

1 **Environmental factors influencing road use in a nocturnal insectivorous bird**

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22

23 **ABSTRACT**

24 Many animals avoid roads due to traffic disturbance, but there are also some species that use  
25 roads in their everyday life and even obtain resources from them. Understanding the factors that  
26 influence the intensity of road use by these species can help understand temporal patterns of  
27 road mortality and thereby maximize the cost-effectiveness of mitigation measures. Here, we  
28 use road transect counts conducted once a week for 9 consecutive years (2009-2017) to  
29 investigate environmental factors influencing road use in the red-necked nightjar (*Caprimulgus*  
30 *ruficollis*), a nocturnal insectivorous bird that frequents roads to forage and thermoregulate. We  
31 found that the intensity of road use by nightjars was affected by ambient temperature, amount of  
32 moonlight, and wind conditions – all factors known to influence their foraging efficiency and  
33 thermoregulatory requirements. Specifically, the highest numbers of nightjars on roads occurred  
34 during no-wind conditions and on either dark-cold or bright-warm nights, suggesting that they  
35 preferentially use roads for thermoregulation under unfavourable weather conditions or to  
36 maximize food intake during periods of increased insect abundance (i.e. warm nights) and  
37 improved conditions for visual prey detection (i.e. full moon). Our results illustrate the role of  
38 environmental conditions as drivers of rapid changes in the use of roads by animals.  
39 Furthermore, this work suggests that analogous studies can be used to inform mitigation  
40 measures, so that mitigation efforts to prevent roadkills can be concentrated during periods of  
41 expected peaks in animal use of roads.

42 **Keywords:** abiotic factors, context-dependence, habitat selection, red-necked nightjar, road,  
43 seasonality.

44

## 45 INTRODUCTION

46 Roads are a ubiquitous feature of the modern landscape and their ecological impact on wildlife  
47 is expected to increase over the next few decades due to the expansion of the road infrastructure  
48 (Laurance et al. 2014). Ecological effects of roads include road mortality, chemical pollution,  
49 dissemination of exotic species, intensification of human presence, habitat fragmentation, and  
50 modification of animal behaviour, among others (reviewed by Forman and Alexander 1998;  
51 Trombulak and Frissell 2000; Coffin 2007). Behavioural modifications in response to roads are  
52 taxonomically widespread and often involve changes in the habitat use and movement patterns  
53 of individuals (Shine et al. 2004; Shepard et al. 2008; Chen and Koprowski 2016). Most often,  
54 animals avoid road environments from a distance due to vulnerability to traffic, such as noise  
55 and lighting (Buchanan 1993; McClure et al. 2013). Behavioural avoidance of roads may also  
56 occur independently of traffic because of reluctance to cross open areas (Ford and Fahrig 2008;  
57 D'Amico et al. 2016) or an aversion to the road surface itself (Shine et al. 2004; McGregor et al.  
58 2008). However, not all animals avoid roads and, although positive effects of roads on wildlife  
59 have been identified (reviewed by Fahrig and Rytwinski 2009; Rytwinski and Fahrig 2013),  
60 they have received comparatively little attention.

61 Many species, from reptiles to birds and mammals, use roads and even benefit from  
62 them depending on their vulnerability to road mortality. For example, small mammals  
63 unaffected by traffic disturbance may benefit from roadside environments due to reduced  
64 predation by road-affected predators (Fahrig and Rytwinski 2009). Roads can act as corridors  
65 that facilitate the movement of terrestrial and aerial animals, from butterflies and birds to  
66 rodents and carnivores (Haddad et al. 2003). Furthermore, some species may be attracted to  
67 roads for a resource. For instance, snakes in temperate regions use the road surface as a  
68 mechanism for thermoregulation (Sullivan 1981, but see Shine et al. 2004), and scavengers and  
69 raptors frequent roads because of the availability of road-killed animals (Dean and Milton  
70 2003). But the relationship between animals and roads is rarely as strong and multifaceted as  
71 that of some caprimulgids, a cosmopolitan family of nocturnal insectivorous birds.

