

1 ARTICLE

2 **'Bodyguard' plants: predator-escape performance influences microhabitat**
3 **choice by nightjars**

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5 CARLOS CAMACHO

6 *Department of Evolutionary Ecology, Estación Biológica de Doñana (EBD-CSIC),*

7 *Américo Vespucio s/n, 41092, Seville, Spain*

8 Tel: +34 954 232 340

9 Fax: +34 954 466 700

10 E-mail address: ccamacho@ebd.csic.es

11

12 **ABSTRACT**

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

31

32 *Keywords:* Antipredator behaviour; Caprimulgidae; Habitat selection; Microhabitat;
33 Predation risk; Red-necked nightjar.

34

35 **1. Introduction**

36 Habitat selection is a major focus of evolutionary and behavioural ecology, as it usually
37 represents a critical process affecting foraging efficiency and individual fitness (Cody,
38 1984). A growing number of studies highlight the influence of habitat features on the
39 spatial behaviour of foraging animals at multiple spatial scales (e.g. Sergio et al., 2003;
40 Whittingham et al., 2005; Barbaro et al., 2007), ranging from the landscape level
41 (Morris et al., 2001; Gilroy et al., 2011) to the home-range scale (Signorell et al., 2010).
42 However, in the context of predation risk, habitat selection by prey species may also
43 apply to increasingly finer levels (Johnson, 1980), which should finally involve the
44 choice of foraging microhabitats within the broad home range (Lima, 1990; Antos et al.,
45 2008). Behavioural responses of a wide array of prey species often include microhabitat
46 shifts that enable individuals to adjust mortality risk by actively selecting particular sites
47 which facilitate escape (e.g. Lima and Dill, 1990; Brown and Kotler, 2004; Creel et al.,
48 2005, Wirsing et al., 2007). For example, white-crowned sparrows (*Zonotrichia*
49 *leucophrys*) and lark buntings (*Calamospiza melanocorys*) inhabiting a floodplain both
50 appear to evaluate predation risk, but exhibit different escape strategies when attacked
51 by raptors: while sparrows always move or fly to vegetation due to the obstruction it
52 provides (i.e. cover-dependent escape tactic), buntings usually require a clear path of
53 escape to the air (i.e. aerial escape tactic; Lima, 1990). Prey behavior-microhabitat links
54 in structurally complex habitats may result in an efficient barrier between predator and
55 prey (Main, 1987). However, differences in the elusive behaviours exhibited by closely
56 related species reflect perception of the safety of foraging sites (i.e. escape options) and
57 could be a function of physical habitat features and its particular escape tactics (see
58 Heithaus et al., 2009; Wirsing et al., 2010).

59 Perceived predation risk may depend on both the likelihood of encountering
60 predators and the probability of escape once attacked (Lima, 1992). According to this
61 theoretical framework, an emerging empirical view holds that prey will actually match
62 the distribution of their predators if evasive behaviours involve particular landscape
63 elements offering the best chance of escape where predators are most abundant
64 (reviewed by Wirsing et al., 2010). Increased predation risk within foraging habitats
65 should lead to rapid evolution of behavioural responses (e.g. microhabitat shifts) to
66 balance antipredator efforts with a minimum reduction in foraging benefits. In contrast,
67 prey species lacking the ability to manage their chances of escape would be expected to
68 seek predator-free and perhaps less profitable foraging areas (Lima and Dill, 1990;
69 Lima, 1992; Cresswell, 2008).

70 My purpose was to assess patterns of microhabitat selection by red-necked
71 nightjars (*Caprimulgus ruficollis*) foraging under risk of predation by red foxes (*Vulpes*
72 *vulpes*) in Doñana National Park, southwestern Spain. Red-necked nightjars (hereafter
73 'nightjars') feed on aerial insects in open spaces and hawk flying insects during short
74 upward sallies from ground perches before returning to exactly the same site (i.e. 'sit-
75 and-wait' foraging strategy; Camacho, 2013). Red foxes are considered to be
76 opportunistic predators on ground-dwelling birds (e.g. Ford et al., 2001; Tryjanowski et
77 al., 2002; Amat and Masero, 2004) including the red-necked nightjar (Aragonés, 2003).
78 Recent studies on microhabitat selection by nightjars and foxes in Doñana indicate that
79 densities of both are highest on roads. While nightjars use roads as their main foraging
80 sites (Camacho, 2013), foxes select human-made corridors as territory boundaries
81 (Suárez-Esteban et al., 2013). Consequently, as encounter probabilities are usually
82 proportional to the abundance of predators (but see Creel and Christianson, 2008), the
83 foraging habits of nightjars are likely to increase the possibilities of encountering

