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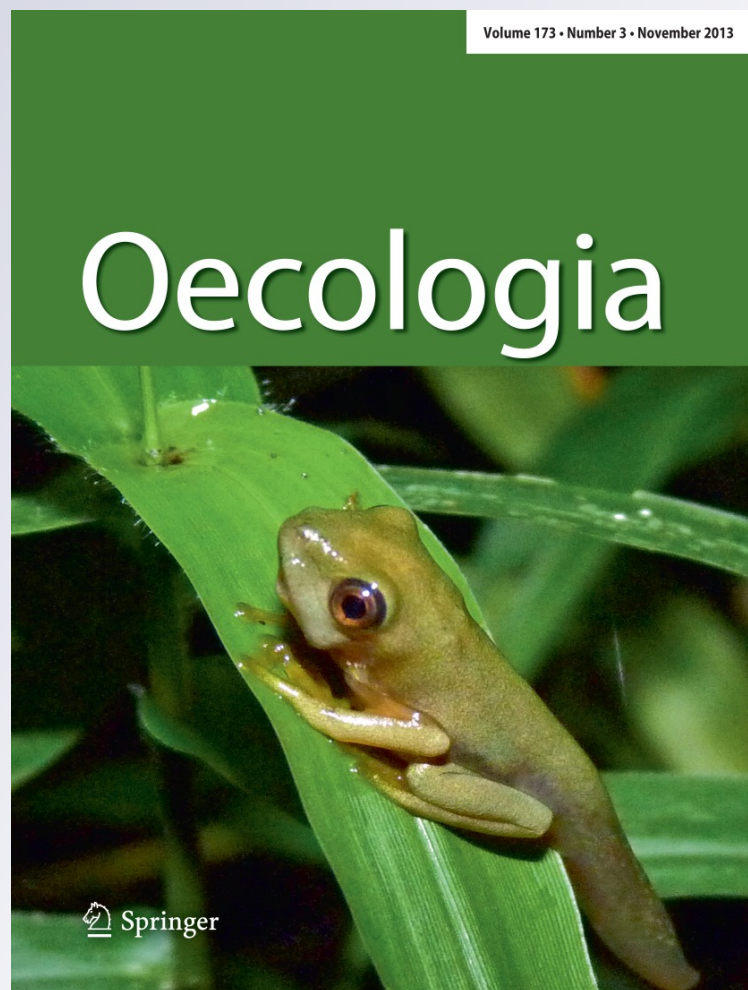
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Responses of a top and a meso predator and their prey to moon phases

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Abstract We compared movement patterns and rhythms of activity of a top predator, the Iberian lynx *Lynx pardinus*, a mesopredator, the red fox *Vulpes vulpes*, and their shared principal prey, the rabbit *Oryctolagus cuniculus*, in relation to moon phases. Because the three species are mostly nocturnal and crepuscular, we hypothesized that the shared prey would reduce its activity at most risky moon phases (i.e. during the brightest nights), but that fox, an intraguild prey of lynx, would avoid lynx activity peaks at the same time. Rabbits generally moved further from their core areas on darkest nights (i.e. new moon), using direct movements which minimize predation risk. Though rabbits responded to the increased predation risk by reducing their activity during the full moon, this response may require several days, and the moon effect we observed on the rabbits had, therefore, a temporal gap. Lynx activity patterns may be at least partially mirroring rabbit activity: around new moons, when rabbits moved furthest and were more active, lynxes reduced their travelling distances and their movements were concentrated in the core areas of their home ranges, which generally correspond to areas of high density of rabbits. Red foxes were more active during the darkest nights, when both the conditions for rabbit hunting were the best and lynxes moved less. On the one hand, foxes increased their activity when rabbits were further from their core areas and moved with more discrete displacements; on the other hand, fox activity in relation to the moon seemed to reduce dangerous encounters with its intraguild predator.

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Introduction

Predator–prey interactions are extremely complex because they are jointly determined by the effect of individual characteristics (e.g. behaviour, physiological condition, phenological traits, human activities), external factors (e.g. landscape, seasons, weather conditions), and certain properties of both the predator and prey populations, such as population demography or the spatial and temporal distribution of individuals (Abrams 2000; Caro 2005; Lima 2002). Predator–prey interactions play a crucial role in animal populations (e.g. Fretwell 1987; Sih et al. 1998), primarily because: (1) predation is one of the most common causes of mortality (and, for prey, there is strong selection pressure towards efficient antipredator defences); and (2) predators' fitness and survival depend strictly on their hunting efficiency. Moreover, predator–prey interactions have deeply influenced the evolution of life history traits and reproductive strategies of interacting species, since successful antipredator behaviours can produce selection for predator traits that can circumvent such prey defence mechanisms (Vermeij 1987).

For the abovementioned reasons, predator–prey interactions have been among the most frequently studied topics in animal ecology and behaviour (e.g. Sih et al. 1998; Lima 2009; Abrams 2000; Caro 2005), and represent fertile ground for theoretical explorations (e.g. Hugie and Dill 1994; van Baalen and Sabelis 1999; Bouskila 2001; Russell et al. 2009). Since the earliest explorations of predator–prey population dynamics by Lotka, Volterra and Gause (Taylor 1984), our know-how of such interactions has increased via the work on:

1. Predator-maintained cycles of prey abundance (e.g. Krebs et al. 1995).
2. The role of predation in regulating species diversity (e.g. Paine 1966).
3. Whether, and, if so, how prey defence strategies change over ontogeny (e.g. Pettersson et al. 2000; Relyea 2003a).

