'Bodyguard' plants: Predator-escape performance influences microhabitat choice by nightjars

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ARTICLE INFO

ABSTRACT

Prey are typically assumed to avoid their predators. However, habitat selection patterns of prey might depend upon their ability to use particular landscape elements to manage their escape options from predator encounters. During two breeding seasons, I studied habitat use and behaviour of red-necked nightjars (*Caprimulgus ruficollis*) foraging under the risk of predation by red foxes (*Vulpes vulpes*) in southwestern Spain. Nightjars exhibited nearly invariable foraging site choice and body positioning behaviour based on the architecture of vegetation near foraging sites. Nightjars actively chose to sit <50 cm from >120 cm-tall shrubs or trees while facing away from vegetation cover. Vegetation behind nightjars significantly increased their aerial escape opportunities from terrestrial attacks during their peak activity period, when nightjars reveal visible feather bands during their foraging sallies from the ground and their cryptic colouration may not always match the background. Spatial overlap of nightjars and foxes along roads suggests that microhabitat selection by these birds may in part depend on the chance of escape from predator encounters rather than on the probability of encountering predators. I conclude that the interplay between high escape efficiency and visibility have probably contributed to the evolution of foraging site selection by caprimulgids using bare grounds and cattle, horse and camel trails as the natural counterpart of roads.

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1. Introduction

Habitat selection is a major focus of evolutionary and behavioural ecology, as it usually represents a critical process affecting foraging efficiency and individual fitness (Cody, 1984). A growing number of studies highlight the influence of habitat features on the spatial behaviour of foraging animals at multiple spatial scales (e.g. Sergio et al., 2003; Whittingham et al., 2005; Barbaro et al., 2007), ranging from the landscape level (Morris et al., 2001; Gilroy et al., 2011) to the home-range scale (Signorell et al., 2010). However, in the context of predation risk, habitat selection by prey species may also apply to increasingly finer levels (Johnson, 1980), which should finally involve the choice of foraging microhabitats within the broad home range (Lima, 1990; Antos et al., 2008). Behavioural responses of a wide array of prey species often include microhabitat shifts that enable individuals to adjust mortality risk by actively selecting particular sites which facilitate escape (e.g. Lima and Dill, 1990; Brown and Kotler, 2004; Creel et al., 2005; Wirsing et al., 2007). For example, white-crowned sparrows (*Zonotrichia leucophrys*) and lark buntings (*Calamospiza*

melanocorys) inhabiting a floodplain both appear to evaluate predation risk, but exhibit different escape strategies when attacked by raptors: while sparrows always move or fly to vegetation due to the obstruction it provides (i.e. cover-dependent escape tactic), buntings usually require a clear path of escape to the air (i.e. aerial escape tactic; Lima, 1990). Prey behaviour-microhabitat links in structurally complex habitats may result in an efficient barrier between predator and prey (Main, 1987). However, differences in the elusive behaviours exhibited by closely related species reflect perception of the safety of foraging sites (i.e. escape options) and could be a function of physical habitat features and its particular escape tactics (see Heithaus et al., 2009; Wirsing et al., 2010).

Perceived predation risk may depend on both the likelihood of encountering predators and the probability of escape once attacked (Lima, 1992). According to this theoretical framework, an emerging empirical view holds that prey will actually match the distribution of their predators if evasive behaviours involve particular landscape elements offering the best chance of escape where predators are most abundant (reviewed by Wirsing et al., 2010). Increased predation risk within foraging habitats should lead to rapid evolution of behavioural responses (e.g. microhabitat shifts) to balance antipredator efforts with a minimum reduction in foraging benefits. In contrast, prey species lacking the ability to manage their chances of escape would be expected to seek predator-free and

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perhaps less profitable foraging areas (Lima and Dill, 1990; Lima, 1992; Cresswell, 2008).

My purpose was to assess patterns of microhabitat selection by red-necked nightjars (*Caprimulgus ruficollis*) foraging under risk of predation by red foxes (*Vulpes vulpes*) in Doñana National Park, southwestern Spain. Red-necked nightjars (hereafter 'nightjars') feed on aerial insects in open spaces and hawk flying insects during short upward sallies from ground perches before returning to exactly the same site (i.e. 'sit-and-wait' foraging strategy; Camacho, 2013). Red foxes are considered to be opportunistic predators on ground-dwelling birds (e.g. Ford et al., 2001; Tryjanowski et al., 2002; Amat and Masero, 2004) including the red-necked nightjar (Aragonés, 2003). Recent studies on microhabitat selection by nightjars and foxes in Doñana indicate that densities of both are highest on roads. While nightjars use roads as their main foraging sites (Camacho, 2013), foxes select human-made corridors as territory boundaries (Suárez-Esteban et al., 2013). Consequently, as encounter probabilities are usually proportional to the abundance of predators (but see Creel and Christianson, 2008), the foraging habits of nightjars are likely to increase the possibilities of encountering predators. Based on field observations of attempted predation and the actual predator–prey overlap, I hypothesized that nightjars would manage their overall risk of predation within preferred foraging habitats (i.e. roads) by seeking sites perceived to be safe (i.e. facilitating the aerial escape tactic of nightjars).