84 predators. Based on field observations of attempted predation and the actual predator-
85 prey overlap, I hypothesized that nightjars would manage their overall risk of predation
86 within preferred foraging habitats (i.e. roads) by seeking sites perceived to be safe (i.e.
87 facilitating the aerial escape tactic of nightjars).

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

94

95 **2. Methods**

96 *2.1. Study area*

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

106

107 *2.2. Field data collection*

108 In June and July 2011 and 2012, I conducted field observations of foraging nightjars
109 during the course of nocturnal vehicle transects along roads. To account for a possible
110 effect of time or variable weather conditions on nightjar behaviour, transects began 1-2
111 h after dusk and were limited to lightly (<30%) clouded nights with no precipitation and
112 low (<10 km/h) wind velocities (Jetz et al., 2003; Ashdown and McKechnie, 2008).
113 Moonlight has no influence on microhabitat selection by red-necked nightjars
114 (Camacho, 2013) and hence was ignored. I detected nightjars from >200 m by their eye
115 shine. Birds were reluctant to flush but remained motionless while the vehicle remained
116 running, which allowed me to record *in situ* their precise location relative to the nearby
117 road verge. Individuals that moved after detection were not included in the analysis to
118 insure that positions recorded from the vehicle were representative of behaviour prior to
119 approaching the birds. Nightjars were captured following the method of Jackson (2003)
120 and individually marked with numbered metal rings. The location of individuals was
121 georeferenced using a Garmin GPS 60 (2-4 m accuracy) and, after trapping or, if the
122 nightjar escaped, flushing the bird, I measured several microhabitat attributes for
123 individuals sitting <1.5 m from either road verge (i.e. 312 out of 320 nightjars detected
124 on roads). I classified body orientation in three angle categories: 0° (tail oriented
125 towards the road verge), 90°-270° (parallel to the road verge) and 180° (head facing the
126 road verge). I measured the distance to the verge to the nearest 1 cm. Canopy height and
127 width of shrub species most commonly used by nightjars (see 3.1) were highly
128 positively correlated ($r = 0.96$, $P < 0.0001$), so I took plant height measurements (to the
129 nearest 1 cm) as a proxy for the structural profile of vegetation. I characterized the
130 roadside vegetation closest to each foraging nightjar (i.e. selected site) and at 160
131 random sites (i.e. randomized kilometric points to the nearest 0.1 km) along the road
132 circuit. The mean height of the two tallest plant stands within a 1.5-m radius of selected

133 sites was averaged to ascertain the structural profile of the adjacent vegetation. To
134 explore nightjar use of plant communities, I identified all individual plants to species
135 level in both selected and random sites. To assess microhabitat selection, the structural
136 and qualitative differences between selected (i.e. microhabitat use) and random sites
137 (i.e. microhabitat availability) were analyzed.

138

139 *2.3. Experimental procedures*

140 Predation attempts are typically rare in nature, and experimental manipulations are
141 therefore necessary to assess the escape abilities of birds (Boland 2003). During the
142 course of vehicle transects, I opportunistically witnessed three actual (2 by foxes and 1
143 by swine) attacks on road-sitting nightjars. Foxes approached to within 1–2 m of the
144 birds from behind, remained motionless for a few seconds, and then suddenly attacked.
145 However, the high (and dense) roadside cover behind the nightjars forced foxes to jump
146 over vegetation, enabling birds to react readily to attacks and escape. Similarly, the
147 attempt by a wild pig *Sus scrofa* also failed because roadside vegetation forced the
148 predator to noisily go through vegetation, thus enabling the nightjar to immediately
149 detect and successfully evade the attack. To experimentally assess the escape efficiency
150 of nightjars relative to vegetation structure, human 'predators' (the author and two
151 experienced field assistants) simulated 65 attacks from the birds' rear (which forced us
152 to avoid vegetation in the road verge) and from the birds' front (where there were no
153 obstacles along the bare road surface). The attack sequence was designed to mimic real
154 (witnessed) predation attempts on road-sitting nightjars, after checking that the escape
155 response elicited by approaching humans was similar to that elicited by real terrestrial
156 predators. Thus, I am confident that the use of humans to simulate attacks was suitable
157 to obtain a reliable estimate of the effect of cover on nightjar escape efficiency. All