4. Prey responses to multiple predators (e.g. Sih et al. 1998; Turner et al. 1999; Relyea 2001, 2003b).
5. Anthropogenic or natural changes in the landscape that can influence predator hunting success and access to forage resources for prey species (e.g. Pedersen et al. 2010; Smee 2012).
6. Predatory interactions among top predators (i.e. intraguild predation; Polis et al. 1989) that can play a crucial role in structuring vertebrate communities through the suppression or release of either the mesopredator or the prey (Palomares et al. 1995; Crooks and Soulé 1999; Fedriani et al. 2000; Sergio et al. 2003).
7. Non-lethal effects determined by the mere presence of predators in ecological systems (e.g. Lima 1998; Peacor and Werner 2004; Pangle et al. 2007; Peckarsky et al. 2008), which may alter prey behaviours (e.g. Crowl and Covich 1994; Doncaster 1994; Sergio et al. 2007; Morosinotto et al. 2010), reduce feeding activity (e.g. Kohler and McPeek 1989), and induce physiological stress responses of prey under a stressful situation (e.g. Skelly and Werner 1990; Monclús et al. 2009).

However, despite the many advances in this field and the several hundred papers on predator–prey interactions published in the past 30 years, at the beginning of the current century we have still to consider our understanding of predator–prey interactions to be limited, mainly because these interactions have been less frequently analysed from a predator perspective (Lima 2002).

This constraint is reinforced by the lack of comparative studies addressing the behaviours of predators and their chief prey (but see Berger-Tal et al. 2010; Kotler et al. 2010), as well as the extent to which behaviours are adaptative to different scenarios and the external constraints under which predator–prey interactions may occur. Among the factors playing a role in shaping the activity of mostly nocturnal predators and prey, moon cycles have recently been shown to affect both predator and prey strategies and behavioural choices (e.g. Brown and Kotler 2004; Kotler et al. 2010; Penteriani et al. 2011 and reference therein). In fact, the changes in illumination conditions determined by the varying brightness of the moon during the lunar cycle generally force prey to be less active and more vigilant and to feed in safer habitats near the time of the full moon (e.g. Vasquez 1994; Brown and Kotler 2004; Griffin et al. 2005). Indeed, on bright moonlit nights: (1) prey shift to more apprehensive foraging strategies (Kotler et al. 2010), and/or (2) are less active (Clarke 1983; Sábato et al. 2006; Berger-Tal et al. 2010). Consequently, selection pressures likely exist on predators to be more active (but see Sábato et al. 2006), as they should search more intensively for prey (although this activity increase depends on the way predators search for their prey, and is

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more likely for active than ambush foragers). However, the predators certainly benefit at the same time from high light levels when hunting (Clarke 1983; Kotler et al. 1988). Actually, predators are most lethal during the brightest hours of the night (Kotler et al. 2002). Despite the long-term interest in the influence of lunar phases on prey behaviour and antipredator strategies (reviewed in Penteriani et al. 2011), less information is available on the response of predators to moonlight (but see Grassman et al. 2005; Di Bitetti et al. 2006; Sábato et al. 2006; Mukherjee et al. 2009). In addition, the interest in the response of predators to moon phases is increased by the evidence that predators at the same trophic level can prey upon each other (with or without consumption; Polis and Holt 1992), a phenomenon that has paramount consequences (e.g. Schmitz et al. 1997). Yet, no study to date has assessed the joint responses of top predators, mesopredators and their shared prey to lunar phases (but see Mukherjee et al. 2009).

By taking advantage of long-term monitoring data of a top predator species, the Iberian lynx (*Lynx pardinus*), a mesopredator, the red fox (*Vulpes vulpes*), and their shared prey, the European rabbit (*Oryctolagus cuniculus*), in the same area (Doñana National Park), we analysed and compared whether the responses of these predators and prey to moon phases are adaptive. Locally, these two sympatric predators (e.g. Fedriani et al. 1999) feed largely upon rabbits (Delibes 1980; Rau et al. 1985; Fedriani et al. 1999) and, therefore, their activity should be synchronised with rabbit activity. However, some differences in the life history of these species may also influence their behaviours. For example, rabbit density determines lynx but not red fox reproductive success (Palomares et al. 2001) and population density (Rodríguez and Delibes 2002). Thus, lynxes should be under stronger selection pressure than foxes to maximize rabbit hunting success by, for instance, following prey responses to lunar phases. Moreover, lynxes in Doñana are mainly crepuscular (Beltran and Delibes 1994; López-Bao et al. 2011) and habitat specialists (Palomares et al. 2000), while red foxes are mainly nocturnal (but they also have crepuscular activity), and habitat generalist (Ginsberg and Macdonald 1991; Fedriani et al. 1999). Finally, since rabbits are also crepuscular (Lombardi et al. 2003), selection for antipredator behaviour is likely to occur in our study system.

For the purposes of this study, we were interested in detecting and comparing general species-specific patterns of behaviours under the effect of moonlight rather than patterns at the level of populations or individuals. By focusing primarily on movement patterns and rhythms of activity, we made a general prediction. Predators and their prey should show opposite activity peaks during moon

cycles because of the changing night brightness. We would therefore expect an increase in the activity of predators near the time of the full moon as a response to the reduced level of rabbit activity (Kolb 1992; Twigg et al. 1998). The same pattern could be predicted during the new moon, because dark nights hamper prey location and capture (Clarke 1983; Kotler et al. 1988, 1991). However, since mesopredators are also potential prey (red foxes may be killed by lynx; Palomares and Caro 1999), they also need to trade-off between food and safety: the same behavioural choices and strategies that make an animal an efficient predator may increase its risk of becoming a prey (Lima 1998). Thus, natural selection should produce adaptive flexible behaviours in mesopredators, allowing them to act according to the trade-off between the benefits of energy intake and the cost of a premature death (Sih 1987; Lima and Dill 1990). Under this perspective, we expected that red fox patterns of activity would be sensitive to the new moon, i.e. that red foxes should be more active on the darkest nights. In particular, we expect that:

1. During the brightest nights, rabbits will reduce their movement rate, increasing activity around new moons because of the safer conditions offered by darkness.
2. Lynx will show a pattern of activity opposite to that of rabbits, e.g. increase their displacements when rabbits are less mobile.
3. Red foxes will show a trade-off in their activities due to the need to increase encounters with rabbits and decrease the risk of being killed by a lynx.

