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Nightjars, rabbits, and foxes interact on unpaved roads: spatial use of a secondary prey in a shared-predator system

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Abstract. Linear developments, such as roads and firebreaks, can increase encounter rates between predator and prey, which could affect predator–prey interactions and community dynamics. However, the extent to which prey responses at the interface between natural and anthropogenic habitats may be compared to those at the interface between natural habitats is unclear. Here, we used a shared-predator system to investigate the spatial response of red-necked nightjars (*Caprimulgus ruficollis*) to changing predation risk on roads, measured as the abundance of red foxes (*Vulpes vulpes*), and their primary prey (rabbits, *Oryctolagus cuniculus*). Because all three species coexist closely on unpaved roads in Doñana National Park (Spain), we predicted that nightjars would experience increased predation risk during periods of high fox and low rabbit abundances. Birds could then modify their space use at a broad scale by moving away from risky unpaved roads or, at a finer scale, by seeking foraging microsites facilitating escape from attacks. Between 2011 and 2012, mean rabbit abundance on roads increased by 50%, and fox abundance decreased by 80%, indicating a substantial decrease in predation risk for nightjars. Unexpectedly, nightjar occurrence on roads did not increase as a consequence of the decrease in fox predation risk. However, nightjars foraging on roads became less apprehensive in their use of linear strips of roadside cover, which is known to function as a physical barrier against fox attacks. Specifically, under high predation risk, most nightjars perched on the ground nearby (<15 cm) tall (>150 cm) vegetation, whereas when predation risk decreased, they shifted to more exposed microsites near shorter (<1 m) stands, but rarely close to cover (>45 cm). Nightjars' preference for areas of high predator abundance strongly suggests that flexible microhabitat selection allows them to manage the overall predation risk independently of predator abundance. Our results highlight the importance of linear developments in determining risk exposure and prey use of apparently dangerous habitats and thus may contribute to a better understanding of risky behaviors of prey.

Key words: *Caprimulgus ruficollis*; escape tactics; habitat selection; linear developments; microhabitat; predation risk; predator avoidance; predator–prey interaction; red-necked nightjar.

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INTRODUCTION

The spatial configuration of habitats (e.g., fragmentation, patch size, patch area/perimeter ratio) critically influences not only species occurrence and abundance, but also the rate and strength of species interactions (Tewksbury et al. 2002, Ries et al. 2004, Suárez-Esteban et al. 2016). In particular, habitat edges are known to alter patterns of abundance and foraging by prey and their predators in diverse ecosystems (Gates and Gysel 1972, Fagan et al. 1999, Ries et al. 2004, Morris 2005, Wirsing et al. 2007*a*, 2010). For example, many nesting birds select edge habitats because of the dual availability of forest cover and foraging areas, but they do so at the expense of increased mortality from edge-foraging generalist predators (e.g., Gates and Gysel 1972, Lima and Dill 1990, Santos and Tellería 1992, Keyser et al. 1998).

Linear developments, such as roads, firebreaks, and railways, can substantially increase the amount of edge habitat and provide a stark juxtaposition of different habitats with contrasting associated predation risks, thus influencing predator–prey interactions (Latham et al. 2011). However, whether edges at the interface between natural and anthropogenic habitats have effects on predator–prey interactions similar to those at the interface between natural habitats is unclear (but see Forman et al. 2003, Latham et al. 2011), even though some linear developments are pervasive worldwide and might lead to critical edge effects (Suárez-Esteban et al. 2016, Torres et al. 2016). In many habitats across the world, vertebrate predators and prey (e.g., carnivores, rabbits, birds) actively use unpaved roads, as they improve their foraging efficiency (Jackson 2003, Barrientos and Bolonio 2009, Suárez-Esteban et al. 2013). However, how prey respond to such dangerous encounters in linear developments is still poorly understood (but see Delgado et al. 2001, Pescador and Peris 2007, Suárez-Esteban et al. 2013).

Prey responses to increased predation risk often consist of spatial shifts to safer habitats (Lima and Dill 1990, Brown and Kotler 2004, Caro 2005). Such prey habitat shifts may occur at multiple spatial scales, usually reflecting those at which risk levels vary (Heithaus and Dill 2006, Cresswell et al. 2010). Predation risk is determined by contrasting factors acting at a hierarchy of levels or spatial scales (Brown and Kotler 2004, Schmitz 2010, Padié et al. 2015) that in turn depend on that over which predators can detect heterogeneity in prey availability (Morgan et al. 1997). At larger scales, predation risk is generally a strong function of predator density (Fedriani et al. 2000). At intermediate scales, predation risk experienced by a particular prey population may be contingent on the availability of alternative prey populations (Latham et al. 2013). At smaller scales, predation risk may vary among habitats and even microhabitats (e.g., Formanowicz and Bobka 1989, Fedriani and Boulay 2006, Heithaus et al. 2009) and thus prey selection of safer habitats is expected when and where predators are most abundant or active (Lima and Dill 1990). Therefore, a comprehensive understanding of prey responses to predation risk requires its assessment at several levels.

