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1 **Diel cycle in a farmland bird is shaped by contrasting predation and human pressures**

2

3 **Running title:** Diel cycle of grey partridge under multiple risks

4

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25 **Abstract**

26 In human-dominated landscapes, human disturbances may contrast (spatially and/or
27 temporally) with risk imposed by non-human predators. However, how prey adjust behaviour
28 to minimize risk from multiple threats remains unclear. In Central-Western France, we
29 investigated patterns of activity, space and habitat use, and causes of variations during the diel
30 cycle of the grey partridge (captive-reared, released), a farmland bird facing multiple risks
31 (nocturnal predation, diurnal hunting pressure). We also investigated influence of individual
32 space use, relative to risk-related features on the fate of birds. Birds adjusted their behaviours
33 in ways consistent with the reduction of risk from nocturnal carnivores at night and hunters
34 during daytime. We recorded bimodal crepuscular activity, likely explained by commuting
35 movements between spatially-separated diurnal and nocturnal sites composed of different
36 habitats: selection of open terrains and avoidance of predator reservoirs at night *versus* use of
37 high-vegetation cover during daytime. We observed space use differences between surviving,
38 hunted and predated birds. Predation and hunting activities act as contrasting pressures,
39 selecting birds based on their spatial behaviour, which has likely shaped diel adjustments at
40 the population level. An improved consideration of temporal variation in environmental
41 pressures would help to reliably address factors constraining populations, so increasing
42 wildlife management efficiency.

43

44 **Key-words:** Diel activity, Global Positioning System, Grey partridge, Habitat selection,
45 Space use, Survival

46 **Introduction**

47 Predation risk and resources are heterogeneously distributed within landscapes (Johnson *et*
48 *al.*, 1992). To fulfill their daily biological requirements, animals must therefore move and
49 adjust their behaviour, trading costs (predation risk, antipredator investment) and benefits
50 (e.g. feeding, resting) (Lima & Dill, 1990). Behavioural adjustments in activity, space and
51 habitat use, are among the most common responses allowing prey to account for variations in
52 predation pressure, and so reduce their direct mortality risk (Lima & Dill, 1990; Lone *et al.*,
53 2015). Such behaviours can, however, carry fitness costs to individuals (Creel & Christianson,
54 2008): some prey respond to a high predation risk by shifting periods of peak activity to
55 lower-risk periods (e.g. at twilight: Monterroso *et al.*, 2013) although this may result in
56 reduced food intake (Lima & Dill, 1990), or by altering their patterns of space and habitat use
57 to lower-risk areas or habitats (Moreno *et al.*, 1996), although these may be of lower-quality
58 (Béchet *et al.*, 2004). Understanding the effects of predation risk on prey is thus crucial, as the
59 outcomes on population dynamics can outweigh the direct effects of predation kills (Creel *et*
60 *al.*, 2005; Creel & Christianson, 2008). Although activity and space use of predators varies
61 during the day, hence affecting the spatio-temporal distribution of risk in prey (Laundré *et al.*,
62 2001), how this translates into behavioural shift by prey across the diel cycle has received
63 little attention (but see Lone *et al.*, 2017; Jucá *et al.*, 2020).

64 In human-dominated landscapes, human diurnal activity (e.g., agricultural field work,
65 outdoor recreational activities such as hiking, or hunting) may induce disturbances of an
66 intensity similar to that of predators, so shaping wildlife behaviour in ways similar to
67 predation risk (Frid & Dill, 2002; Gaynor *et al.*, 2018; Shamoan *et al.*, 2018). Such
68 cumulative human and non-human risks can, however, vary in their spatio-temporal
69 patterning. For example, Lone *et al.* (2014, 2015) found that risk imposed by hunting
70 disturbance on the European roe deer, *Capreolus capreolus*, occurring by day in open areas

71 (greater visibility and so easier shots, see also Ciuti *et al.*, 2012), both add to and contrast with
72 risks imposed by nocturnally-active predators (carnivores) in dense understory cover. This
73 may lead to risk enhancement in prey due to the overall impacts of conflicting antipredator
74 responses (e.g. Gehr *et al.*, 2018; Bonnot *et al.*, 2020). Indeed, prey response to one predator
75 may result in an enhanced risk of exposure to a second predator (Sih *et al.*, 1998), and thus
76 induce additional lethal and/or non-lethal predation effects on prey populations (Cresswell &
77 Quinn, 2013). In this context of multiple and contrasting risks in both space and time,
78 complex behavioural adjustments may be critical to avoid the predator most active at a given
79 time (Lone *et al.*, 2017). However, empirical evidence of such adjustment processes (i.e. how
80 prey switch between predator-specific responses), and consequences for survival, remain rare
81 in vertebrates (Sih *et al.*, 1998; Cresswell & Quinn, 2013).