In addition to the main hypothesis and expectations, we suppose that individual activity should also vary due to some other aspects acting on the individuals, like several internal (e.g. age, sex, the need for foraging efficiency during reproduction), as well as external factors (e.g. landscape structure and composition).

Materials and methods

Study area

Radio-tracking of all three species was carried out in the Doñana National Park (south-western Spain). Two main environments characterize the Doñana area: scrubland and marshland. The scrubland area, on sandy soils, is made up of patchy, heterogeneous landscapes with a great variety of different habitats. The marshland remains flooded for a portion of the year and it is not relevant for this study.

Collection of data from radio-tagged individuals: predators

Lynxes

We radio-tagged 32 lynxes (15 males and 17 females) from a population that has been intensively studied during the past 25 years (e.g. Ferreras et al. 1997, 2004; Palomares et al. 2001; López-Bao et al. 2010). Between 1993 and 2007, lynx were captured with box traps (50 × 50 × 200 cm) baited with live domestic rabbits subjected to sanitary control. Trapped lynxes were checked for any damage associated with the capture (no damage was found) and were fitted with collars, keeping the compromise of a weight (200 g) less than 5 % of the absolute weight of the smallest lynx captured (Kenward 2001). Radio-tracking procedures were the same for all individuals. Lynxes were located according to two schedules: (a) between two and four times per week; and (b) during weekly intensive 24-h radio-tracking sessions, where we recorded their position and activity on an hourly basis (Ferreras et al. 1997; Palomares et al. 2001; López-Bao et al. 2010). Lynx activity was determined by means of activity sensors incorporated into the collars. Overall, lynx were tracked during a total of 246 nights, and a total number of 2,082 nocturnal locations were collected.

Foxes

We radio-tagged 33 red foxes (18 males and 15 females), which were followed during 5 years (1993–1997). Red foxes were captured using coil-spring traps (Victor no. 2; Woodstream, PA) and box traps baited with pieces of chicken. Once captured, the animals were fitted with radio-collars (150 g) equipped with an activity sensor; the tracking system and procedures for red foxes were similar to those described for lynx (see also Ferreras et al. 1997). Intensive radio-tracking periods were conducted during 86 nights (for 902 locations), during which red fox locations were determined at 1-h intervals.

Collection of data from radio-tagged individuals: prey

Rabbits

A total of 55 individuals (32 males and 23 females) were trapped and radio-tagged during 2 years (1993–1994). Rabbits were trapped and managed following the methods described in Lombardi et al. (2003, 2007). During trapping sessions, rabbits were flushed out of their warrens by muzzled ferrets (*Mustela furo*) and then captured in nets. Each rabbit was equipped with a 20-g radio-collar with activity sensors (Biotrack) and the weight of the transmitters were less than 3 % of the weight of

the smallest adult male (750 g; mean ± SD = 990 ± 37.4 g). We obtained three radio locations per week from each rabbit during regular monitoring periods and from seven to 14 locations per week during intensive monitoring periods (30 days every 3 months; Lombardi et al. 2003, 2007). The tagged individuals were tracked during 120 nights, for a total of 414 nocturnal locations.

Moon phases

The different phases of the lunar cycle were calculated as in Penteriani et al. (2011). In particular: (1) the daily moon phase at the geographic location of the study area was obtained from the Naval Oceanography Portal (http://aa.usno.navy.mil/data/docs/RS_OneDay.php) and expressed in terms of the fraction of the moon disk illuminated and whether the moon was waxing or waning; (2) the fraction of the moon disk illuminated was converted into radians (θ), with one lunar cycle corresponding to a gradual change from 0 to 2π radians (0 and 2π radians correspond to the full moon, and π radians corresponds to the new moon). $\cos(\theta)$, $\sin(\theta)$, $\cos(2\theta)$ and $\sin(2\theta)$ transformations were included in the statistical model as explanatory variables to investigate the possible lunar effects on individual activity throughout the lunar cycle (deBruyn and Meeuwig 2001; Kuparinen et al. 2010).

General movement patterns and rhythms of activity

Nocturnal movement patterns and the rhythms of activity of the three target mammals were calculated separately and at two different spatial scales, the home range and the core area(s). For each night of radio tracking, we first estimated the home range size using fixed-kernel methods (Worton 1989) with a least squares cross-validation process to determine the optimal value of the smoothing parameter for a given kernel and sample size. To establish the home range boundaries, we used density isopleth values of 90 % (Seaman and Powell 1996). We characterised the internal structure of the home ranges by estimating the core area(s) of each home range, defined by the 50 % density isopleths. Movements at the home range spatial scale were described by two variables (Delgado et al. 2010a, b; Penteriani et al. 2011): (a) total distance, the sum of the distance between successive steps on the same nightly path; and (b) speed, the value obtained by dividing the step distance by the time interval between successive locations. To determine the rhythms of activity, we used: (1) core area activity, the time an individual spent in the core area(s); (2) the number of movements within the core area(s); and (3) percentage of locations of active individuals, which was determined by means of activity sensors incorporated into the collars.