72 Nightjar (family Caprimulgidae) attraction to roads has long fascinated ecologists and  
73 some research efforts have been made in North America, Europe and Africa to understand the  
74 reason for this intriguing behaviour (e.g. Poulin et al. 1998; Jackson 2003; Camacho 2013a).  
75 From these studies, it is clear that there is no single explanation. Nightjars are sit-and-wait  
76 foragers and routinely use the clean surface of roads as an observation platform to improve  
77 detection of flying prey (Jackson 2003). Moreover, the open space above roads allows nightjars  
78 to safely launch into the air in pursuit of flying insects (Jackson 2003). Nightjars may also pick  
79 up beetles and crickets directly from the road surface and, importantly, roads can act as a source  
80 of grit material that facilitates the mechanical digestion of their exoskeletons (Jenkinson and  
81 Mengel 1970). However, roads can serve other non-foraging functions, such as dust bathing on  
82 sandy stretches (Abdulali 1948), thermoregulation on a surface that remains warmer than the  
83 surroundings (Camacho 2013a) and a courtship and/or mating platform (Sáez and Camacho  
84 2016). Finally, foraging nightjars in predator-rich environments regularly use the roadside  
85 vegetation as a physical barrier to increase their chance of escaping attacks from terrestrial  
86 predators (Camacho 2014; Evens et al. 2018).

87 Not surprisingly, the extensive use of roads makes nightjars extremely vulnerable to  
88 road mortality to the extent that road traffic is the most common cause of non-natural mortality  
89 in caprimulgids (Jackson and Slotow 2002; Camacho 2013a). Nevertheless, previous studies  
90 conducted in tropical and temperate regions indicate that nightjar numbers on roads may  
91 fluctuate over time (Ashdown and McKechnie 2008; Camacho 2013b), and so may the risk of  
92 road mortality (Mizuta 2014). Detailed knowledge on the factors affecting road-use behaviours  
93 in species that obtain resources from them is necessary to understand variation in the risk of  
94 traffic-induced mortality and thus inform mitigation efforts.

95 Here we used road transect counts of red-necked nightjars (*Caprimulgus ruficollis*)  
96 conducted for 9 consecutive years (2009-2017) to assess whether environmental factors  
97 influence their road-use behaviour. Every night, red-necked nightjars ('nightjars' hereafter)  
98 travel from their nesting and roosting sites to nearby gravel and paved roads to forage,

99 thermoregulate, and evade predation (Camacho et al. 2014). However, previous studies indicate  
100 that road affinity changes over time and that some factors influencing the foraging efficiency  
101 (i.e. moonlight, temperature and wind) and thermoregulation patterns (i.e. temperature, rainfall)  
102 of nightjars can determine their abundance on roads independently of seasonality (Ashdown and  
103 McKechnie 2008; Camacho 2013a; Camacho et al. 2014). Compared to other long-distance  
104 migrants, nightjars spend a disproportionately long period (7 months) on the breeding grounds  
105 in seasonal habitats of North Africa and the Iberian Peninsula (Cleere 2010; Camacho 2013b).  
106 Nightjars must therefore face a wide range of environmental conditions, which provides an  
107 excellent opportunity to investigate the context dependence of road-use behaviours. We  
108 hypothesized that nightjars would adjust their road-use behaviour to current environmental  
109 conditions to reduce energy expenditure for thermoregulation and/or increase food intake rates.  
110 Nightjars should therefore use roads more on cold nights, especially under poor conditions for  
111 detection and capture of aerial insects (i.e. insufficient lunar illumination and strong wind),  
112 and/or during periods of presumed high insect abundance (i.e. warm nights) and good foraging  
113 conditions (i.e. full moon, calm nights) (Table 1). Second, we hypothesized that nightjar  
114 numbers on roads would fluctuate not only on a seasonal basis, but also on a weekly or even  
115 daily basis due to changes in environmental conditions. To test these hypotheses, we examined  
116 the relationship between the number of road-sitting nightjars and physical aspects of the  
117 environment, including moonlight, temperature, humidity, and wind conditions.