158 simulated attacks were conducted between 23:00 h and 2:00 h during the course of car
159 transects in July 2012. Humans quietly approached the birds on foot prior 'attacking'
160 from 1-2 m from the bird. We used an 80-cm diameter butterfly net to 'catch' birds so as
161 to not injure them. To avoid the net becoming entangled in vegetation, and thus
162 ensuring that attacks in the open had the same chance of success as in the cover, the net
163 was never casted but we always held it above the backing vegetation until flushing or
164 trapping the bird on the bare ground. As premature detection of the 'predators' by prey
165 would undermine the validity of experimental attacks, we used a LED torch in the two
166 contexts (with and without plant barrier) and hid ourselves behind the light beam. The
167 use of LED light as a camouflage device did not appear to reduce the escape abilities of
168 nightjars, as subtle noises from footsteps are generally enough to cause dazzled birds to
169 flush (Jackson 2003; pers. obs). Capturability of nightjars could be unequal among age
170 classes, so recently-fledged and juvenile birds were omitted from the experiment. Data
171 on radiotagged nightjars in the study population reveal that adult individuals often
172 forage along the same stretch of road (<200 m length), usually near the nest (Camacho,
173 Palacios and Sáez, unpublished data). For this reason, predation attempts were
174 conducted at least 300-m apart to ensure that the same individuals were not tested twice.
175 I defined trapping success (%) as a measure of the escape efficiency of nightjars in
176 relation to microhabitat architecture.

177

178 *2.4. Statistical analyses*

179 To assess habitat selection, I tested for structural differences between selected and
180 random sites using a Generalized Linear Model (GLM) with Poisson error distribution
181 and log link function. The model included vegetation height as the dependent variable
182 and site type (class variable: selected and random) as a fixed effect. Foraging sites were

183 sometimes found in close proximity (within 20 m). Since nearby sites were almost
184 certainly not independent, I only considered the closest one (i.e. encountered first along
185 the route) to reduce pseudoreplication and stops to collect data often caused other
186 nearby birds to flush. Mean vegetation height (but not species composition) of the road
187 verge plant community was not significantly different between the managed and the
188 protected area ($F_{1,159} = 0.16$, $P = 0.69$), so I pooled data from the two study plots for
189 structural analyses. To determine fine-scale habitat selection with regard to the
190 adjoining vegetation cover, I used the Wilcoxon signed rank test (T). I applied Chi
191 square tests (χ^2) to test whether birds positioned randomly or selected particular plant
192 species and also to evaluate the trapping success in experimental attacks. I undertook all
193 statistical analyses using the software package R (version 2.15; R Core Team 2012).
194 Differences were considered to be significant at $P < 0.05$.

195

196 **3. Results**

197 Data on microhabitat selection by foraging nightjars included 312 field observations
198 (170 and 142 in the managed and the protected area, respectively). I characterized the
199 structural profile of 209 foraging sites noted to be used by nightjars, 38 of which (18%)
200 were consistently used (2–7 times) by the same or different individuals (≤ 4 birds).

201

202 *3.1 Effect of vegetation cover*

203 The direction nightjars oriented on roads was not random. Most individuals ($>75\%$, $n =$
204 209) sat <50 cm from the road verge (mean \pm SD = 35.1 ± 32.1 cm), and nearly all
205 (95.7%) faced away from the verge ($\chi^2_1 = 89.65$, $P < 0.0001$). Nightjars actively
206 selected particular foraging sites according to the architecture of nearby vegetation:
207 despite the low ($<25\%$) availability of tall (>120 cm) and medium height plant stands in

208 either area, birds settled near tall stands (mean \pm SD, selected sites: 159.9 ± 102.9 cm;
209 random sites: 66.6 ± 102 cm; $F_{1,368} = 7\ 060.2$, $P < 0.0001$; Fig. 1). Microhabitat
210 selection also occurred at finer scales, with most individuals (76%) choosing taller plant
211 stands than available in the immediate surroundings ($T = 16\ 518.5$, $n = 209$, $P <$
212 0.0001). In contrast to the managed property, where no selection of particular plants was
213 detected ($\chi^2_{19} = 24.8$, $P = 0.17$), nightjars in the protected area actively sat nearby tall
214 dense stands of *Juniperus phoenicea*, but avoided the medium-height stands of
215 *Rosmarinus officinalis* ($\chi^2_{19} = 54.61$, $P < 0.0001$).

