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Plasticity in daily activity patterns of a key prey species in the Iberian Peninsula to reduce predation risk

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Abstract

Context. Some prey species can shift their daily activity patterns to reduce the risk of encountering predators, and, in turn, predators develop strategies to increase their chances of meeting prey. European rabbit (*Oryctolagus cuniculus*) is a key species in Iberian Mediterranean ecosystems. It is the main prey for many vertebrate predators. It is also a game species and is often the target of management measures such as translocations.

Aims. To test whether rabbits adjust their activity patterns in response to differing predation regimes in a management context.

Methods. Rabbits were translocated from a donor area, with a high rabbit density, to a release area in central Spain, with a semi-permeable fenced plot and an unfenced plot, which had no rabbits before the translocation. We estimated daily activity patterns and relative abundance index (RAI) for mesocarnivores and rabbits by using camera-traps, and calculated Jacobs selection index (JSI) to classify each species in a diel period. Additionally, we calculated the activity overlap between prey and mesocarnivores in the different areas.

Key results. Rabbits were nocturnal in the donor area, where only two mesocarnivore species were detected, red fox (*Vulpes vulpes*, with a high RAI) and Egyptian mongoose (*Herpestes ichneumon*, with a low RAI). However, in the unfenced area, where five mesocarnivore species were present, rabbits showed a crepuscular trend with two activity peaks, around sunrise and around sunset. In contrast, rabbits showed a nocturnal activity in the fenced plot, where four mesocarnivore species were detected but where only the Egyptian mongoose (strictly diurnal) had a high RAI value.

Conclusions and implications. The results suggest that rabbits in the fenced plot adapted their activity to avoid the diurnal mongooses. Conversely, rabbits in unfenced areas showed a trend towards day/twilight activity patterns as an adaptation to a diverse community of mesocarnivores. Rabbits can adapt their daily activity patterns to reduce predation risk depending on the pressure exerted by different predator species, with conservation and management implications. These adaptations would allow higher success of rabbit translocations despite the risk of predation by carnivores and could help in the management design of future translocations of this key species.

Keywords: European rabbits, predator–prey relationship, red fox, Egyptian mongoose, adaptive behaviour.

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Introduction

Activity patterns of animals depend on resource availability, intraspecific interactions, habitat selection, reproductive season and predation risk (Villafuerte *et al.* 1993; Rouco *et al.* 2008; Monterroso *et al.* 2013; Díaz-Ruiz *et al.* 2016). Some small mammals show variations in activity patterns as a consequence of resource use and predation pressure (Vieira and Baumgarten 1995). Fear towards predators modulates the dynamics of prey more than does predation itself (Brown *et al.* 1999; Preisser *et al.* 2005; Rouco *et al.* 2011). Thus, prey activity patterns can also change depending on moon phase, to reduce predation risk

(Harmsen *et al.* 2011). Some studies report adaptations in activity patterns of prey species to reduce their risk of encounter with their predators (Hoogmoed and De Avila-Pires 1989; Fenn and Macdonald 1995; Harrington *et al.* 2009). However, some management actions intended to facilitate the success of translocations, such as fences to exclude predators (Rouco *et al.* 2008), may actually increase the risk of predation by creating hotspots of activity of some predators that have access to the fenced areas.

The European rabbit (*Oryctolagus cuniculus*, rabbit hereafter) is a key native prey species in southern Europe (Delibes-Mateos

et al. 2007). Rabbits are prey for more than 40 nocturnal and diurnal predators (Delibes-Mateos *et al.* 2008a; Fernandez-de-Simon *et al.* 2011). Rabbit is an opportunistic species with high adaptability, which allows a high colonising ability (Gibb 1990). This prey has an important role in Mediterranean ecosystems (Valverde 1967; Delibes-Mateos *et al.* 2008a), through its effects on vegetation (Willott *et al.* 2000; Delibes-Mateos *et al.* 2008a, 2018), the use of latrines as food by some invertebrate species (Delibes-Mateos *et al.* 2008a; Gálvez Bravo *et al.* 2009), or the use of rabbit burrows as refuge by other species (Delibes-Mateos *et al.* 2008c; Gálvez Bravo *et al.* 2009). Rabbits have declined in some areas in the past decades, mainly owing to habitat loss (Delibes-Mateos *et al.* 2010) and the incidence of two viral diseases (rabbit haemorrhagic disease and myxomatosis, Delibes-Mateos *et al.* 2008b; Villafuerte *et al.* 2017). Because of that, the species has been recently classified as endangered by the IUCN (Villafuerte and Delibes-Mateos 2019). Besides, it is an essential prey for endangered specialist predators, such as the Iberian lynx (*Lynx pardinus*; Ferreras *et al.* 2010) and the Spanish imperial eagle (*Aquila adalberti*; Ferrer and Negro 2004).