82 In farmland landscapes, predation risk by nocturnal carnivores is expected to be high
83 at night near habitats such as woodlands and built-up areas, which are carnivore reservoirs,
84 and along hedgerows and roads, which are carnivore corridors (Pereira & Rodríguez, 2010;
85 Krauze-Gryz *et al.*, 2012; Bischof *et al.*, 2019). The reverse is expected during daylight hours,
86 when open habitats should be more dangerous as a result of higher risk of being shot by
87 hunters, disturbed by agricultural work in open fields, or being target of diurnal birds of prey
88 (Moreno *et al.*, 1996). Here we investigated such behavioural adjustments in space and habitat
89 use across the diel cycle for an iconic gamebird species living in a farmland landscape: the
90 grey partridge, *Perdix perdix*. In addition to increased chick mortality caused by agricultural
91 intensification (Kuijper *et al.*, 2009; Gée *et al.*, 2018), this species has suffered increased
92 predation and shooting pressure over the last decades, with the latter two being identified as
93 two of the main proximal causes of population decline (Kuijper *et al.*, 2009; Aebischer &
94 Ewald, 2012). Main partridge predators are mammalian carnivores (involved in about 70% of
95 predation kills in France, Bro *et al.*, 2001, 2013), including red fox, *Vulpes vulpes*, (65-80%

96 of carnivore kills: Bro *et al.*, 2013), mustelids and the domestic cat, *Felis catus*, (Bro *et al.*,
97 2001; Buner & Schaub, 2008). All are mainly active at night (Pereira & Rodríguez, 2010;
98 Krauze-Gryz *et al.*, 2012). In contrast, human disturbance (agriculture, hunting) and raptor
99 predation risk occur mainly during the day (Moreno *et al.*, 1996; Gaynor *et al.*, 2018). The
100 latter is mainly attributed to the hen harrier, *Circus cyaneus*, hunting partridges in open cereal
101 plain of French agrosystems (Reitz & Mayot, 1999; Bro *et al.*, 2013; personal observation).
102 Despite recent and extensive work documenting the effect of predation on habitat selection
103 (Bro *et al.*, 2004; Rantanen *et al.*, 2010a; Harmange *et al.*, 2019), very little is known about
104 partridge behavioural adjustments to the multiple risks and how they vary across the diel
105 cycle.

106 Using individual-based GPS locations for the first time with grey partridge individuals
107 (captive-reared, released), we addressed the following questions: (i) given that night and day
108 predation risks differ, will the partridge, as a potential prey, adjust its activity patterns, i.e.
109 space and habitat use, accordingly?, and (ii) what are the consequences of space use patterns
110 for individual survival? Although we monitored naïve (captive-reared) birds, we expected to
111 observe immediate behavioural adjustments after release into the wild, as previously reported
112 in the current (e.g. in response to interspecific competition: Rinaud *et al.*, 2020) and other
113 species (Sih *et al.*, 2010; Reyna & Newman, 2018). We particularly expected that partridges
114 would adjust their space use according to spatio-temporal variation in predation risk, shifting
115 from selection of open habitat (or avoidance of carnivore-rich features) at night, to selection
116 of permanent and/or high-vegetation cover providing good refuges against human disturbance
117 (agriculture, hunting) and raptor predation risk during the day (Moreno *et al.*, 1996; Tillmann,
118 2009; Potts, 2012). The type of response to risky situations may, however, differ substantially
119 between individuals, based on their phenotypic traits and sensitivity or tolerance to stress
120 (Koolhaas *et al.*, 2007; Sih *et al.*, 2012) and, accordingly, result in differential survival (Ciuti

121 *et al.*, 2012; Lone *et al.*, 2015). We test this hypothesis by linking space use behaviour,
122 presence of risk-related landscape features in the surroundings, and partridge survival
123 expectancy.