Status and internal state of individuals

Lynxes

We considered four explanatory variables representing additional potential sources of variation in individual activity:

(a) The different phases of the biological cycle. We defined three seasons according to lynx behaviour and rabbit abundance (López-Bao et al. 2008)—mating season and medium rabbit abundance (December–March; 1); cub-rearing and high rabbit abundance (April–July; 2); females accompanied by juveniles, pre-dispersal phase and low rabbit abundance (August–November; 3).
(b) Lynx age. Since age was known for all individuals (Ferreras et al. 2004; Palomares et al. 1996; López-Bao et al. 2009), lynx were categorized as young (<2 years, all individuals in the predispersal phase; Ferreras et al. 2004), or adults (≥2 years).
(c) Sex of lynx.
(d) Status of lynx, i.e. resident or dispersing individual. We considered all adult lynx maintaining site fidelity for at least 10 months as resident individuals (Palomares et al. 2000).

Because of the increasing experience of juvenile individuals (López-Bao 2010), both age and status can potentially affect individual behaviour.

Foxes

Following Fedriani et al. (1999) we included the following five additional variables:

(a) Three different seasonal periods influencing red fox behaviour—mating season (November–February; 1), cub rearing (March–June; 2), and dispersal (July–October; 3).
(b) Two different periods corresponding to high (1) and low (2) rabbit abundance.

Additionally, we also included:

(c) Sex of foxes.
(d) Age of foxes—juvenile (<1 year), subadult (1–2 years), adult (≥2 years)—which was based on tooth wear.
(e) The activity status of the fox (active or inactive), which was based on the collar-sensor signal.

Rabbits

Five additional explanatory variables were also included:

(a) The different phases of the biological cycle for rabbits—pre-breeding (when the number of reproducing females is relatively low; November–January; 1); breeding (February–May; 2); post-breeding (June–July; 3); non-breeding (when the number of reproducing females is close to zero; August–October; 4).
(b) Sex of rabbits (all animals were sexed based on their external genitalia).
(c) Age of rabbits (determined by individual weight) (Soriguer 1981; Villafuerte 1994).

In addition, two specific variables for the rabbit were considered, which might also affect individual behaviours:

(d) Status of rabbits [representing a native (1) or a reintroduced individual (2)].
(e) A rabbit's location [inside (1) or outside (2) a fenced area; the fence never restricted the access of lynxes or foxes to the area inhabited by rabbits].

External cues influencing individual activity

For the two predators and the prey, we tested the possible effect of habitat heterogeneity and composition on individual behaviour. We used edge density (i.e. the total length of the patch edge per unit area within each landscape) and Shannon's diversity index as proxies for the effect of habitat heterogeneity (Donovan et al. 1995; Elkie et al. 1999; Kie et al. 2002; Anderson et al. 2005). To evaluate habitat composition, we first reclassified the map into ten main land cover elements: crop areas, water bodies, eucalyptus forest, dense scrubland, open scrubland with scattered trees, pasture, open scrubland with pasture, sand dunes, woody crops and herbaceous crops. Then we calculated the proportion of each habitat type within the area traversed by individuals on each radio-tracking session. The calculated home range areas (in raster format; cell size: 0.5×0.5 km) were used as a basic input data layer for measuring all landscape metrics. Both landscape structure and composition were estimated using ArcMap in ARCGIS version 9.0. Because habitat changes over the study years were minimal in Doñana, we did not use year-specific habitat cover.

Statistical analyses

To analyse how the lunar cycle may affect individual behaviour, we built general linear mixed models with movement parameters and rhythms of activity as the dependent variables and (1) moon phase, (2) individual status/internal state, and (3) external cues as the explanatory variables. Given that the probability to have a cloudy night is equally distributed over the study period and, consequently, among all moon phases, we considered such

Table 1 Model outputs of the tested variable for rabbits, lynxes and red foxes

		Moon phase				Status/internal				External cues			
		predictor	β	SE	t-value	CIs	predictor	β	SE	t-value	CIs	predictor	β	SE	t-value	CIs
Rabbits																
Total distance	Cos(θ)		44.81	16.17	2.77	13.11, 76.50	Period 2[b]	−107.57	39.44	−2.73	−184.87, −30.28	ED	−2,289.52	372.58	−6.15	−3,019.76, −1,559.28
	Sin(θ)		−369.17	46.57	−7.92	−460.45, −277.89	Period 4[b]	292.84	40.16	7.29	214.12, 371.55					
Speed	Sin(2θ)		−0.68	0.16	−4.32	**	Status[c]	64.22	23.03	2.79	19.07, 109.37	ED	−8.51	1.32	−643	**
							Period 4[b]	0.89	0.14	6.59	**					
T core area	Cos(θ)		69.30	25.36	2.73	19.60, 119.00	Period 2, 1 & 3[b]	−129.81	53.86	16.53	−235.38, −24.25	No effect				
	Sin(θ)		87.12	37.74	2.31	13.16, 161.08										
N core area	No effect						No effect					No effect				
Lynxes																
Total distance	No effect						No effect					ED	−6.91	1.55	−4.46	−9.95, −3.87
												SDI	858.35	195.09	4.40	475.97, 1,240.72
												Habitat type[d]	−36.39	17.82	−2.04	−71.32, −1.46
Speed	No effect						Age[f]	0.45	0.12	3.67	**	ED	−0.002	0.0004	−4.69	**
												SDI	0.34	0.05	6.93	**
T core area	No effect						Period 2 & 3[b]	65.83	25.19	2.61	16.46, 115.19	No effect				
							Age[f]	−115.78	41.33	−2.80	−196.79, −34.76					
N core area	Sin(2θ)		0.16	0.06	2.92[a]	*	Period 2 & 3[b]	−0.28	0.07	−3.69[a]	**	No effect				
	Cos(θ)		−0.14	0.05	−2.91[a]	**										
Foxes																
Total distance	No effect						Sex (female)	560.92	243.33	2.30	83.99, 1,037.85	ED	−28.69	2.92	−9.82	−34.42, −22.97
							Period[g]	658.34	232.04	2.84	203.54, 1,113.14	SDI	2,099.23	296.32	7.08	1,518.45, 2,680.01
Speed	No effect						No effect					ED	−0.013	0.001	−10.05	−0.02, 3.21
												SDI	0.87	0.13	6.64	0.57, 10.9
T core area	No effect						No effect					ED	−0.46	0.21	−2.15	−0.89, −0.04
N core area	No effect						No effect					ED	−0.004	0.0009	−4.16	**
Activity status	Cos(θ)		−0.24	0.11	−2.08	*	Period[g]	0.76	0.22	3.37	**	Habitat type[e]	−0.014	0.004	3.77	**