Here, we used a shared-predator system to investigate the antipredator response at different spatial scales of a secondary prey—the red-necked nightjar (*Caprimulgus ruficollis*)—to natural variation in predation risk from an opportunistic predator, the red fox (*Vulpes vulpes*) along unpaved roads in Mediterranean Spain. Specifically, we studied rabbits, foxes, and nightjars coexisting closely on unpaved roads in the Doñana National Park (SW Spain; Penteriani et al. 2013, Suárez-Esteban et al. 2013, Camacho 2014). Foxes are edge-foraging generalist predators that locally rely on rabbits (*Oryctolagus cuniculus;* Fedriani 1996, Ferreras et al. 2011, Palomares 2003), though they may occasionally prey upon alternative prey, including the red-necked nightjar (Forero et al. 2001, Aragonés 2003, Camacho 2014). Because rabbit numbers in Doñana fluctuate widely from year to year (Palomares 2003), predation pressure by the red fox on nightjars is likely to increase in years of low rabbit abundance (Fedriani et al. 1998, Ferreras et al. 2011).

During nighttime, nightjars sit-and-wait on the ground in open clearings, typically unpaved roads, since they are a suitable observation platform to detect flying insects and launch into the air to pursue them (Jackson 2003). Moreover, unpaved roads may be used to pick up insects from the ground and to take grit to aid in food digestion (Jackson 2003; C. Camacho and P. Sáez-Gómez, *personal observation*). For all these reasons, roads play a critical role as a foraging habitat for nightjars. In Doñana, foraging nightjars tend to settle in areas of sparse roadside cover, in front of tall shrubs or trees facilitating escape from fox attacks (Camacho 2014), at the cost of impaired detectability of their prey (Jackson 2003). It seems that nightjars fearing attack by a fox could feel safe on the roadside because