118

## 119 **METHODS**

### 120 *Study area*

121 We carried out fieldwork in a 2000-ha area of the Doñana Natural Park, SW Spain (37°7'N,  
122 6°33' W). Many aspects of the movement ecology and habitat selection of nightjars have been  
123 studied in the study area over the past decade (e.g. Camacho 2013a, b; Camacho et al. 2014,  
124 2017). Because this study focuses on nightjar use roads, the sampling area consisted of a 24-km

125 network of paved (7 km) and gravel (17 km) roads crossing a mosaic landscape of sparse  
126 Mediterranean shrublands, cattle-grazed grasslands, and pine tree plantations (see Camacho  
127 et al. 2014 for a detailed description of the study site). Human access is not allowed, except for  
128 scientific research, small-game hunting, and livestock management; therefore, traffic density  
129 ranges from limited (<10 vehicles/day) to negligible (<1 vehicle/night). The lack of traffic  
130 disturbance, together with the high abundance of road-sitting nightjars (up to 3 birds/km) and  
131 the regular road layout (3.5–4 m wide), provide an excellent set up for assessing road-use  
132 responses of birds to changing environmental conditions.

### 133 *Field procedures*

134 We conducted road transect counts on a weekly basis between July and October of 2009-2010  
135 and April and October of 2011-2017, which encompasses the early arrival and late departure  
136 dates of nightjars (Camacho 2013b). Nightjars use gravel and paved roads alike, although their  
137 relative numbers on each surface may change depending on ambient temperature (Camacho  
138 2013a). Nocturnal censuses began 1–2 h after sunset from fixed starting points by driving a  
139 vehicle at a constant speed of 30 km/h until the full route was completed in both directions  
140 (Camacho 2013a). Nightjars sitting on roads can easily be located by their eye-shine using the  
141 headlights of the car on full beam, as nearly all of them (> 95%) sit perpendicular to the road  
142 axis (Camacho 2014). Nightjars occur in the study area only during the dry season and,  
143 therefore, we undertook all counts on clear nights (< 30% cloudiness and no rain). Censuses  
144 were also limited to nights with low (< 10 km/h) wind speed due to methodological constraints  
145 imposed by other studies conducted at the same time (e.g. Camacho 2013a; Camacho et al.  
146 2014).

### 147 *Meteorological data*

148 Nightjars use roads mainly for foraging and thermoregulation (Jackson 2003), as confirmed in  
149 our study population by direct observation and telemetry data (Camacho 2013a, Camacho et al.  
150 2014). Therefore, we considered abiotic factors known to influence the thermal requirements

151 and foraging efficiency of caprimulgids (Jetz et al. 2003; Ashdown and McKechnie 2008;  
152 Camacho 2013a; English et al. 2018; see Table 1). We took meteorological information from  
153 the two nearest meteorological stations around the study site. Data on daily mean, maximum  
154 and minimum air temperature were taken from the Doñana Biological Reserve  
155 (<http://icts.ebd.csic.es>), located 17 km from the study site. Data on mean, maximum and  
156 minimum humidity, as well as wind speed, were taken from the IFAPA agro-climatic station of  
157 the Andalusian Regional Government  
158 (<https://www.juntadeandalucia.es/agriculturaypesca/ifapa/web/>), located 6 km from the study  
159 site. To assess the effect of moonlight conditions, we calculated the proportion of the lunar disk  
160 illuminated each night using the R package ‘lunar’ (Lazaridis 2014).