CI Confidence interval, *ED* edge density, *SDI* Shannon's diversity index

* $P < 0.01$, ** $P < 0.001$

[a] z-value

[b] Factor levels were joined in the model simplification process

[c] Reintroduced rabbits

[d] Cultivated habitat

[e] Dense habitat

[f] Adult individuals

[g] Spring and summer periods

variation to lead to additional noise, which is likely to weaken the signal strength in our results rather than to create systematic biases. The total distance and time spent in the core area were modelled using linear mixed models with follow-up time (tsessions) included as an offset. This is because total distance and time spent in the core area depend on the duration of the radio-tracking session and, then, these variables need to be standardized by tsessions. Hence, the variation arising from different lengths of the follow-up session was accounted for by considering the length of the period as an offset variable. To include the offset function, the linear mixed models were built using the lmer function, and therefore, confidence intervals (25 % CI and 95 % CI), not *P*-values, are reported for these models. To ensure normality, both total distance and speed were log-transformed. We used generalised linear mixed model to analyse the number of movements in the core area(s), assuming quasi Poisson distributed data (to control for the overdispersion), with the logarithm of the follow-up time (tsessions) included as an offset (normal choice in Poisson models). Because we had repeated measures of the same individual within and between years, we considered the individual and year as random effects. Because only a few individuals occupied territories that partially overlapped, we could not consider the territory as a random factor (i.e. the number of levels of this factor was not enough to get an accurate characterization of the mean and variance; Zuur et al. 2009). Following Pinheiro and Bates (2004), the significance values of random effects were estimated using the Akaike information criterion. As
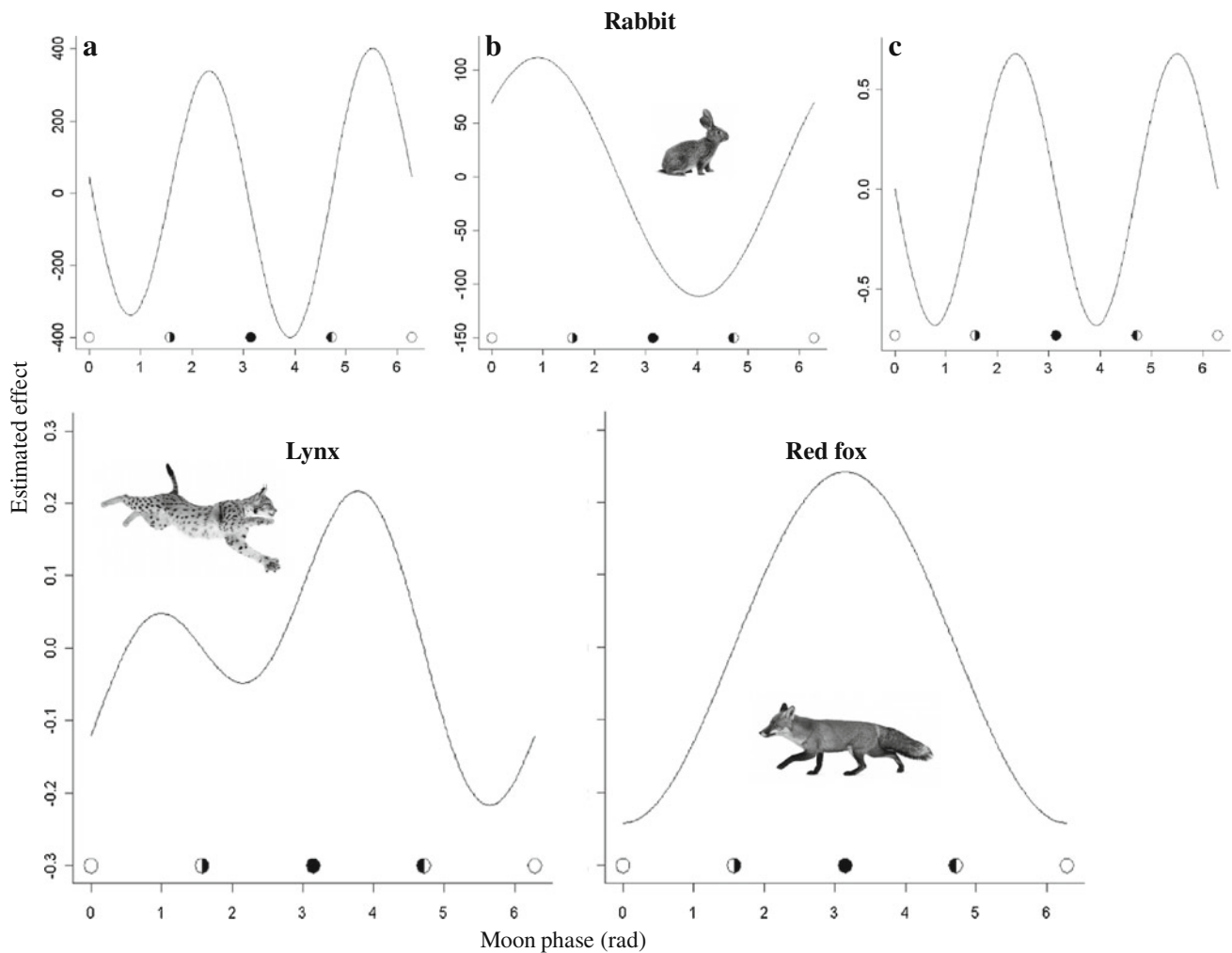