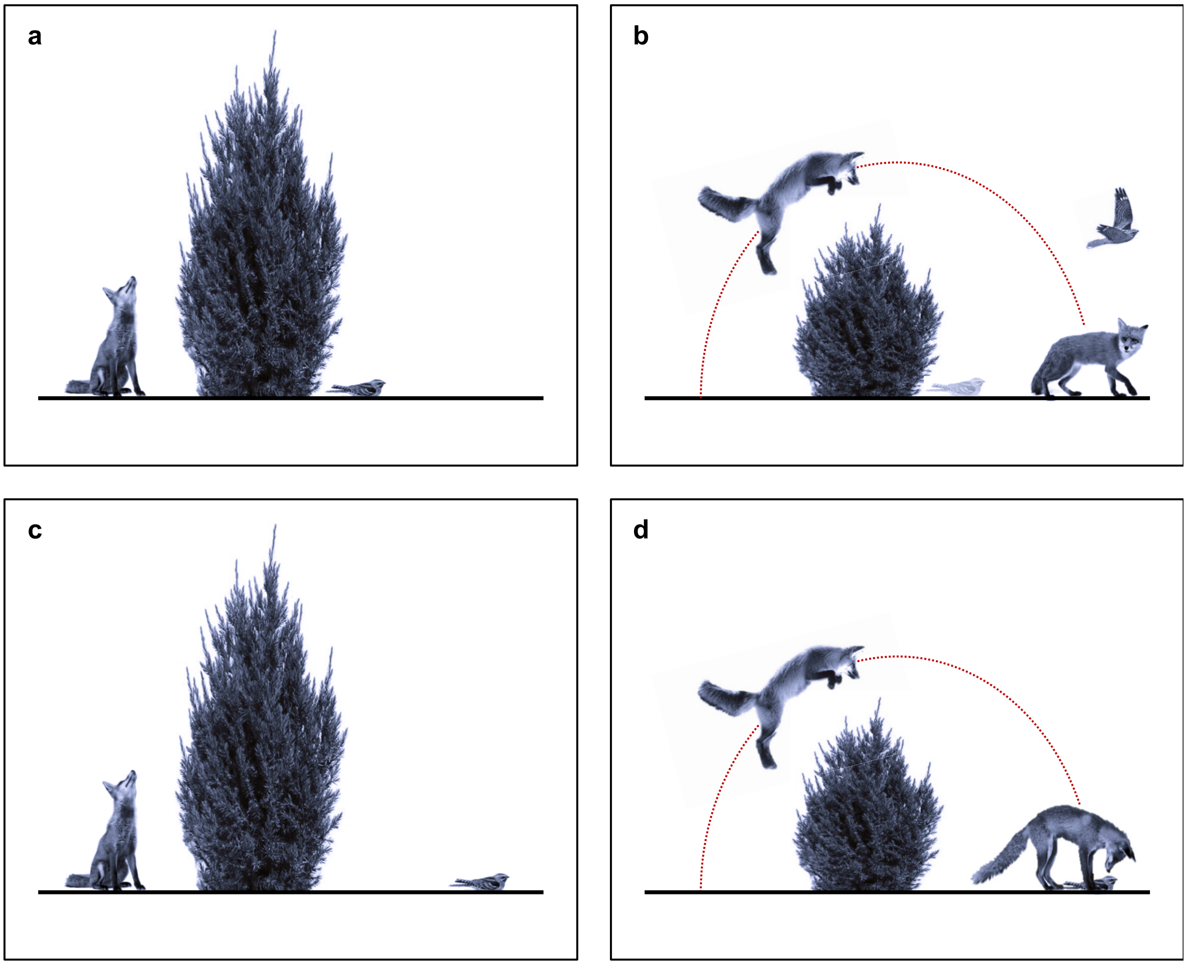

Fig. 1. Four possible red fox-red-necked nightjar hunting scenarios illustrating variance in predation risk for nightjars according to variation in vegetation height and the distance birds perch away from it. (a) Tall vegetation and short distance—relatively low predation risk: The plant(s) represent a nearly insurmountable barrier to foxes approaching from the rear; (b) low vegetation and short distance—medium predation risk: In this case, plant height does not preclude fox attack but hampers the fox to land on the bird, allowing it to fly toward any of the two sides; (c) tall vegetation and large distance; this is also a scenario of medium risk; (d) low vegetation and large distance; relatively high predation risk: Plant height does not preclude fox attack, nor hamper it to land on the bird.

(1) the backing vegetation might act to conceal it from potential predators prowling the adjacent habitats (Lima et al. 1987) and also restricts the number of direct attack routes (i.e., without any obstacle) to those from the open road (Fig. 1a), allowing early detection of terrestrial predators approaching from the front or the sides; (2) if attacked from the rear, the roadside cover would force the fox to jump over or pass through vegetation and impede it to land directly on the nightjar, allowing the latter to evade the attack (Fig. 1b) and (3) unpaved roads may provide nightjars a measure of protection from terrestrial predators, which may find it difficult to walk silently on uneven surfaces (Jackson 2003). However, a major disadvantage is that the view of the sky for nightjars would become narrower as the height of nearby vegetation and proximity to the roadside increase. Consequently, the safety provided by the roadside strip may at the same

time make it more difficult to detect flying insects, thereby reducing the foraging efficiency of nightjars (Jackson 2003).

Like many other prey species (Forstmeier and Weiss 2004, Pascual and Senar 2015, but see Schmitz 2006), predator abundance (direct cue) and availability of alternative prey (indirect cue) are chief determinants of the predation risk experienced by nightjars, and they are expected to respond to temporal changes in such critical variables (Sih et al. 2000, Camacho 2014). Nightjars may modulate risk exposure by moving to alternative foraging habitats away from the roads frequented by foxes to reduce the likelihood of encountering them (pre-encounter risk; Lima and Dill 1990) or, at a finer scale, by seeking safe microsites, allowing early detection of foxes and/or acting as a physical barrier against fox attacks (post-encounter risk; Lima and Dill 1990). Specifically, we compared patterns of habitat use by nightjars between two consecutive years of high and low relative predation risks and addressed two non-mutually exclusive predictions: (1) Nightjar occurrence on roads should respond to temporal increases in the probability of encountering foxes, so that during years of relative high fox activity along unpaved roads, birds should move to non-preferred (but safer) foraging habitats, and (2) nightjars foraging on roads in years of relative high predation risk by foxes should show a stronger selection for safe microhabitats (i.e., those located at short distances from tall roadside cover) as compared with years of relative low predation risk by foxes.