Previous studies have found that rabbit activity is predominantly crepuscular and shows two activity peaks, namely, one at sunrise and another at sunset (Villafuerte *et al.* 1993; Martín-Díaz *et al.* 2018; Moseby *et al.* 2005; Fernández de Simón *et al.* 2009; Monterroso *et al.* 2013; Penteriani *et al.* 2013). Rabbit activity pattern has been interpreted as an adaptation to avoid the activity of its predators, so as to decrease predation risk (Moreno *et al.* 1996; Lombardi *et al.* 2007; Monterroso *et al.* 2013). Daily activity patterns of rabbits show seasonal changes related to environmental conditions such as weather (Villafuerte *et al.* 1993), and rabbits in semi-natural conditions also change their activity patterns gradually throughout the year, depending on sunrise and sunset times (Diez *et al.* 2007). Rabbits are also known to modify their activity pattern in response to the specialised behaviours of their predators (de Matos-Dias *et al.* 2018; Martín-Díaz *et al.* 2018). For instance, rabbits show more diurnal activity when they are under scrub cover because predation risk by carnivore mammals in daytime is lower there than in grassland. Conversely, rabbits are more nocturnal when they are in grassland because the risk of predation by raptors is higher during the daytime than at night (Moreno *et al.* 1996; Lombardi *et al.* 2007).

Diel activity patterns of Iberian mesocarnivores differ among species. Some species are strictly nocturnal, such as stone marten (*Martes foina*), Eurasian badger (*Meles meles*) and common genet (*Genetta genetta*; Monterroso *et al.* 2014), whereas others are facultative nocturnal such as red fox (*Vulpes vulpes*), wildcat (*Felis silvestris*) and Iberian lynx (Penteriani *et al.* 2013; Monterroso *et al.* 2014; Díaz-Ruiz *et al.* 2016). The only strictly diurnal carnivore in south-western Europe is the Egyptian mongoose (*Herpestes ichneumon*; Monterroso *et al.* 2014). Some Iberian mesocarnivores such as Egyptian mongoose, red fox, or Eurasian badger have generalist feeding habits, although rabbits constitute a large part of the consumed biomass when they are abundant (Delibes *et al.* 1984; Fedriani *et al.* 1998; Delibes-Mateos *et al.* 2008c). Therefore, we would expect that these carnivore predators represent different predation risks for rabbits according to the predator diet and prey abundance.

Although some studies have described activity adaptations of rabbits, activity changes under several scenarios have been

rarely studied (e.g. Rouco *et al.* 2008). The objective of the present study is to test whether rabbits can adapt their activity depending on different predation risks associated with different management scenarios. An additional objective is to assess whether predation risk differs between inside and outside of fenced areas. Our hypothesis is that rabbits change their daily activity patterns according to the predation risk and activity patterns of their predators. We tested whether activity patterns of translocated rabbits differed between fenced and unfenced areas. We expected that rabbits would reduce the overlap in activity patterns with their predators as an adaptation to reduce the risk of predation.

Materials and methods

Study area

Rabbits were translocated from an area, with a high rabbit density (La Nava (donor area), 1.26 rabbits ha⁻¹, 0.053 s.e.), located close enough to the release area (32 km) to prevent introducing rabbit genetic lineages different from the native ones (Delibes-Mateos *et al.* 2008d). La Nava is a 985-ha private property located in Almagro municipality (Ciudad Real province, central Spain), covered mainly by cereal fields and, secondarily, by Mediterranean scrubland and sparse patches of holm oak. A high density of red fox (1.6 ind. km⁻²) was previously estimated in the donor area (Jiménez *et al.* 2019). The release area was located in Picón municipality (39°5'0"N, 4°5'0"W, Ciudad Real province, central Spain; Fig. 1). This area is dominated by holm oak (*Quercus ilex* subsp. *rotundifolia*) and crimson-spot rock-rose (*Cistus ladanifer*), with some areas of olive crops (Fig. 1). The climate is Mediterranean, with wet and mild winters and dry and hot summers. A 0.42 ha plot was surrounded by a 1.5 m high wire netting fence with a 0.85-m-wide overhang outwards (hereafter, fenced plot). This fence was established at least 10 years before the study by local hunters (1) to recover the rabbit populations through reintroductions because the species was virtually extinct, and (2) to exclude mesocarnivores. The fenced plot was semi-permeable for most wildlife, with passageways (66 cm wide, 8 cm high) for rabbits to enter and exit the plot, allowing them to colonise the surrounding area. Artificial warrens built by local hunters were present in the area within and outside the fenced plot (hereafter, unfenced area). Some warrens were made of rocks, sand and a layer of polyethylene, and others were made of just rocks. In addition, we calculated the scrub cover in the donor and release areas (both fenced and unfenced plots). We used an aerial photograph (Bing aerial) from a geographic information system (QGis, version 2.18.17). An imaginary 130 m line from the camera-traps (see below) was drawn in a random bearing, and the proportion of the line crossing areas of shrub was measured and assigned to the proportion of shrub cover. We estimated that the average scrub cover in the fenced plot (61.92%) was larger than in the unfenced release area (54.23%) and the donor area (31.44%), although differences among the areas were not significant (ANOVA test, $F_{2,17} = 2.185$, $P = 0.143$, see Supplementary material Table S1, Fig. S1).