Fig. 1 Moon-phase effect on rabbits: **a** the total distance moved during the night shows two peaks within a lunar cycle, with the higher peak during the darker period, whereas **b** the time spent in the core area at night increases with the intensification of nocturnal brightness; log-transformed speed at night (**c**, *solid line*) shows a pattern similar to that of the total distance. The pattern is slightly shifted to the right of the full (*white circle*)/new moon (*black circle*), i.e. there might be a delayed response to the full/new moon. The number of lynx nightly locations in the core area peaks near the time of the new moon, which is the darkest period, and is always lower near the brightest nights. The probability of finding an active red fox increases at new moon

the random factor year did not improve the model's likelihood value, we built a less complex model class. As suggested by Crawley (2007): (1) model simplification was performed by backwards selection of variables from the full model, and (2) models were compared using likelihood ratio tests until a minimal adequate model was obtained. In the case of the different phases of the biological cycle factor, model reduction was performed by joining the factor levels closest to each other, after which nested models were compared using likelihood ratio tests until the minimal adequate model was found. For each analysis, we used slightly different sub-samples of the data. These sub-samples represented those individuals for which it was possible to collect the specific information sought. The residuals of the final models were explored to verify the normality, homogeneity (except in the case of the generalised linear model), and independence assumptions. All statistical analyses were performed in R 2.10.1 statistical software (R Development Core Team 2009) with the nlme (Pinheiro et al. 2009), lme4 (Bates and Sarkar 2007) and MASS (Venables and Ripley 2002) packages. Statistical significance was set at $\alpha < 0.05$.

Results

Moon phase effects

Our analyses of rabbit radio-tracking data revealed that lunar cycle had a significant effect on the following response variables (Table 1): (1) the total distance moved during the night (intercept: $\beta \pm SE = -372.65 \pm 41.30$, t-value $= -9.02$; CIs -453.60, -291.71; Fig. 1a); (2) the time spent at night in the 50 % core area (intercept: $\beta \pm SE = -176.01 \pm 44.34$, t-value $= -3.97$; CIs -262.91, -89.10; Fig. 1b); and (3) the movement speed (intercept: $\beta \pm SE = -1.11 \pm 0.13$, t-value $= -8.31$, $P < 0.0001$; Fig. 1c). Together, the effect of moon cycle on rabbit movement and rhythms of activity parameters seemed to determine three different behavioural strategies. First, at the time of the full moon, rabbit movement rate was low (i.e. short total distances and low speed; Fig. 1a, c, respectively) within their core area (Fig. 1b). Second, rabbits increase their movement activity (i.e. long total distances and high speed; Fig. 1a, c, respectively) both within and outside their core area (Fig. 1b) around new moon, when darkness potentially offers the safest opportunities for movement. Thirdly, on the darkest nights, rabbits moved far from their core area (Fig. 1b) and seemed to optimise this strategy by using oriented movement patterns, i.e. covering long distances away from their core area(s) by using few number of steps and, therefore, reducing the total distances moved (Fig. 1a). The rabbit

pattern is slightly shifted to the right from the full/new moon, i.e. there might be a delayed response to the full/new moon and/or to predator activity peaks that correspond to the full/new moon (see below).

A significant moon effect was also found in the number of nightly locations in the core areas for lynxes (intercept: $\beta \pm SE = -4.84 \pm 0.08$, z-value $= -58.68$, $P < 0.0001$; Fig. 1b; Table 1), which peaked near the time of the new moon (i.e. during the darkest period), clearly contrasting with the rabbit activity pattern. That is, lynxes moved further from core areas when rabbits were mostly active within their core areas. However, when rabbits moved away from the core areas, lynxes tended to move less by spending more time within their core area(s).

The effect of the moon cycle on red fox behaviour was weaker than for rabbit and lynxes, only indicating a slight increase of the probability of being active around new moon, i.e. when nights are darker (intercept: $\beta \pm SE = -0.85 \pm 0.25$, z-value $= -3.36$, $P < 0.0001$; Fig. 1c; Table 1). That is, red foxes showed the highest activity: (1) when rabbits mostly moved away from their core area(s); but (2) lynxes were moving less, due to longer settlement within the core area(s), which could have maximised and minimized encounters with fox prey (rabbit) and intraguild predator (lynx), respectively.

Additional effects

The moon's effect on the rabbits' nocturnal behaviour was also associated with different phases of the biological cycle (Table 1): the total distance moved during the night, time spent in the core areas and speed all increased during the non-breeding period. In addition, reintroduced rabbits tended to move longer distances than native individuals. Furthermore, the structure of the habitat, in particular edge density, also affected total distance and movement speed: rabbits moved short distances and at slow speed when crossing fragmented habitats.

Total distance moved by lynxes (intercept: $\beta \pm SE = 5{,}403.50 \pm 1{,}868.07$, t-value $= -2.89$; CIs 1,742.15, 9,064.86; Table 1) and their movement speed (intercept: $\beta \pm SE = 0.69 \pm 0.19$, t-value $= 3.54$, $P = 0.0004$; Table 1) were affected by habitat structure and composition. Lynxes moved short total distances and at slow speed when moving in fragmented but less diverse habitats, especially when crossing areas of cultivated crops. Additionally, movement speed was influenced by individual age, with adults generally moving faster than juveniles. The number of lynx nocturnal movements (intercept: $\beta \pm SE = -4.84 \pm 0.08$, z-value $= -58.68$, $P < 0.0001$; Fig. 1b; Table 1) and the time spent (intercept: $\beta \pm SE = -315.30 \pm 37.84$, t-value $= -8.33$; CIs -389.47, -241.14; Table 1) within the core area were

related to their biological cycle: individuals moved close to their core areas during the central phases of lynx reproduction (from kitten rearing to the pre-dispersal phase of juveniles).