216

217 3.2 Attack experiments

218 High dense plant stands commonly used by foraging nightjars hindered human
219 predators from launching silent precise attacks, so the escaping efficiency of nightjars
220 sitting near cover was significantly higher (96%, $n = 25$ attacks) compared to that in
221 attempts by subjects facing no obstacles when approaching the prey (7.5%, $n = 40$
222 attacks; $\chi^2_1 = 47.80$, $P < 0.0001$; Fig. 2). The most common escape mode consisted of a
223 rapid short flight upward just before the human predator attacked, but some escaping
224 birds remained fluttering above for a few seconds.

225

226 4. Discussion

227 Red-necked nightjars exhibited microhabitat choice based on the architecture of
228 vegetation, which also influenced the body positioning behaviour within foraging sites.
229 During their peak activity, foraging microhabitats provided nightjars with overhead
230 cover that increased their chances of escape from approaching human predators and,
231 assuming that humans and predators elicit similar responses, therefore likely also from
232 real predator attacks.

233 Besides the availability and energetic value of prey and the density of
234 competitors, the risk of predation is a major factor contributing to selection of foraging
235 sites by prey (e.g. Ekman, 1986; Rosenzweig, 1987; Lima, 1990; Suhonen, 1993 a,
236 1993b). Feeding and vigilance are mutually exclusive activities, which often leads to a
237 higher vulnerability to predators as foraging activity increases (Lima and Dill, 1990). In
238 daylight, roosting nightjars exhibit secretive behaviour and a strong preference for
239 substrates resembling their plumage to avoid detection by diurnal predators (Holyoak,
240 2001). However, foraging individuals not only reveal their highly visible wing and tail
241 bands (i.e. increased signalling), but their cryptic coloration may not always match the
242 background of roads (i.e. reduced plumage crypsis), thus increasing conspicuousness to
243 predators (Aragonés et al., 1999). In addition, nightjars sitting on the ground might
244 allow terrestrial predators to detect and access them in a relatively easy way (Doucette
245 et al., 2011). At my study site, red foxes positively select roads (Suárez-Esteban et al.,
246 2013) so, under the assumption that attack probabilities following an encounter are
247 equal both near and far from roads, use of roads by nightjars probably translates into
248 increased likelihood of fox attack therein during the night. In this scenario, the nightjar-
249 'plant screen' association might function as a solid barrier to (human and possibly fox)
250 predation attempts. By facing away from the road verge and sitting nearby (but not
251 under) tall dense cover, nightjars may reduce the likelihood of fox predation in two
252 different ways. First, the 'plant screen' would restrict the number of direct attack routes
253 (i.e. with no obstacles) to those from the open road, facilitating an early detection of
254 approaching predators. Second, the roadside cover would force foxes to jump over the
255 'plant screen', providing a head start for nightjars to escape to the open. Thus, nightjars
256 seem able to manage their overall risk of death within preferred foraging habitats,

257 suggesting that selection of foraging sites by nightjars is more based on the chance of
258 escaping predators than on the risk of encountering them (see Lima, 1992).

259 Experimental attacks indicated that 'plant screens' significantly increased the
260 aerial escape abilities of nightjars from simulated attacks. However, due to conscious or
261 unconscious bias from observers, some caution is required in extrapolating the escape
262 response to human approaches to the responses to real attacks. The strongest inference
263 could have been made by comparing the behaviour of the same individual in the two
264 contexts, but this was unfeasible with free-ranging individuals. It is likely that the
265 nightjar-'plant screen' association evolved long before the advent of the automobile,
266 when cattle, horse and camel trails acted as the 'natural' counterpart of roads (see
267 Jackson 2003 and references therein). Therefore, due to facilities for access and animal
268 detection, roads represent a reasonable way to assess birds' behaviour. Although the
269 experimental results are suggestive, data in this study do not rule out other plausible
270 explanations influencing the evolution of microhabitat use by nightjars. Visibility,
271 thermal properties or availability of sheltering sites have been proposed as alternative
272 explanations that I will briefly discuss below.