Rabbit translocation

Prior to the study, rabbit abundance was negligible in the release area. We conducted an experimental rabbit translocation in

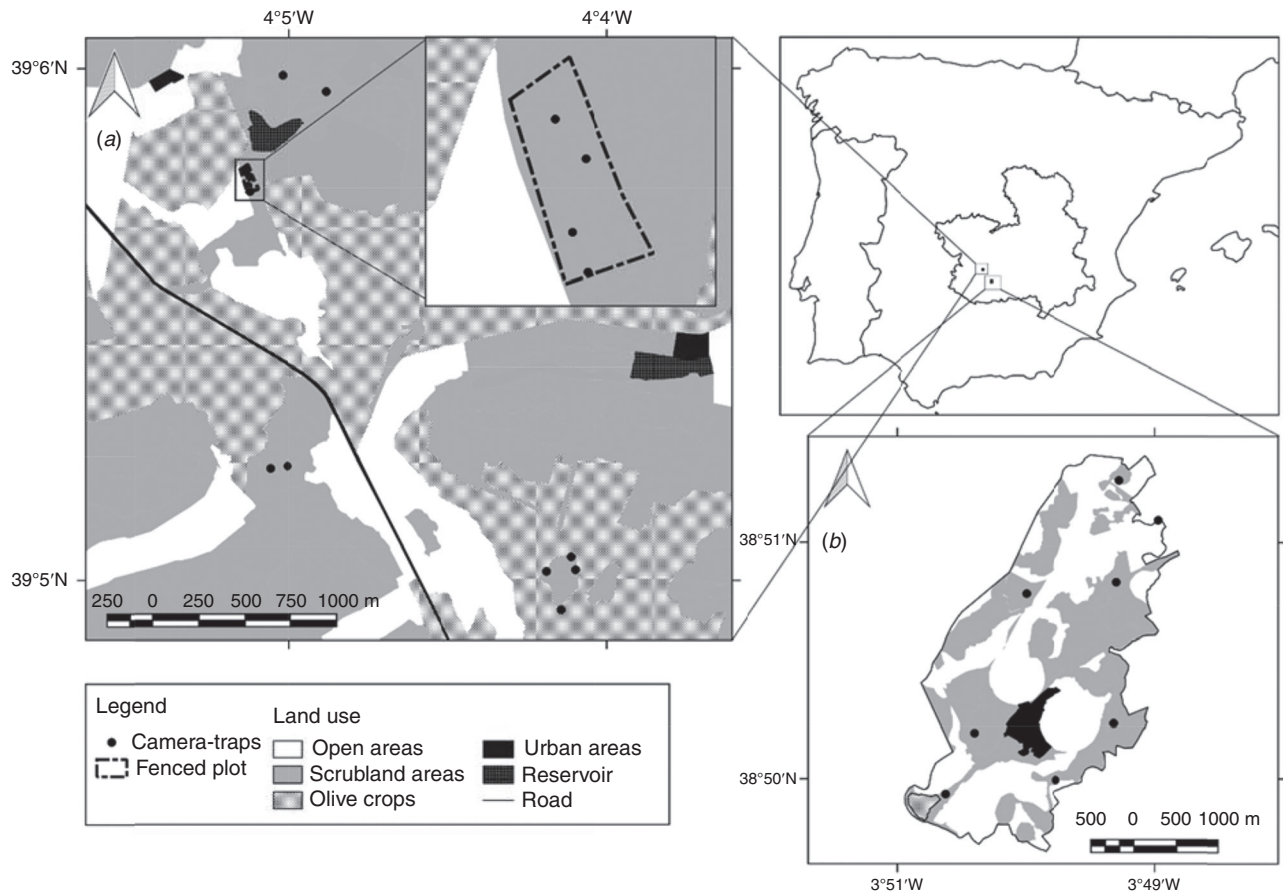


Fig. 1. Study area in (a) Picón and (b) Donor area (Ciudad Real province, Castilla-La Mancha region, outlined area, central Spain).

December 2016 as part of a study on conditioned food aversion (Tobajas *et al.* 2020). Rabbits were captured with ferrets (*Mustela putorius furo*) and nets in the donor area between 12 and 15 December 2016 and transported within 12 h of capture in metal cage carriers to the release area. A total of 108 rabbits was translocated to the main release area, including 34 (15 males and 19 females) to the fenced plot and 74 (35 males and 39 females) to the surrounding unfenced area. Four rabbits were released in each artificial warren, with an average sex ratio male:female of 0.86. Rabbits were ‘hard released’ without any kind of acclimation (Bright and Morris 1994; Machado *et al.* 2017). One of the authors (RM), registered veterinarian, supervised all the procedures during animal capture, handling, and post-release for wellbeing of animals.

Field surveys

Eight camera-traps were deployed in the donor area and were active from October 2015 to March 2016. Lynx urine and valerian extract were used as attractants to increase the detectability of mesocarnivores at the cameras (Ferrerías *et al.* 2018) in the donor area. In the release area, four camera-traps were deployed in the fenced plot and eight in the unfenced areas near warrens where rabbits were released, and cameras remained active from October 2016 to March 2017. Spartan SR1-BK® (HCO Outdoor Products, Georgia, USA) and Reconyx HC500

Hyperfire (Reconyx, Wisconsin, USA) cameras were used. Spartan cameras were programmed to record 10-s videos, with a minimum time delay (0 s) between consecutive records, whereas Reconyx cameras (with no video option) were programmed to take three consecutive photos per trigger, with a minimum time delay (0 s). The mean distance between the nearest camera-traps was $300 \text{ m} \pm 100 \text{ m}$ (s.d.). A bait of rabbit meat was placed 1.5–2 m from each camera-trap as part of the mentioned experiment on conditioned food aversion (Tobajas *et al.* 2020) in the release area. Camera-traps were checked every 7 days to replace memory cards, baits, and batteries when necessary.