I used a combination of nighttime observations and experimental simulations of predation attempts by humans to: (1) determine the influence of landscape features (i.e. vegetation structure and composition) on the spatial behaviour of nightjars foraging under risk of predation, and (2) to test the hypothesis that microhabitat architecture contributes to the safety of foraging sites by increasing the escape options of ground-sitting nightjars.

2. Methods

2.1. Study area

I measured nocturnal microhabitat choice by nightjars along 35-km of roads crossing the protected core of Doñana National Park (37°0′N, 6°30′W) and its managed periphery (37°8′N, 6°34′W). The two sites have different vegetation communities that include autochthonous Mediterranean shrublands dominated by *Halimium halimifolium*, *Ulex* spp., *Erica* spp. and *Juniperus phoenicea* in the protected area, and a mixture of cattle-grazed grassland with scattered exotic trees (e.g. *Acacia saligna*, *Nicotiana galuca*, *Casuarina equisetifolia*) and pine plantations in the managed area. Vegetation along road verges is made up of sparse tall (>2 m) and medium-height (1–2 m) clumped shrubs or single trees with sparse herbaceous cover.

2.2. Field data collection

In June and July 2011 and 2012, I conducted field observations of foraging nightjars during the course of nocturnal vehicle transects along roads. To account for a possible effect of time or variable weather conditions on nightjar behaviour, transects began 1–2 h after dusk and were limited to lightly (<30%) clouded nights with no precipitation and low (<10 km/h) wind velocities (Jetz et al., 2003; Ashdown and Mckechnie, 2008). Moonlight has no influence on microhabitat selection by red-necked nightjars (Camacho, 2013) and hence was ignored. I detected nightjars from >200 m by their eye shine. Birds were reluctant to flush but remained motionless while the vehicle remained running, which allowed me to record in situ their precise location relative to the nearby road verge. Individuals that moved after detection were not included in the analysis

to insure that positions recorded from the vehicle were representative of behaviour prior to approaching the birds. Nightjars were captured following the method of Jackson (2003) and individually marked with numbered metal rings. The location of individuals was georeferenced using a Garmin GPS 60 (2–4 m accuracy) and, after trapping or, if the nightjar escaped, flushing the bird, I measured several microhabitat attributes for individuals sitting <1.5 m from either road verge (i.e. 312 out of 320 nightjars detected on roads). I classified body orientation in three angle categories: 0° (tail oriented towards the road verge), 90–270° (parallel to the road verge) and 180° (head facing the road verge). I measured the distance to the verge to the nearest 1 cm. Canopy height and width of shrub species most commonly used by nightjars (see Section 3.1) were highly positively correlated ($r = 0.96$, $P < 0.0001$), so I took plant height measurements (to the nearest 1 cm) as a proxy for the structural profile of vegetation. I characterized the roadside vegetation closest to each foraging nightjar (i.e. selected site) and at 160 random sites (i.e. randomized kilometric points to the nearest 0.1 km) along the road circuit. The mean height of the two tallest plant stands within a 1.5-m radius of selected sites was averaged to ascertain the structural profile of the adjacent vegetation. To explore nightjar use of plant communities, I identified all individual plants to species level in both selected and random sites. To assess microhabitat selection, the structural and qualitative differences between selected (i.e. microhabitat use) and random sites (i.e. microhabitat availability) were analyzed.

2.3. Experimental procedures

Predation attempts are typically rare in nature, and experimental manipulations are therefore necessary to assess the escape abilities of birds (Boland, 2003). During the course of vehicle transects, I opportunistically witnessed three actual (2 by foxes and 1 by swine) attacks on road-sitting nightjars. Foxes approached to within 1–2 m of the birds from behind, remained motionless for a few seconds, and then suddenly attacked. However, the high (and dense) roadside cover behind the nightjars forced foxes to jump over vegetation, enabling birds to react readily to attacks and escape. Similarly, the attempt by a wild pig *Sus scrofa* also failed because roadside vegetation forced the predator to noisily go through vegetation, thus enabling the nightjar to immediately detect and successfully evade the attack. To experimentally assess the escape efficiency of nightjars relative to vegetation structure, human 'predators' (the author and two experienced field assistants) simulated 65 attacks from the birds' rear (which forced us to avoid vegetation in the road verge) and from the birds' front (where there were no obstacles along the bare road surface). The attack sequence was designed to mimic real (witnessed) predation attempts on road-sitting nightjars, after checking that the escape response elicited by approaching humans was similar to that elicited by real terrestrial predators. Thus, I am confident that the use of humans to simulate attacks was suitable to obtain a reliable estimate of the effect of cover on nightjar escape efficiency. All simulated attacks were conducted between 23:00 h and 2:00 h during the course of car transects in July 2012. Humans quietly approached the birds on foot prior 'attacking' from 1 to 2 m from the bird. We used an 80-cm diameter butterfly net to 'catch' birds so as to not injure them. To avoid the net becoming entangled in vegetation, and thus ensuring that attacks in the open had the same chance of success as in the cover, the net was never casted but we always held it above the backing vegetation until flushing or trapping the bird on the bare ground. As premature detection of the 'predators' by prey would undermine the validity of experimental attacks, we used a LED torch in the two contexts (with and without plant barrier) and hid ourselves behind the light beam. The use of LED light as a camouflage device did not appear to reduce the escape