MATERIALS AND METHODS

Study area and species

The study was carried out in the protected core of Doñana National Park and a nearby managed area (37°1–7′ N, 6°32–33′ W; see Camacho et al. 2014 for a detailed description of the study site) in two consecutive years with contrasting rainfall: 2011 and 2012 (713 vs. 330 mm, respectively). Heavy rains in Doñana often lead to drastic declines in rabbit density as a result of the flooding and collapsing of their warrens (Palomares 2003). Overall, the 2 years of study provide a good opportunity to investigate the opportunistic interaction between foxes and nightjars as mediated by rabbit numbers, since fox occurrence at the foraging sites of nightjars—and presumably also the real risk of predation—decreased substantially from the first year to the next with the increase in rabbit numbers (see *Results*). The study area consists of a 35-km road circuit of unpaved roads of 3.5−5 m width along which areas of dense tall roadside vegetation alternate with areas of sparse or absent vegetation (Appendix S1: Fig. S2). The roadside vegetation consists of tall (>2 m) and medium-height (1–2 m) shrubs (mainly *Juniperus phoenicea*, *Halimium halimifolium*, *Rosmarinus officinalis*, and *Ulex* spp.) with sparse herbaceous cover. There were no differences in the structure of roadside vegetation between the protected and the managed area (Camacho 2014). Despite the overall availability of safe microhabitats along roads is not high (Appendix S1: Fig. S1), safe microhabitats should not be considered as a limiting resource given that many of them keep unoccupied during nighttime due to relatively low nightjar abundance. Climate in Doñana is Mediterranean sub-humid with temperate wet winters and hot dry summers, although annual rainfall varies widely from year to year (range 170−1028 mm; mean ± SD 550 ± 217 mm for the period 1978−2012; data available at http://www.rbd.ebd.csic.es).

In Doñana, and possibly elsewhere, the red-necked nightjar does not make up a significant proportion of the fox diet (Fedriani 1996). Nevertheless, a previous study conducted in the same study area revealed that red foxes can strongly affect nightjar survival in some years (Forero et al. 2001). Here, the nightjar appears to be a suitable alternative prey for the red fox when rabbits are less abundant, mainly for three reasons. First, nightjars and foxes are mostly nocturnal and coexist closely along unpaved roads, since these are positively selected by the two species in the study area (Suárez-Esteban et al. 2013, Camacho et al. 2014). Fox abundance is, indeed, over five times higher along unpaved roads than in contrasting adjacent habitats (Suárez-Esteban et al. 2013), and nightjar numbers along roads can reach up to six birds/km in some stretches (C. Camacho and P. Sáez-Gómez, *personal observation*). Second, the cryptic coloration of nightjars would seldom match the background of their foraging sites, thus increasing conspicuousness to predators (Aragonés et al. 1999). Finally, nightjars spend most of the night sitting on the ground, and this may allow foxes to detect and access them relatively easily (Doucette et al. 2011). In fact, foxes have been occasionally observed attempting predation on road-sitting nightjars during the night, which they generally do by approaching the birds perpendicularly from the rear and pouncing on them by jumping over the roadside vegetation (Camacho 2014). Because roads play a critical role as a foraging habitat for nightjars compared with other habitats (Camacho et al. 2014) and, therefore, their foraging habits involve the sites where red foxes are most frequent at night (Suárez-Esteban et al. 2013), the probability of encountering predators, and thus perceived predation risk, should be highest at their foraging sites.

Annual changes in rabbit and fox abundance

Rabbit abundance was estimated in April, June, and September 2011 and 2012 from transect counts conducted by driving a vehicle at a constant speed of 10–15 km/h along six different road stretches of 15 km each, all located in the vicinity of the study area (0–18 km away). Rabbit counts began 1 h before dusk and finished 0.5 h after dusk and were repeated during three consecutive days. We used the mean number of rabbits counted during three transect replicates as a monthly value of rabbit abundance at each road stretch. Fox occurrence at the foraging site of nightjars was estimated as the total number of fox sightings during the nightjar counts conducted between April and September 2011 and 2012 (see *Nightjar use of roadside cover and occurrence on unpaved roads*). Mean fox sightings (individuals/10 km) in each year was used as a proxy for nightjar perceived predation risk.