Finally, fox movement behaviour was affected by several internal and external factors. Like rabbits and lynxes, foxes moved a short total distance (intercept: $\beta \pm SE = 2{,}369.87 \pm 292.18$, t-value $= 8.11$; CIs 1,797.21, 2,942.53; Table 1) and at slow speed (intercept: $\beta \pm SE = 2.98 \pm 0.09$, t-value $= 31.79$; CIs 2.80, 3.16; Table 1) in fragmented habitats. Individuals moved longer total distances in spring and summer, especially females (Table 1). The number of fox nocturnal movements (intercept: $\beta \pm SE = -0.0048 \pm 0.0009$, z-value $= -4.16$; Table 1) and the time spent (intercept: $\beta \pm SE = -98.12 \pm 15.99$, t-value $= -6.13$; CIs -129.47, -66.77; Table 1) within the core area were also related to the structure of the habitat: individuals spent less time within their core area when inhabiting fragmented habitats than when in continuous landscapes. Finally, the probability of being active was higher in spring and summer, especially when individuals were crossing dense habitats (Table 1).

Discussion

As expected, moon phases played a role in both predator and prey activity, potentially affecting predator–prey interactions. Three main points emerged from our analyses. Firstly, the moon has a stronger effect on the behaviour of the prey than on the behaviour of both species of predator. Because prey foraging and, more generally, prey displacements are undoubtedly riskier than predator movements, rabbit is the most constrained species during bright nights. We observed that the alternation of extremely different types of moonlight led to a complex anti-predatory rabbit strategy. On the darkest nights, rabbits took the risk to move further from their burrows (located in their core areas); however, they seemed to reduce the risk to be far from cover by moving with direct movements (i.e. they reduced the total distance they moved by decreasing the number of movement steps). That is, when the costs of movements were high, a safe movement strategy evolved to decrease the time spent in an inhospitable environment (Delgado et al. 2010a, b). Other studies have found that rabbit movements and activity are affected by predation risk (Kolb 1992; Twigg et al. 1998), which is one of the crucial, extrinsic factors influencing the behaviour of individuals and their habitat selection (Bos and Carthew 2003; Kotler 1997; Lima and Dill 1990).

Secondly, and due to the dependence of lynx on rabbits (Fedriani et al. 1999; López-Bao et al. 2008), the activity of lynxes and rabbits may be connected during the different moon phases. This pattern may be at least partially the result of the level of rabbit activity, which is higher during the darkest nights (Kolb 1992; Twigg et al. 1998). Consequently, the lynxes are not forced to move throughout their whole home range to find a prey, and their movements are thus mainly performed in the close surroundings of their core areas, which generally correspond to areas of high density of rabbits (Palomares et al. 2001).

Thirdly, the rather weak link between moon phases and red fox activity seems to indicate that fox patterns of activity are: (1) relatively more independent of those of rabbit, although foxes are more active when the conditions for rabbit hunting are the best; but (2) are inverse to the activity patterns of lynxes. There might be at least two not mutually exclusive explanations for these patterns. The first may be found in the characteristics of the diet and hunting behaviour of foxes. Because foxes are trophic generalists (Fedriani et al. 1999), their activity patterns are likely influenced by prey species other than rabbit (rodents, insects, etc.). In addition, red foxes, chase their mobile prey (Kleiman and Eisenberg 1973; Murray et al. 1995), which is typical of canids, and do not sit and wait like lynxes (Delibes 1980). Thus, red foxes would need to increase their activity during the darkest nights to elevate the probability of encountering rabbits, which would be further from their core areas and moving with more discrete displacements. Moreover, rabbit hunting may be less effective during bright nights, fox predation on rabbit being generally lower on full moon nights than during other moon phases (Molsher et al. 2000). Lastly, the opposite patterns of activity we recorded between the top and the mesopredator could represent a fox-avoidance strategy attained by temporal segregation: the mesopredator alters its activity times to avoid encounters with the top predator. In many systems, smaller predators forage at risk from top predators, which do not only kill or injure but may also induce fear, and this influence the behaviour and the ecology of mesopredators (Mukherjee et al. 2009). Actually, foxes perceive moonless nights to be safer and, when coexisting with top predators, tend to increase their activity on darker nights when top predators are less active (Mukherjee et al. 2009).

We consider it important to highlight that the lack of temporal overlap of our data does not affect our inferences and conclusions. This is because, for the purposes of this study, we were interested in detecting and comparing general species-specific patterns of activity under the effect of moonlight rather than patterns at the level of populations or individuals. More interesting, the importance of examining a system comprising two predators and their common prey lies in the possibility that multiple predators may have effects that cannot be predicted simply by summing up the effects of single predator types on the same prey (Sih et al. 1998).

The study of moon-related patterns of activity may help to understand the coexistence of carnivores

Fedriani et al. (1999) suggested that one of the possible mechanisms explaining the coexistence of lynxes and red foxes in Doñana was that foxes reduced the risk of being killed by a lynx by their spatial behaviour, as has been recently observed in Doñana (Viota et al. 2012), where lynx and Egyptian mongoose coexist (*Herpestes ichneumon*). Specifically, Fedriani et al. (1999) proposed that foxes reduced using the richest rabbit habitat during the activity period (i.e. at night) to avoid encounters with lynxes, which mainly frequented this habitat.