### 161 *Statistical analyses*

162 All analyses were performed using the R environment (R Development Core Team, 2017). We  
163 reduced the initial dataset was reduced from 8 to 4 variables (Table 1) after checking for  
164 interrelations between them using a Farrar-Glauber Test (F-G test). To evaluate the  
165 environmental correlates of nightjar abundance on roads, we used a Linear Model (LM) with  
166 normal distribution for errors and identity link function. We included nightjar abundance  
167 (birds/km) as the response variable in the model after square-root transformation to meet  
168 assumptions of normality. Our covariates were moonlight, minimum air temperature, wind  
169 speed, and maximum humidity. Moonlight and thermal conditions are considered as major  
170 environmental determinants of the foraging efficiency and energetic requirements of nocturnal  
171 aerial insectivores (Jetz et al. 2003; Ashdown and McKechnie 2008; Camacho 2013a), so it is  
172 possible that the interplay between them influences the foraging activity and road-use behaviour  
173 of nightjars. To examine this possibility, we included in the model the interaction between  
174 moonlight and minimum air temperature as a fixed effect. Finally, we also included in the  
175 model week number (week 1 = 4-10 January) and its quadratic to control for seasonal changes  
176 in nightjar numbers due to their migratory behaviour. Examination of the data from the subset  
177 of nightjars captured for other purposes in the study area (e.g. Camacho 2013b, Camacho et al.

178 2014) revealed no differences in the number of males and females using roads (unpubl. data),  
179 suggesting that any effect of environmental factors may be uniform across the sexes. Data from  
180 9 different years were pooled, as a comparison between models including and excluding the  
181 term ‘year’ as a random effect revealed no confounding effects of year-specific conditions  
182 (Likelihood ratio test,  $\text{Chi} = 2.229$ ,  $\text{d.f.} = 1$ ,  $\text{P} = 0.135$ ).

183 To avoid misleading conclusions based on statistical artefacts, we performed diagnostic  
184 statistics (e.g. inspection of residuals plotted against predicted values and examination of  
185 influential data points and interrelations between predictor variables). None of these showed  
186 obvious deviation from the assumptions of normality and homogeneity of residuals or revealed  
187 influential cases or outliers, confirming model stability.

188

## 189 **RESULTS**

190 From 2009 to 2017, we conducted a total of 218 transect counts. Nightjar abundance varied  
191 substantially throughout the breeding season, ranging from 0.04 to 3.61 birds/km in April and  
192 August, respectively. Environmental factors also varied widely throughout the study period, as  
193 shown in Table 1.

194 Multiple physical aspects of the environment affected nightjar use of roads, but the  
195 direction and strength of this effect varied among variables (Table 2). Nightjars responded  
196 negatively to wind speed, to the extent that an increase in wind speed of 3 km/h resulted in a  
197 41,5% decrease in nightjar abundance on roads (Figure 1). Moonlight also affected the spatial  
198 behaviour of nightjars with respect to roads, but the statistical significance of the moonlight  $\times$   
199 minimum temperature interaction indicated that this effect varied depending on the thermal  
200 environment (Table 2). Specifically, under new moon conditions, nightjar abundance decreased  
201 by 41.5% as temperature increased from 5 to 23°C, while this temperature change resulted in a  
202 17.6% increase in nightjar abundance under full moon conditions (Figure 2). We found no  
203 effect of environmental humidity (Table 2).

204 **DISCUSSION**

205 By monitoring a red-necked nightjar population from arrival at the breeding grounds to autumn  
206 departure over nearly a decade, we provide evidence for context-dependent use of roads by  
207 nightjars. The number of nightjars sitting on roads fluctuated markedly according to  
208 environmental conditions, independently of seasonality. Moonlight, minimum temperature and  
209 wind speed jointly explained 41,5% of the variance in nightjar numbers on roads, suggesting  
210 that microhabitat use in this species is largely a function of extrinsic abiotic factors.

211 The effect of physical aspects of the environment on road use by animals, such as  
212 ambient temperature or light, has been previously reported for different taxa, from amphibians  
213 (Gravel et al. 2012) and reptiles (Sullivan 1981) to mammals (Milling et al. 2017; Myczko et al.  
214 2017) and birds, including caprimulgids in tropical and temperate regions (Jetz et al. 2003;  
215 Ashdown and McKechnie 2008; Camacho 2013a) and several other diurnal and nocturnal birds  
216 (e.g. Whitford 1985, Mizuta 2014). These studies found a positive role for temperature and  
217 nocturnal light in the activity and behaviour of various bird species. Our results agree with these  
218 previous findings that both temperature and moonlight affect the road-use behaviour of  
219 nocturnal birds and furthermore reveal that the effects of abiotic factors are not as simple as  
220 previously thought (Table 2).