Data analysis

Our target species were the rabbit and its mesocarnivore predators. Consecutive records (photos or videos) of the same species were considered as independent events when at least 30 min elapsed between them (O’Brien *et al.* 2003). A relative abundance index (RAI) was calculated for each species as the number of independent events divided by the total number of days in which camera-traps were active, multiplied by 100 (O’Brien *et al.* 2003). RAI represents a measure of activity or ‘density of detections’ rather than an abundance index (Monterroso *et al.* 2013) because it does not consider detection probability and home-range size of each species (Sollmann *et al.* 2013; Palmer *et al.* 2018).

So as to classify each species according to its selection of diel periods, we considered the following four periods, as described in Monterroso *et al.* (2013): Day, defined as the period between 1 h after sunrise and 1 h before sunset; Night, the period between 1 h after sunset and 1 h before sunrise; Dawn, the period between 1 h prior and 1 h after sunrise; and Dusk, the period between 1 h prior and 1 h after sunset. The selection/avoidance for a period of the diel cycle was assessed using the Jacobs selection index (JSI), a common measure to quantify preference of a resource (Jacobs 1974; Revilla *et al.* 2000):

$$JSI = \frac{r - p}{r + p - 2 * r * p}$$

where *r* represents the used proportion and *p* the available proportion. In this case, *r* is the proportion of independent events obtained for the species during the period considered (day, night, dusk, or dawn) and *p* is the proportion of the daily 24 h corresponding to the period considered. JSI ranged between +1 for maximum preference and -1 for maximum avoidance. The estimated JSI for the four periods of diel cycle were employed to define the following three behaviourally distinct groups: diurnal (JSI_{day} of ≥ 0.8), nocturnal (JSI_{night} of ≥ 0.8), and facultative nocturnal ($0.4 \leq JSI_{\text{night}} \leq 0.8$) (Jacobs 1974; Monterroso *et al.* 2013). We calculated 95% confidence intervals with the boot package within R 3.6.1 (R Core Team 2018). Significant selection (JSI of > 0) or avoidance (JSI of < 0) were considered when 0 was not included in the confidence interval.

The Overlap package (Ridout and Linkie 2009; Meredith and Ridout 2017) within R 3.6.1 (R Core Team 2018) was used to estimate the activity patterns for each species and the overlap between rabbits and mesocarnivores in the unfenced areas, fenced plot and donor area. Clock times were fitted to a sunset and sunrise (determined according to the dates and locations provided) fixed through 'sunTime' topic of Overlap package.

The coefficient of overlap $\Delta 1$ was used as recommended for small sample sizes (Ridout and Linkie 2009). Diel activity patterns were estimated for each species when sample size was representative ($N \geq 30$). Overlap values ≥ 0.70 were considered high, moderate when $0.45 \leq \Delta < 0.7$, and low when $\Delta < 0.45$, following Monterroso *et al.* (2014).

Results

Total sampling effort was 2692 camera-trap-nights in the study area (928 in the donor area, and 1764 in the release area, 588 in the fenced plot and 1176 in unfenced areas, Table 1). Five mesocarnivore species were detected, namely, stone marten, Eurasian badger, common genet, red fox and Egyptian mongoose. RAI values were higher for red fox and Egyptian mongoose (Table 1) than for the other mesocarnivore species, although badger RAI was also high. Mongoose RAI was almost double in the fenced plot than in unfenced areas (Table 1).

Rabbits and some mesocarnivores (stone martens, genets, Eurasian badger and Egyptian mongooses) were able to get in and out of the enclosure through the passageways in the fence. Red fox was not detected in the fenced plot, and few detections of common genet and Eurasian badger were recorded (Table 1). Overlap of diel activity patterns between mesocarnivores and rabbits in the fenced plot was limited to Egyptian mongooses because detection sample sizes were too low for all other mesocarnivores. In unfenced areas, RAI and time overlap with rabbits were estimated for all carnivore species except for the stone marten due to its small sample size (Table 1). The low sample size for Egyptian mongoose in the donor area prevented the calculation of RAI value and activity overlap with rabbits, which were only calculated for red fox (Table 1).