Nightjar use of roadside cover and occurrence on unpaved roads

Between April and September 2011 and 2012, we conducted weekly counts of road-sitting nightjars by driving a vehicle along a 35-km road circuit at a constant speed of 30 km/h, beginning 1–2 h after dusk. During these transects, nightjars were captured by using a flashlight and a handheld net, individually marked with numbered metal bands, and aged as either hatch year or after hatch year (i.e., adults; see Camacho 2013 for details on the field procedures). In June and July 2011 and 2012, coinciding with the breeding season, we examined the patterns of microhabitat selection by foraging nightjars encountered during the nocturnal transects. Nightjars were detected from >200 m by their eye shine, as they sit on roads perpendicularly, with the tail oriented toward the roadside (Camacho 2014). After approaching to within 10–15 m of the bird, they were reluctant to flush and remained motionless while the vehicle motor remained running and the car lights on, which allowed us to record in situ (to the nearest 1 cm) their proximity to roadside vegetation, measured as the perpendicular distance from the roadside, and vegetation height. Individuals that moved after detection were not included in the analysis to ensure that positions recorded from the vehicle were representative of behavior prior to approaching the birds (Camacho 2014). Microsites used by nightjars were georeferenced using a Garmin GPS 60 (2–4 m accuracy) and those located $\leq$ 300 m apart were not considered in the analyses to avoid non-independence of the points (Camacho 2014). Only adult nightjars were included in the analyses, because the presence of hatch-year birds on roads early in the season was comparatively small (n = 36 vs. 224 captures during June and July 2011−2012).

Statistical analyses

All statistical analyses were done using R 2.14.0 (http://www.r-project.org). Between-year differences in rabbit abundance and nightjar occurrence on roads were evaluated by paired t tests, after log-transformation of the relative abundance of rabbits only to meet normality assumptions (Shapiro–Wilk normality tests: $W_{\text{rabbit}} = 0.95$, $P = 0.12$; $W_{\text{nightjar}} = 0.98$, $P = 0.56$). In the case of foxes, most counts yielded zero values, particularly in 2012. For this reason, no test was performed to assess annual differences in fox occurrence on roads; instead, they were determined by the cumulative number of foxes counted in each season in relation to the total distance covered by transects (840 km/season).

By comparing the distribution of microsite attributes (i.e., vegetation height and proximity) in 2011 and 2012, we tested for differences in the antipredator behavior of foraging nightjars naturally exposed to different levels of predation risk. A left-skewed distribution of vegetation heights at the foraging sites would reflect the occurrence of highly apprehensive behaviors, with nightjars sitting preferably near tall, obstructive cover. On the other hand, regarding distances to nearby vegetation, more fearful behaviors would be associated with right-skewed distributions, with nightjars sitting more closely to obstructive cover. Separate Kolmogorov–Smirnov (KS) two-sample tests were performed for vegetation height and distance to vegetation. KS tests were implemented using the function *ks.boot* (10,000 simulations) in the R-package "Matching" (Sekhon 2011), which enables the test to be conducted on data containing ties.

RESULTS

Annual changes in rabbit and fox abundance

Fox abundance on unpaved roads decreased 79% from 2011 to 2012 (Fig. 2a). Mean rabbit abundance on unpaved roads increased 53% between these years ($t = 3.284$, df = 16, $P = 0.005$, $n = 17$ and 18 counts in 2011 and 2012, respectively; Fig. 2b). Based on the observed annual differences in fox and rabbit abundance at the foraging sites of nightjars, we classified 2011 as a period of "increased predation risk" for nightjars caused by the regular presence of foxes on roads and low rabbit abundance and 2012 as a period of "decreased predation risk" caused by the limited presence of foxes and high rabbit abundance.

Nightjar responses to changing predation risk on unpaved roads

Contrary to our expectations, nightjar numbers on unpaved roads decreased 43% from 2011 (high predation risk) to 2012 (low predation risk; $t = -3.931$, df = 23, $P = 0.0007$, $n = 24$ counts per year; Fig. 2c). Our second level of analysis at a finer spatial scale includes 209 field observations (147 and 62 in 2011 and 2012, respectively) concerning microhabitat selection by foraging nightjars in unpaved roads. As predicted, during the year of high predation risk (2011), nightjars chose to forage nearby obstructive, tall stands (≥150 cm; Fig. 3a) of, for example, *Halimium halimifolium* and *Juniperus phoenicea*, while they avoided venturing