221 Moonlight and thermal conditions jointly influenced nightjar abundance on roads, as  
222 shown by the statistical significance of the temperature x moonlight interaction. Not  
223 unexpectedly, the highest numbers of nightjars on roads occurred on either dark-cold or bright-  
224 warm nights. Following the expected environmental effects on nightjar use of roads, several  
225 hypotheses can be advanced to explain this duality. For example, the use of roads on dark-cold  
226 nights could represent a thermoregulatory strategy. Measurements of the surface temperature of  
227 roads taken at the study site during cold spells indicate that, during the night, the thermal  
228 difference between roads and adjacent areas ranges from +3 to +4.5 °C (Camacho 2013a). By  
229 perching on a surface that is significantly warmer than the surroundings, nightjars can mitigate

230 heat loss and thereby reduce energy expenditure for thermoregulation during periods of food  
231 shortage and/or insufficient lunar illumination (Camacho 2013a). Furthermore, nightjars using  
232 roads in dark-cold nights may take the advantage of the aerial insects that tend to be attracted to  
233 the warmth of roads at night (Lehtonen 1972; Jackson 2003) and that can be scarce in cold  
234 environmental conditions (McGeachie 1989; Choi 2008).

235 Nightjar abundance also peaked on bright-warm nights. Clearly, thermoregulation  
236 should not be an issue during warm weather, suggesting that additional mechanisms must be  
237 operating. For instance, nightjars might find it easier to spot insects silhouetted against the  
238 background skylight on moonlit nights (Jackson 2003). Many caprimulgids indeed exhibit the  
239 most intense foraging behaviour under good conditions for visual prey detection (Jetz et al.  
240 2003; Ashdown and McKechnie 2008), supporting the role of moonlight intensity in  
241 determining road-use behaviours in nightjars. Food supply might also account for the observed  
242 pattern. Aerial insect abundance may fluctuate considerably over short periods of time, although  
243 typically peaks in warm weather (McGeachie 1989; Choi 2008). Nightjars could thus maximize  
244 their food intake by increasing their foraging activity –and, hence, their occurrence on roads–  
245 during periods of increased insect abundance (i.e. warm nights) and improved conditions for  
246 visual prey detection (i.e. full moon).

247 Foraging nightjars also appear to be extremely sensitive to wind speed, as evidenced by  
248 the dramatic decrease (40%) in nightjar abundance on roads as a result of a slight increase  
249 (3km/h) in wind speed. Conceivably, the use of open and exposed surfaces in windy nights  
250 could be thermoregulatory inefficient compared to other more closed habitats adjacent to roads,  
251 like scrublands or pine tree plantations (Bakken 1991). Dramatic effects of wind in terms of  
252 thermoregulation have been previously noted, for instance, in small passerines, for which an  
253 increase in wind speed of 9 km/h can lead to an increase of up to 14% in thermoregulatory costs  
254 (Wolf and Walsberg 1996). Second, aerial insectivorous like nightjars foraging in windy  
255 conditions may experience major insect-hunting difficulties, not to mention that insect  
256 availability may also decrease substantially (Teather 1992; Møller 2013).

257 Overall, our results suggest that nightjars use roads either as a thermally favourable  
258 microhabitat that enables them to conserve energy under poor foraging conditions, or as a  
259 profitable foraging area to maximize food intake under optimal conditions. However, due to the  
260 correlative nature of this study, further experimental evidence is needed to unambiguously  
261 elucidate the mechanisms driving variation in road use. In addition, the spatial behaviour of  
262 nightjars may be affected by physical factors other than those considered here, such as  
263 cloudiness (Ashdown and McKechnie 2008). Biotic factors might also account for the 58% of  
264 the variance not explain by the measured variables. For instance, predation risk could influence  
265 the spatial decisions of foraging nightjars (Lima and Dill 1990; Lima 1998). However, the risk  
266 of predation on the surveyed roads rarely changes at time scales as short as a few days or weeks  
267 (Camacho et al. 2017). Fluctuations in the availability of both flying insects (e.g. moths and  
268 lacewings) and other prey occasionally consumed by nightjars (e.g. beetles and crickets) could  
269 also shape their road use behaviour, but there are no data available to examine this possibility.  
270 Future studies in which the availability of different potential prey is measured on roads and out  
271 roads would clearly allow stronger inference as to microhabitat use by nightjars.