Rabbits in the donor area showed a nocturnal activity pattern with high overlap with the mesocarnivore community (0.70, 95% CI of 0.64–0.72; Fig. 2a). This was primarily a result of red

Table 1. Camera-trap data in the release area (Picón) and the area where the translocated rabbits were captured (donor area)

Number of camera-traps, effort (trap-nights), number of independent events corresponding to each species, values of relative abundance index (RAI), time overlap between rabbits and predators, and 95% confidence intervals (CI (95%))

Area	Number of camera-traps	Effort (trap-nights)	Species	Number of independent events	RAI	Time overlap ($\Delta 1$) with European rabbits	CI (95%)			
Donor area	8	928	Egyptian mongoose ^A	5	–	–	–			
			Red fox	261	28.12	0.68	0.62–0.71			
			European rabbit	889	95.79					
Picón	8	1176	Stone marten ^A	16	–	–	–			
			Common genet	35	2.98	0.49	0.32–0.59			
			Egyptian mongoose	149	12.67	0.33	0.23–0.35			
			Red fox	181	15.39	0.73	0.58–0.79			
			Eurasian badger	116	9.86	0.42	0.27–0.45			
			European rabbit	118	10.03					
			Fenced plot	4	588	Stone marten ^A	1	–	–	–
						Common genet ^A	18	–	–	–
						Egyptian mongoose	121	20.58	0.26	0.18–0.26
						Red fox ^A	0	–	–	–
Eurasian badger ^A	4	–				–	–			
			European rabbit	595	101.19					

^ASample size of predator species was too small (< 30 independent events) to calculate time overlap with rabbit.

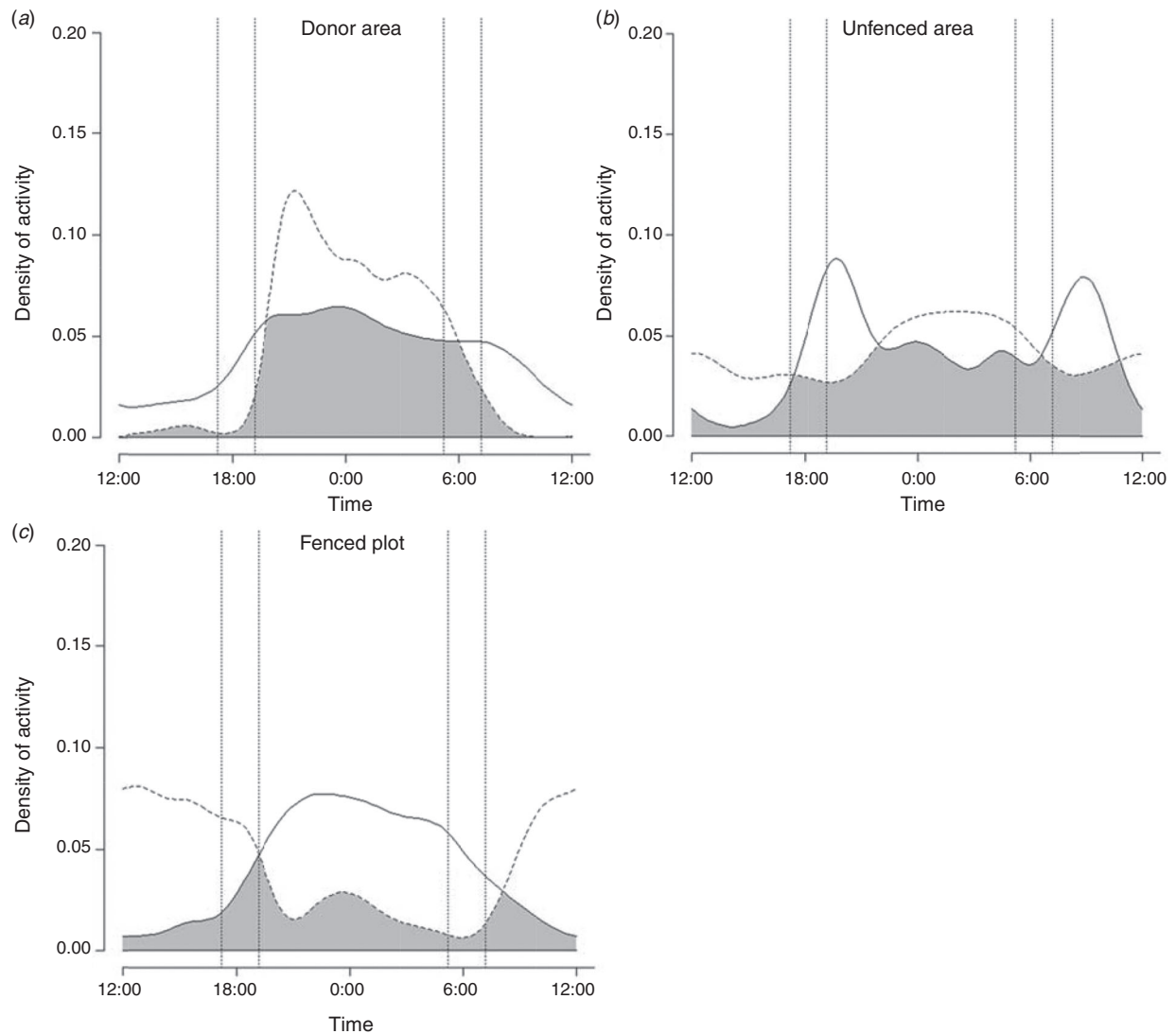


Fig. 2. Activity overlap (grey area) between the mesocarnivore community (dashed line) and rabbits (solid line) in (a) donor area (mesocarnivore community: Egyptian mongoose and red fox), (b) unfenced area (mesocarnivore community: Egyptian mongoose, red fox, Eurasian badger, common genet, and stone marten), and (c) the fenced plot (mesocarnivore community: Egyptian mongoose, Eurasian badger, and common genet). Vertical dashed lines represent approximate sunset and sunrise times.

fox activity (RAI = 261; Table 1), whose overlap with rabbits was 0.68, 95% CI of 0.62–0.71 (Table 1, Fig. 2a).