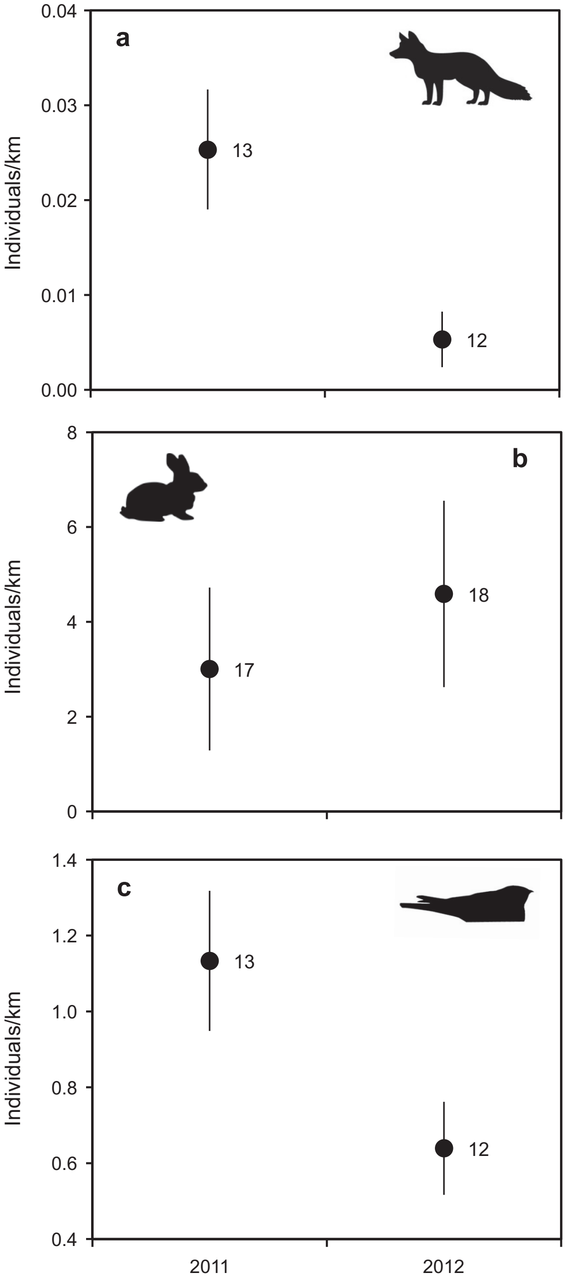

Fig. 2. Mean abundance of red foxes (a), rabbits (b), and red-necked nightjars (c) coexisting in Doñana during 2011 and 2012. Note that, unlike in the statistical analyses, only the months for which count data for all the three species are available (April, June, September) are depicted here. Bars denote SE. Figures besides the dots are annual numbers of counts.