272 It is also known from previous telemetry and observational studies in this population  
273 that not all individuals use roads to the same extent, and that this difference is unrelated to nest  
274 proximity to roads (Camacho et al. 2014). It is not known, however, whether individuals  
275 differing in road affinity respond differently to physical environmental conditions. Differences  
276 in road affinity between individuals might relate to their dominance rank, age class, sex,  
277 physiological state, or personality, but a full understanding of the continuum of road use  
278 behaviours is still lacking. Future research on individual variation in road affinity may open  
279 new avenues for research into the role of roads as a selective force, as individuals killed by  
280 vehicles may not be a random sample of the population.

281 In summary, we illustrate the role of environmental conditions as drivers of rapid  
282 changes in the use of roads by a bird species severely affected by roadkill mortality. Even  
283 though these particular findings may not apply to all systems, they strongly suggest that

284 research on context dependency in road use can be used to inform mitigation measures so that  
285 regional resources and efforts to prevent roadkills can be concentrated during periods of  
286 expected peaks in animal use of roads.

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- 398 Wolf BO, Walsberg GE (1996) Thermal effects of radiation and wind on a small bird and  
399 implications for microsite selection. Ecology 77:2228-2236.

400 Table 1. Description of the abiotic factors considered in the present study. The ‘Range’ column summarizes variation for each variable throughout the  
 401 study period, while the remnant fields summarize the effect (positive, negative or neutral) of each variable on thermoregulatory costs, prey availability,  
 402 and prey detection of red-necked nightjars.  
 403

<b>Variable</b>	<b>Range</b>	<b>Thermoregulatory costs</b>	<b>Prey availability</b>	<b>Prey detection</b>	<b>References</b>
Minimum temperature (°C)	5-23	-	+	0	Camacho 2013a; McGeachie 1989; Ashdown & McKechnie 2008; Choi 2008
Maximum humidity (%)	58.4-100	+	0/+	0	Choi 2008; Lin et al. 2005
Moonlight (% of visible disk)	0-100	0	0	+	Ashdown & McKechnie 2008
Wind speed (km/h)	0.6-3.6	+	-	-	Wolf & Walsberg 1996; McGeachie 1989; Choi 2008; Møller 2013

404 Table 2. Results of the LM examining the effect of environmental variables on red-necked  
 405 nightjars abundance on roads, measured as birds/km. Note that week and quadratic week are  
 406 included in the model to account for seasonal variation in nightjar abundance due to their  
 407 migratory behaviour. Model statistics:  $F = 22.8$ , d.f. = 7, adjusted  $r^2 = 0.412$ ,  $P < 0.001$ .  
 408

	<b>Estimate</b>	<b>SE</b>	<b>t</b>	<b>P</b>
(Intercept)	-2.979	0.412	-7.226	<0.001
Minimum temperature	-0.069	0.040	-1.735	0.084
Maximum humidity	0.000	0.021	0.004	0.997
Moonlight	0.024	0.054	0.437	0.663
Wind speed	-0.102	0.026	-3.900	<0.001
Week	0.285	0.029	9.747	<0.001
Quadratic week	-0.005	0.000	-9.682	<0.001
Minimum temperature × Moonlight	0.129	0.056	2.313	0.022

410 **Figure legends:**

411

412 Figure 1: Effect of wind speed (standardized) on red-necked nightjar abundance on roads. The  
413 plotted points correspond to the fitted values of the model, and the shaded area denotes the 95%  
414 confidence interval of the regression slope.

415

416 Figure 2: Effect of the interplay between minimum air temperature and moonlight (estimated as  
417 the percentage of the moon's visible disk illuminated) on red-necked nightjar abundance on  
418 roads.