Rabbit activity in unfenced areas tended to be crepuscular, with peaks around dusk and dawn, although these periods were not being significantly selected (Table 2, Fig. 2b). Rabbits in unfenced areas showed an intermediate–high overlap with the mesocarnivore community (0.69, 95% CI of 0.51–0.72; Fig. 2b). The Egyptian mongoose showed diurnal activity patterns in unfenced areas (Table 2, Fig. 3a), whereas the red fox showed a mainly nocturnal activity (Table 2, Fig. 3c). The Eurasian badger and the common genet showed nocturnal activity patterns (Table 2, Fig. 3d, e). Activity overlap between red fox and rabbits was high outside the enclosure ($\Delta \geq 0.73$, 95% CI of 0.59–0.80; Table 1, Fig. 3c). Activity overlap between rabbits and Egyptian mongooses was low in unfenced areas (0.33, 95% CI of 0.23–0.35; Table 1, Fig. 3a) and moderate

($0.45 \leq \Delta < 0.70$) with the common genet and the Eurasian badger (Table 1, Fig. 3d, e).

Like in the donor area, rabbit activity in the fenced plot was almost exclusively nocturnal (Table 2, Fig. 2a, c). Activity overlap between the whole mesocarnivore community and rabbits was low–intermediate (0.41, 95% CI of 0.31–0.45). Egyptian mongoose showed a diurnal activity (Table 2, Fig. 3b) and a low activity overlap with rabbits (0.26, 95% CI of 0.18–0.26; Table 1, Fig. 3b).

Discussion

Our results support the hypothesis that the plasticity of rabbit activity patterns was likely to be due to an adaptation to reduce predation risk. Despite the fact that all of the rabbits were translocated from the same area, rabbit activity patterns in the

Table 2. Mean Jacobs selectivity index (JSI) and 95% confidence intervals (in square brackets) for each of the defined periods of the diel cycle of night, dawn, day and dusk in the study area Picón (fenced plot and unfenced areas) and the donor areaSignificant selection was considered whenever the 95% confidence interval of the JSI did not overlap zero (i.e. used as expected by chance). Negative values mean that the species avoids these periods and positive values mean that the species selects these periods. * $P < 0.05$ (significant)

Area	Species	JSI day	JSI night	JSI dawn	JSI dusk	
Donor area	European rabbit	-0.24 [-0.31, -0.17]*	0.25 [0.18, 0.31]*	0.04 [-0.08, 0.16]	-0.22 [-0.35, -0.08]*	
	Red fox	-0.9 [-0.97, -0.84]*	0.77 [0.70, 0.85]*	0.08 [-0.12, 0.29]	-1 [-1.00, -1.00]*	
Picón	Unfenced areas	European rabbit	-0.06 [-0.25, -0.13]*	0.13 [-0.04, 0.30]	-0.26 [-0.62, 0.16]	-0.05 [-0.37, 0.33]
		Egyptian mongoose	0.69 [0.59, 0.79]*	-0.88 [-0.96, -0.80]*	-1.00 [-1.00, -1.00]*	0.45 [0.29, 0.63]*
		Red fox	-0.23 [-0.38, -0.07]*	0.28 [0.15, 0.42]*	0.15 [-0.07, 0.40]	-0.78 [-1.04, -0.51]*
		Eurasian badger	-0.94 [-1.02, -0.85]*	0.76 [0.65, 0.87]*	0.16 [-0.11, 0.48]	-1.00 [-1.00, -1.00]*
		Common genet	-0.90 [-1.08, -0.71]*	0.13 [-0.19, 0.46]	0.76 [0.61, 0.93]*	-0.51 [-1.13, 0.26]
		Fenced plot	European rabbit	-0.51 [-0.59, -0.43]*	0.45 [0.38, 0.52]*	0.04 [-0.10, 0.18]
Egyptian mongoose	0.71 [0.61, 0.82]*		-0.93 [-0.93, -0.86]*	-1.00 [-1.00, -1.00]*	0.46 [0.29, 0.66]*	