However, they also hypothesized that some other temporal avoidance behaviours should act to facilitate the coexistence of these two sympatric carnivore species (Fedriani 1997). Information from our novel analyses on moon-mediated patterns of activity shed light onto the relationships between top and mesopredators. The coexistence of predators that overlap in foraging habitats certainly may be facilitated by the changing light of contrasting lunar phases. Different moonlight responses may be especially useful in giving an alternative explanation as to how carnivores may coexist when, as is the case in this study, overlapping food among predators challenges the view that food is the resource towards which spatial and behavioural means of distinguishing niches by predators are ultimately directed (e.g. Hespenheide 1975). The lunar effects documented in this study are indeed consistent with MacArthur and Pianka (1966) and MacArthur and Wilson (1967), who predicted that for coexisting predators it is easier to adjust behaviour to reduce competition, than to change food habits.

The temporal gap in the prey response

Interestingly, rabbits delayed their response to the full/new moon and/or to predator activity peaks that correspond to the full/new moon. A similar lack of synchrony might be a neglected feature of other predator–prey interactions if one species responds to the other species with a time lag. This delayed response of the rabbit to the lunar cycle might result more from being alert to increasing predation than directly from the effect of lunar brightness, i.e. the rabbits are not necessarily aware that they risk more during the brightest nights, as is generally believed (e.g. Clarke 1983; Kotler et al. 2010). If predation increases because the moonlight assists predators to find and pursue prey, the prey respond to this increased predation rate by reducing their activity. This reduction, however, can take several days, and this time delay could be the source of the temporal gap we observed in the moon's effect on rabbits.

This situation can also hold for sit-and-wait predators such as lynxes (López-Bao 2010) and eagle owls (*Bubo bubo*; Penteriani et al. 2008) because rabbits live in groups, and a predation event may be observed by the neighbouring conspecifics of the targeted individual. This delay in the rabbit response under predation agrees with the previously studied interactions between a diurnal avian predator (the Spanish imperial eagle *Aquila adalberti*) and rabbits (Penteriani et al. 2006); the primary factor influencing a predator's occupancy of a foraging patch being the time taken by the rabbits to change their activity timetable under predation pressure. Foraging predators can affect prey availability and, consequently, capture success (Neill and Cullen 1974; Parrish 1992; Loggerwell and Hargreaves 1996; Ainley et al. 2003). Thus, if the lowered availability of rabbits decreases predation, the rabbits resume their previous behaviour and consequently become available again to the predators. Clearly, all these cycles of availability show a temporal range of perception of predation risk and/or recovery from fear of predation. This predator–prey 'game' might be the source of the temporal gap between moon phases and rabbit behaviours. Relationships between predators (for better hunting) and prey (for better predator avoidance) are typical examples of coordinated behaviours (Rosenzweig et al. 1997; Bahr and Bekoff 1999; Brown et al. 2001). Thus, these results support previous evidence that predators may influence the activity and spatial patterns of prey (Lagos et al. 1995; Brown and Kotler 2004; Yunger 2004), and also highlight the importance of comparative studies of predators and prey. Thus, we revealed a functional response (i.e. the rabbits shift to a more concealed behaviour pattern if predation pressure increases) that is influenced in part by spontaneous patterns: the rabbits could not be aware of the pattern that they created (i.e. behavioural variations following lunar cycles).

Other effects

It is also interesting to underscore the important role evidently played by the diverse constraints resulting from the diverse tasks required by the reproductive period. The different periods of the year always played an important role in determining the behaviours of all three species. For example, both the predators and the prey restricted their activities to the core areas during reproduction. Note, in addition, that the contribution of the landscape structure in terms of ecotone density affected the behaviours of foxes and rabbits similarly, decreasing their nightly total distances travelled. Specifically, the edge density played a role in determining both total distance and speed: in the most heterogeneous landscapes (higher values of edge density), the rabbits moved shorter distances and at a slower speed. Previous radio-tracking studies showed the importance of

cover for rabbits (Sacramento et al. 1996; Lombardi et al. 2007). These studies showed that vegetation patches providing refuges were used in higher proportions than their availability. Because rabbits are hunted by most Mediterranean mammals and avian predators (Fedriani et al. 1999; Forero et al. 2002), their habitat use and spatial activity appear to be substantially related to the availability of refuges and to predator avoidance (Lombardi et al. 2007). In conjunction with the previously unexplored effect of the moonlight, predation could have determined the differences formerly recorded in home range size and core areas, primarily as a function of the availability of shelter providing predator avoidance rather than because of pasture availability (Lombardi et al. 2007). Finally, in light of the results of this study, the previously unexplained long foraging excursions into the pasture areas and a greater use of space at night (Lombardi et al. 2007) may now be related to the darkest nights. During these nights, the rabbits increased their activity because obscurity offered the safest opportunities for movement even in open (risky) habitats.

The results of the current work present two non-mutually exclusive possibilities. First, prey appear to be adapted to reduce their activity near the full moon because of the high associated risk of predation. Consequently, they become less active and show a greater tendency to remain concealed (Clarke 1983). Second, though, the temporal gap shown by the rabbit response to moon phases under brighter moons must be considered. The predators initially take advantage of the easier visual location of prey to increase their (successful) predation rates. In response, the prey modify their behaviour and become increasingly wary. Thus, the potential for predators to visually detect prey increases with increasing light, but the probability of encountering active prey then decreases and the effort associated with such encounters increases (Lockard and Owings 1974; Clarke 1983; Sábato et al. 2006) because of the increasing fear shown by the prey in response to the increase in predation rates. On the other hand, foxes appeared to display a trade-off between the two needs to maximise and minimise encounters with their prey (rabbits) and top predators (lynx), respectively.

The results of this study suggest that predator–prey interactions still merit deeper investigation. As emphasised by Lima (2002), and recently shown by Berger-Tal et al. (2010), Kotler et al. (2010) and Cozzi et al. (2012), a more global approach to predator–prey interactions might change the way we think about such interactions and bring to light complex foraging games between multiple predators and their prey.

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