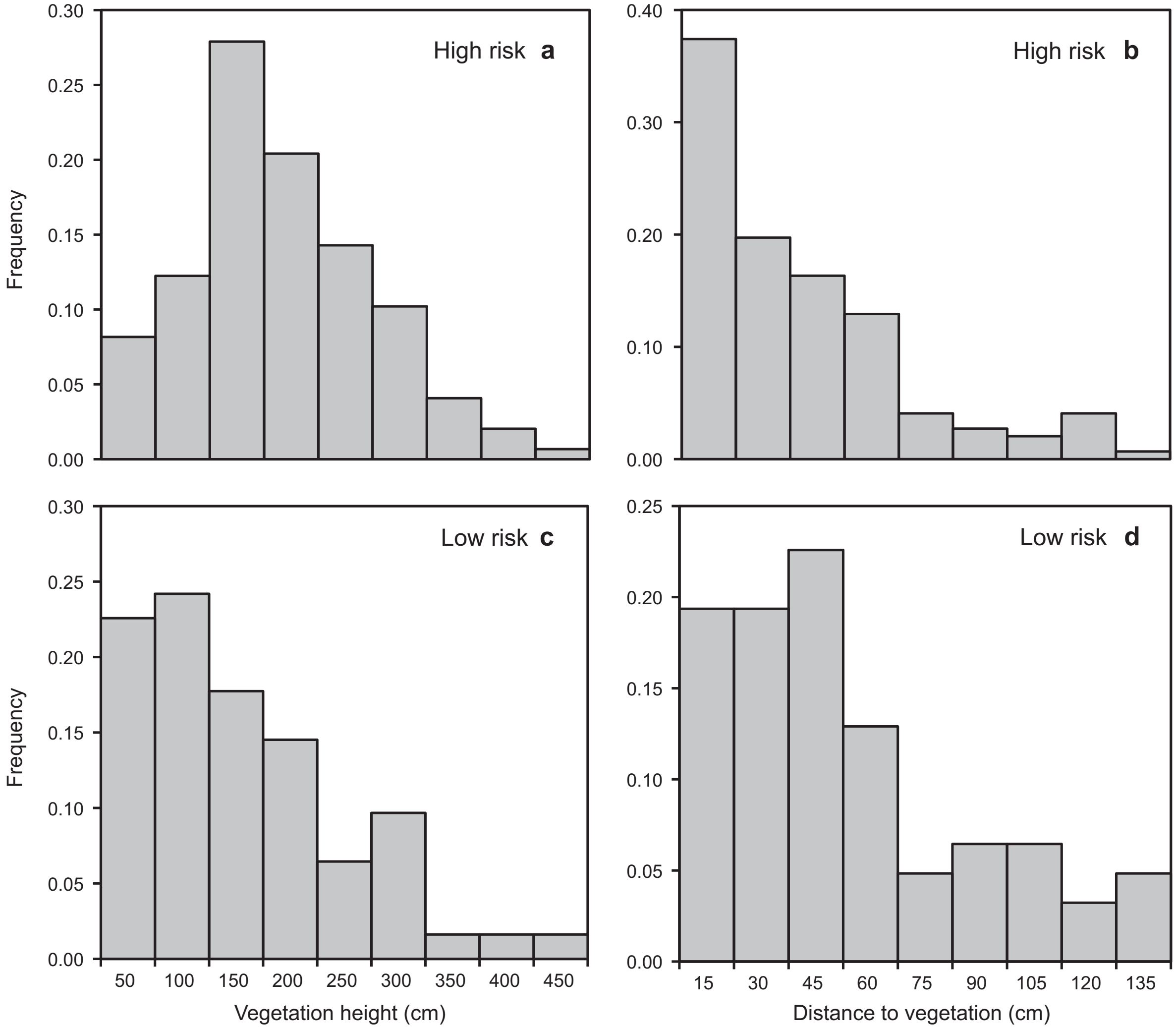

Fig. 3. Frequency distributions of vegetation heights (left) and distances to vegetation (right) at the foraging sites of nightjars under contrasting predation risks. Note that more apprehensive behaviors would be associated with left-skewed distributions of vegetation heights and right-skewed distributions of distances to vegetation, that is, nightjars sitting preferably at minimum distances from tall, obstructive cover. The reverse would be true for risky behaviors.

>15 cm away from cover, as shown by the right-skewed distribution of distances to obstructive cover (Fig. 3b). However, foraging nightjars shifted their microhabitat selection to less apprehensive choices during 2012, when fox occurrence decreased. Specifically, they sat nearby shorter plants (≤1 m; Fig. 3c) and ventured ≥45 cm away from cover (Fig. 4d). Thus, the differences between both years in the antipredator behavior of nightjars were highly significant, as shown by the comparison of the distributions of both plant heights (*D* = 0.29, *P* = 0.001) and nightjars' distances to vegetation (*D* = 0.22, *P* = 0.027).

DISCUSSION

Our results strongly suggest that nightjars can modulate risk exposure according to perceived predation risk through flexible microhabitat selection in roadside strips. Based on the results from this and our previous work (Camacho et al. 2014), it seems that short-term changes in the antipredator responses of nightjars are scale-dependent. Birds preferentially foraged on unpaved roads over the entire study period (Camacho et al. 2014), indicating no effect of changing predation risk at the broad spatial scale. However, their spatial behavior changed from year to year at the microhabitat scale. Nightjars facing reduced predation risk shifted from safer microsites offering the best chance of escaping predation to more exposed ones that, however, probably offer greater foraging efficiency. Our findings therefore indicate that predation risk shapes nightjar use of unpaved roads, shed light on the spatial scale at which nightjars respond to predation risk, and give support to the idea that habitat spatial configuration influences the rate and strength of species interactions (Tewksbury et al. 2002, Ries et al. 2004, Suárez-Esteban et al. 2016).

During 2011 and 2012, both direct (fox abundance) and indirect (rabbit abundance) cues indicated decreased predation risk for nightjars in 2012. Our results show that, as in other Mediterranean birds (Carpio et al. 2015), short-term changes in rabbit abundance may mediate the opportunistic interaction between generalist predators and nightjars. Fluctuations in rabbit numbers usually lead to prey switching by the red fox and thus may affect predation pressure on nightjars to the same extent as changes in fox abundance (Pech and Hood 1998, Ferreras et al. 2011). Both cues could therefore be considered useful criteria to assess predation threats (Forstmeier and Weiss 2004, Pascual and Senar 2015). Whether nightjars rely mostly on rabbit or fox abundance to index predation risk, however, cannot be determined, as they both acted in the same direction during our study and indicated a release of fox predation risk for nightjars.

Contrary to our expectations, foxes and nightjars co-occurred closely on roads during the first year of study and to a lesser extent in the following year. Nocturnal monitoring of radiotagged nightjars in 2011 and 2012 showed that they selected roads as their main foraging habitat during the two study years, although they occasionally travelled to alternative foraging habitats in nearby crops and natural clearings (Camacho et al. 2014). However, this rarely occurred in the year when foxes were most abundant; instead, they continued foraging on roads, thereby increasing the probability of encountering the predator (Camacho et al. 2014). Nightjars' preference for unpaved roads even during risky periods supports the idea that these are the most profitable habitats for them (Jackson 2003) and indeed suggests that, as some marine mammals like bottlenose dolphins and dugongs, nightjars prefer to forage in areas with high predator abundance than shifting to safer but less profitable habitats (Heithaus and Dill 2006, Wirsing et al. 2007*a*, *b*).