release area markedly differed between the unfenced areas, where they showed a trend to crepuscular activity, and the fenced plot, where they were nocturnal. Our hypothesis explains the adaptation of rabbits to the receiver areas; they avoided Egyptian mongooses in the fenced plot where the fox was excluded, so they had nocturnal activity. However, we cannot fully explain why rabbits were also nocturnal in the donor area, where the red fox (also nocturnal) was the main predator. The activity overlap between the Egyptian mongoose and rabbits was low both in the fenced plot and unfenced areas. These results could be due to the importance of rabbits in mongoose diet when the former are abundant (Delibes *et al.* 1984; Palomares *et al.* 1995; Rosalino *et al.* 2009), causing the temporal avoidance of mongooses by rabbits. On the contrary, the overlap between the red fox and rabbits was high in the unfenced areas and in the donor area. This suggests that rabbits in our study area were adapting their activity patterns to reduce the risk of encounter with the Egyptian mongoose in the fenced plot rather than with the red fox in unfenced areas. This was supported by the higher activity of the Egyptian mongoose inside (RAI = 20.6) than outside (RAI = 12.7) the enclosure. However, the calculation of the overlap between rabbits and both Egyptian mongoose and red fox was possible only at the unfenced area because of the absence of the red fox inside the fenced plot. Our hypothesis does not explain why rabbits also showed a nocturnal activity in the donor area where the red fox was nocturnal and in high density (Jiménez *et al.* 2019), apparently representing the main predation risk. The nocturnal activity of rabbits in the donor area could be due to their high abundance, because rabbits in big groups reduce the predation risk (Villafuerte and Moreno 1997). This possibility was not tested because of lack of data, although it would be interesting to test in future studies. Even if different bait/attractant were used in the cameras in the donor and release areas, it is not expected that this difference could affect the rabbit activity patterns and explain its nocturnal activity in the donor area. The high activity overlap between rabbits and mesocarnivores in the donor area may be due to other factors that were overlooked in our study, such as the activity of diurnal raptors, hunters, or other human activities (Fernández de Simón *et al.* 2009). Moreover, given that diurnal raptors hunt more effectively in open areas (Lombardi *et al.* 2003), the lower vegetation

cover of the donor area, although not significant, may explain these differences in rabbit activity.

The moderate time overlap of rabbits with the Eurasian badger and the common genet in the unfenced areas suggests that rabbits did not adapt their activity patterns to avoid these mesocarnivores. This was probably because they do not represent a high predation risk (Delibes 1978; Genovesi *et al.* 1996). The common genet is a specialist predator of small mammals (Larivière and Calzada 2001), whereas the European badger is a feeding generalist, which mainly hunts juvenile rabbits in their burrows at the time of the year when rabbits are an important part of their diet (Fedriani *et al.* 1998). The resulting optimal activity pattern in unfenced areas was the trend towards the typical twilight pattern adapted to a high diversity of predators, as previously reported (Diez *et al.* 2007; Monterroso *et al.* 2013). In several areas of the same region, a previous study reported a low (0.24–0.49) temporal overlap between foxes and rabbits because of high fox activity during twilight–night when rabbits decreased theirs (Díaz-Ruiz *et al.* 2016). In a study performed in two Iberian National Parks, the activity overlap between the mesocarnivore community and rabbits was 0.52 (Monterroso *et al.* 2013), being similar to our results from unfenced areas (0.52–0.68). These authors suggested, in agreement with our results, that rabbits adapt their behaviour in response to predation risk. In a study in Africa, Tambling *et al.* (2015) argued that predator pressure in fenced areas was higher than in unfenced areas where prey used large-scale spatial avoidance patterns that cannot be used in fenced areas. In contrast, we observed that despite the fact that rabbits in the fenced plot apparently had a high predation pressure (assuming that mesocarnivore RAI is correlated with predation pressure), they coped with it by adapting their activity to reduce the risk of predator encounters.

Previous studies have shown that aboveground rabbit activity is higher during twilight and night than during daytime, not only in the Iberian Peninsula, but also in areas where rabbits have been introduced (Jilge 1980; Wallage-Dress 1989). These patterns show seasonal variation being likely due to environmental conditions and predation pressure (e.g. Jilge 1980; Wallage-Dress 1989; Villafuerte *et al.* 1993). This activity pattern is related to the rabbit visual adaptation to low light conditions during the night, and especially twilight (Nuboer 1971).

