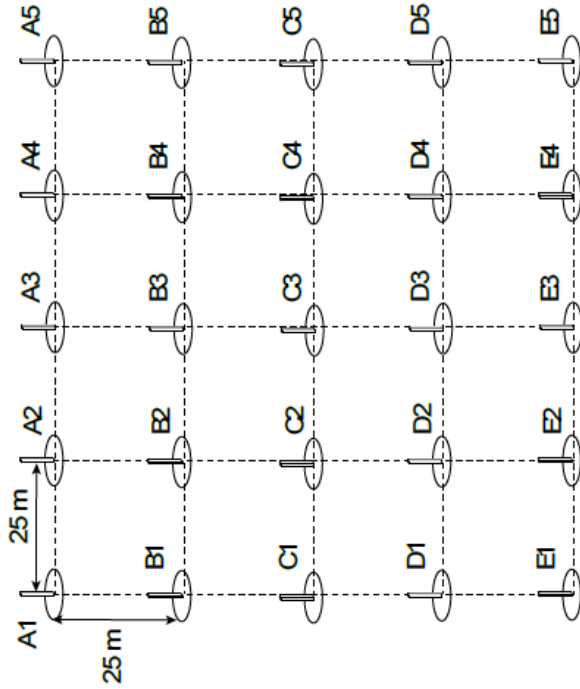
### Indícios de predadores

Código	Tipo	Idade	Recolha	Espécie

Tipo: P= Pegada; E= Excremento; L= Latrina; C= Cadáver  
 Idade: F= Fresco; V= Velho; MV= Muito Velho  
 Recolha: S= Sim; N= Não\*

1 2 3 4 5

### Contagem de Excrementos Dispersos



	A	B	C	D	E