Caution is required when interpreting these results, since the relative availability of aerial insects on unpaved roads and nearby habitats could also play a part in our study system (Jackson 2003). In addition, nightjar use of roads could have been affected by thermoregulatory constraints. Nightjars are attracted toward warm surfaces when the air temperature drops below 14°C (Camacho 2013). However, based on the mild ambient temperature in the study area during the fieldwork seasons 2011 and 2012 (mean night temperatures: 22.7°C and 22.2°C, respectively), it appears that the observed decrease in nightjar numbers on roads does not reflect a thermoregulatory response. Taken together, our results strongly support the idea that predation risk is a major factor impinging on nightjar use of unpaved roads (Camacho 2014).

Linear strip-cover habitats such as roadsides can provide undisturbed nesting habitat and concealment from predators and therefore attract numerous bird species in manmade habitats (Warner 1992, Bergin et al. 2000). Nightjars have previously been shown to use linear strips of vegetation along unpaved roads as an effective antipredator strategy to facilitate escape from terrestrial attacks (Camacho 2014). Moreover, the results of this study suggest that the spot nightjars choose to sit on roads are determined by perceived predator risk. Roadside vegetation can act as a solid barrier against fox attacks and possibly also makes the approach of foxes easily detected by sound, thereby increasing their chances of survival. But the backing vegetation could also make nightjars more vulnerable to predation by altering their escape trajectory and velocity (Kullberg and Lafrenz 2007). However, according to our observations of fox attacks, it appears that nightjars sitting at the base of a tall shrub or tree can still perform evasive maneuver and escape into the open at a safe distance from the fox (Camacho 2014).

Besides predation risk, the ground spot nightjars choose to sit could be influenced by perceived risk from vehicles, but this seems unlikely given the negligible night traffic volume along the surveyed roads. Nightjar use of roadsides could also reflect some advantage in territorial or courtship display to other nightjars or, alternatively, the shading provided by shrubs adjacent to roads during the day might affect the surface temperature during the first hours of the night and thus confound the choice of the foraging sites by nightjars (Camacho 2013). It should be noted, however, that despite only males are territorial and perform courtship displays (Aragonés et al. 1999, Aragonés 2003), both males and females select road sections with tall vegetation regardless of their breeding status and the ambient temperature (C. Camacho and P. Sáez-Gómez, *personal observation*).

Our results indicate that the efficiency of nightjars' escape strategy may vary at extremely fine-grained scales and that birds may respond to annual changes in predation risk in a threat-sensitive manner (Lima et al. 1987, Helfman 1989). By shifting from safer microsites nearby tall shrubs to more exposed ones near the middle of the road, nightjars are apparently able to modulate their chances of escape and thereby manage the overall predation risk independently of predator abundance (Lima and Dill 1990). It may be argued, however, that nightjars reveal their safest habitat only at low densities, when those preferred sites are available to most birds. But this seems unlikely, as safe plant stands did not appear to be a limiting resource for nightjars according to their abundance along roads. Despite the availability of the safest microhabitats in the roadside, that is, shrubs >150 cm—was only 30% of all the plants, during the surveys we observed plenty of safe plant stands unoccupied by nightjars, even during the year of high nightjar abundance (2011).

Overall, our findings support the notion that linear developments, and unpaved roads in particular, can strongly influence predator–prey interactions. However, they are in marked contrast to those of an analogous study suggesting that an increase in predator presence on linear developments results in prey avoidance of such structures and in the subsequent loss of functional habitat (Latham et al. 2011).

Ideally, a field test comparing the same individuals exposed to different threat levels at the same site and period or during a greater number of years would allow us to exclude potentially confounding factors and provide stronger support to our finding that the threat of fox attack actually mediates habitat selection of nightjars. However, such an approach is hard to carry out under natural conditions (Heithaus et al. 2009, Pascual and Senar 2015), particularly when direct and indirect cues of predation risk may vary unpredictably (see Davies and Gray 2015). During our survey, 45% of the adult nightjars escaped before their identity was determined, and only approximately 20% of the individuals captured during the 2011 season were recovered in 2012. As a result, the sample size of repeated measures of the same individuals in the two study years was very limited. Experimental manipulations of predation risk and/or food availability for nightjars are therefore needed to determine the generality of our results. But, in any case, the observed response of nightjars to changing predation risk at the interface between natural and anthropogenic habitats strongly supports the idea that habitat spatial configuration in general, and habitat edges in particular, has a major role in determining the rate and outcome of predator–prey interactions.

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