273 It is well known that reduced visibility strongly affects the foraging behaviour of
274 nightjars (Mills, 1986; Jetz et al., 2003; Ashdown and McKechnie, 2008). Along roads,
275 visibility for ground-sitting individuals is conditional to road width and the cover height
276 on either road verge (Jackson, 2003). Birds sitting on an open road are certainly in a
277 favoured position to detect and hawk flying insects silhouetted against the twilight sky.
278 But if visibility were the main factor determining nightjars' choice of foraging sites,
279 then the highest bird numbers should be expected to be found in the open, with no side
280 vegetation or canopy above. Despite the tendency for the abundance of several
281 Afrotropical caprimulgids to increase with a greater arc of sky visible, most birds

282 encountered by Jackson (2003) during a field survey on roads viewed only half the sky,
283 since vegetation partially covered one of the road verges. Therefore, consistent with
284 Jackson (2003) and my own results, enhanced visibility alone does not explain the
285 birds' choice of structural attributes during the night.

286 Birds may also accrue thermal benefits from microhabitat selection (Wolf and
287 Walsberg, 1996; Wolf, 2000). Red-necked nightjars are attracted towards the warmth of
288 paved roads when the air temperature drops substantially (Camacho, 2013) suggesting
289 that microhabitat choice could have been influenced by thermoregulatory requirements
290 during cold weather. Different shading of gravel and paved roads during daylight would
291 slightly affect the temperature of surfaces at night and, hence, foraging site choice.
292 However, mean cover height does not differ between surface types in the study area
293 and, consequently, I dismissed the possibility that the observed use of microhabitats was
294 driven by thermoregulatory constraints (Camacho, 2013).

295 Anecdotal observations supported the role of plant cover as protective barriers
296 for road-sitting nightjars. The three real attacks I opportunistically witnessed
297 resoundingly failed, as the obstruction provided by vegetation enable all nightjars to
298 react readily and evade the attacks. Some of the foraging sites repeatedly used by
299 different individuals could be the consequence of the low availability of sheltering sites,
300 but might also indicate that nightjars perceive certain vegetation attributes as offering
301 better protection than others (i.e. plant height and appearance vs. plant species).
302 Composition of vegetation itself was not crucial for selection of foraging sites, as the
303 preference for *Juniperus phoenicea* trees and saplings in the protected area is likely
304 attributable to their tall height and dense appearance affording birds increased
305 protection.

306 The nightjars' tendency to face the open and sit at short distances from the
307 vegetation probably relates to increasing both safety and foraging opportunities (Lima,
308 1990). Ground hunting perches in the roadside afford nightjars increased aerial escape
309 options and, at the same time, broaden the field of view to detect prey (Jackson, 2003)
310 and predators (Amat and Masero, 2004). Therefore, the interplay between selective
311 forces appears to be the most likely mechanism underlying the evolution of nocturnal
312 microhabitat choice by nightjars. Yet, the extent to which low predation risk or
313 relatively wide visibility have contributed to nightjar-plant associations is difficult to
314 judge.

315

316 **5. Conclusions**

317 Results of this study suggest that the success rate of attacks on foraging nightjars by
318 ambush predators would increase with no cover offering a means to facilitate aerial
319 escape. However, this study shows that the presence of a physical structure alone may
320 not necessarily provide complete protection from terrestrial predators, but the interplay
321 between predator-avoidance behaviours and habitat structure might result in an efficient
322 barrier against predators increasing survival when predators and prey coexist in high-
323 profitable habitats for prey. My findings lend support to the idea that prey would
324 actually match the distribution of the predators and highlight the role of predator
325 avoidance in the evolutionary ecology of habitat selection.

326

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336

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436 **Figure legends:**

437

438 **Fig. 1.** Range of vegetation heights available along road verges and red-necked
439 nightjars' preference for the height of the adjoining (<1.5 m) cover when perched on
440 roads.

441

442 **Fig., 2.** Escape efficiency (i.e. trapping success) of red-necked nightjars from
443 experimental nighttime attacks with protective ($n = 25$ attempts) and no protective ($n =$
444 40 attempts) vegetation cover.