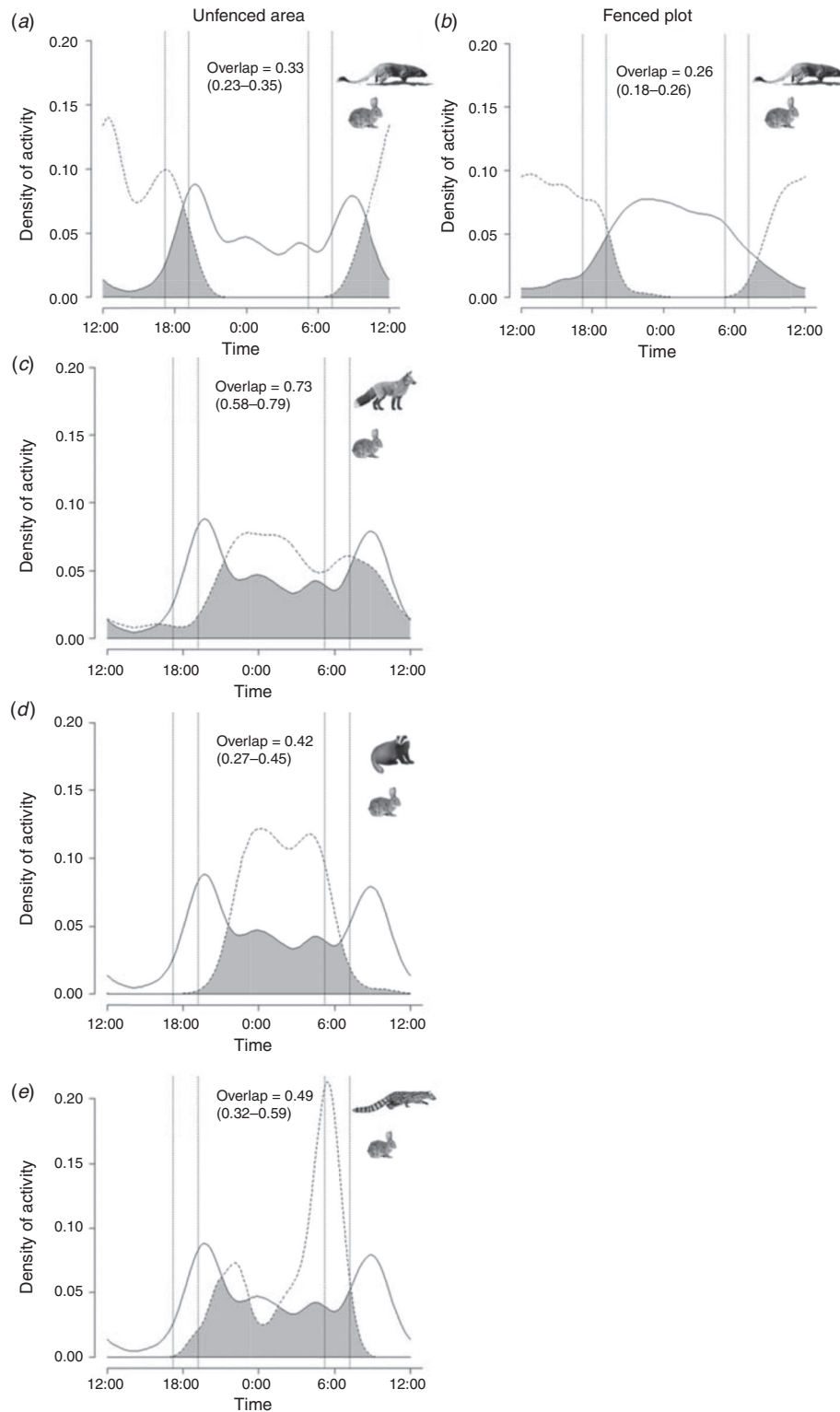


Fig. 3. Activity overlap (grey area) between rabbits (solid line) and Egyptian mongoose (dashed line) in (a) unfenced areas and (b) the fenced plot, and between rabbits (solid line) and (c) red fox, (d) Eurasian badger and (e) common genet (dashed lines) in unfenced areas. Dashed vertical lines represent approximate sunset and sunrise times.

Similar adaptations of activity patterns to avoid predators have been reported for other prey species. Daily activity patterns of Norway rats (*Rattus norvegicus*) changed from mainly nocturnal to diurnal activity to avoid being predated by red foxes, the only nocturnal predator in that study area (Fenn and Macdonald 1995). Other studies have reported similar adaptations in other taxa such as lizards (Hoogmoed and De Avila-Pires 1989), American mink (*Mustela vison*; Harrington *et al.* 2009), cane toad (*Rhinella marina*; Doody *et al.* 2019), other lagomorphs (Arias-Del Razo *et al.* 2011), and bearded pigs (*Sus barbatus*; Ross *et al.* 2013).

Prey species often use scrub cover as shelter, even though cover can be associated with higher predation risk during some periods (Moreno *et al.* 1996). For instance, rabbits hide in scrub cover to protect themselves from diurnal raptors during the day, but this strategy is not safe during the night because of predation risk by stalking carnivores (Moreno *et al.* 1996). Therefore, rabbits show a more nocturnal activity in grassland areas (Lombardi *et al.* 2003). Rabbits in our study showed a more nocturnal activity in the fenced plot where scrub cover was almost identical to that in unfenced areas. These results confirmed that differences in rabbit activity between the fenced plot and unfenced areas were due to differential predation risk during the diel cycle rather than due to differences in habitat cover.

Rouco *et al.* (2008) did not find differences in rabbit survival following translocation between fenced and unfenced areas. In their study, the risk of predation was high in the unfenced areas because of mesocarnivores, but it was compensated in the fenced plot by the risk because of raptors. The authors suggested that the higher predation by raptors in the fenced plots was a consequence of an attraction of these predators by the higher rabbit density (González 1989; Viñuela *et al.* 1994; Rouco *et al.* 2008). In our study, we cannot discard the possibility that the nocturnal activity patterns of rabbits in the fenced plot could be also an adaptation to avoid the predation risk by diurnal raptors. Although we did not observe raptors during the study, the lack of systematic surveys to obtain information on the presence and activity of raptors in our study prevented testing this hypothesis.

Despite the limitations in our study to compare one fenced plot and one unfenced area, the study suggests that rabbits can modulate their daily activity patterns to reduce the risk of predation according to the presence and activity of different mesocarnivores. The knowledge of the factors affecting these adaptations could help in the design of future rabbit translocations for management and conservation purposes, so as to allow a higher success of the translocations. We suggest that future investigations should focus on how fast this process of adaptation could be, how long rabbits take to change their habits to improve their survival, and which factors might accelerate or modulate this adaptation.

Conflicts of interest

Rafael Villafuerte is an Associated Editor. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. The authors have no further conflicts of interest to declare.

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