124

125 **Material and methods**

126 Study site

127 The study was carried out from 2015 to 2018, on the Long-Term Socio-Ecological Research
128 (LTSER) platform « Zone Atelier Plaine & Val de Sèvre », *Département des Deux-Sèvres*,
129 Central Western France. Land-use of this 435km² site is dominated by intensive cereal
130 agriculture. Land-cover use has been exhaustively surveyed annually since 1994, and is
131 characterized by winter cereals (41.5%, mean value calculated over the years 2009–2016),
132 sunflower (10.4%), corn (9.6%), rape (8.3%), meadow (13.5%), woodlands (2.9%), and built-
133 up areas (9.8%) (Bretagnolle *et al.*, 2018). In the LTSER, the breeding density of raptors that
134 might prey upon grey partridge is relatively low: e.g. an average of 20 pairs of hen harrier for
135 450 km² (Millon *et al.*, 2002), 2 pairs of marsh harrier, *Circus aeruginosus*, a low density for
136 Eurasian sparrowhawk, *Accipiter nisus*, (no detailed count available, but very few forests
137 fragments), and extremely low for northern goshawk, *Accipiter gentilis*, (1-3 pairs in total).
138 The breeding density of common buzzard, *Buteo buteo*, is about 50-100 pairs for 450 km², but
139 the latter species' predation on grey partridge is anecdotal in France (Valkama *et al.*, 2005). In
140 winter, counts at roosts indicate that some 25-50 hen harriers are present.

141 Grey partridge density at the study site was very low (around 1 male/pair per 400 ha;
142 Harmange *et al.*, 2019). For recreational activity, game management associations have
143 therefore relied heavily on annual releases of captive-reared partridges (on average 250 birds
144 are released per 1700 ha, i.e. the mean area of a local municipality; Harmange *et al.*, 2019), as
145 is common in France (Bro & Crosnier, 2012). Locally in the LTSER, bird releases generally

146 take place in late August/early September, just before the onset of the hunting season in mid-
147 September. Standard game release protocol consists in the release of birds artificially reared
148 in commercial game farms: First, rearing farms receive 1-day-old chicks from egg production
149 farms (ca. 30 generations bred in captivity). Then, chicks are reared without parents, with an
150 approximate space of 3-6 square meters per bird. Finally, captive-reared birds are released at
151 the age of 19 to 21 weeks, to reach 21 to 23 weeks at the onset of the hunting season. In
152 addition, in France, hunting activity is usually organized at the local municipality scale, with
153 each of these having officially-regulated hunting societies (50 to 75 hunters in the LTSER), as
154 well as an obligation to designate non-hunting areas that, on average, constitute about 10% of
155 the municipal territory. Hunting activity occurs twice a week in the LTSER (Thursdays and
156 Sundays; Casas *et al.*, 2009) during daylight hours (from 1 hour before the sunrise to 1 hour
157 after the sunset). For partridges, the hunting season starts in mid-September and ends mid-
158 November thus resulting in 17 to 19 shooting days (depending on the year) over a two-month
159 period. However, partridge disturbance from hunting extends for 5 months and a half because
160 of shooting of other game species. The hunting quotas allow hunters to harvest a maximum of
161 three partridges per hunting day. However, estimating reliably hunting bags is complex, and
162 has been only partially addressed through national surveys in France performed every 10
163 years (e.g. Aubry *et al.*, 2016), but reliable records of hunting kills at the regional scale are
164 lacking. In the study region, since there is no hunting plan for any of the gamebird species,
165 and because of the absence of consistent schemes to report the hunting kills, there is no data
166 available on the number of birds harvested by hunters at the scale of local hunting societies.

167

168 GPS surveys

169 The first set of individuals were fitted with CatLog-S2 (Catnip Technologies Ltd, Hong
170 Kong), on their breast using a necklace (2015 and 2016). A second set consisted of birds fitted

171 with GPS trackers enabling remote data transmission (5 units of UvA-BiTS GPS-trackers,
172 www.uva-bits.nl, Bouten *et al.*, 2013, at Marigny in 2016; and 2 units of Milsar
173 GsmRadioTag-S9 units, www.milsar.com, at Marigny in 2017). These devices were fitted on
174 the backs of birds with a harness. Birds were also ringed with colour rings and an additional
175 alphanumeric metal gamebird ring. Total load was maintained below the recommended limit
176 of 5% of the bird weight (Kenward, 2001). Owing to the trade-off between maximizing
177 battery lifespan and obtaining more fixes, in 2015, the first year of monitoring, loggers were
178 programmed to switch-on 1 week before the hunting season onset (the dispersion phase was
179 not captured as birds were already out of pens), with 1 fix/30 min during daylight, and no
180 nocturnal data recorded. From 2016, the programming was adjusted so that all loggers turned-
181 on at the release time, recorded 1 fix/15 min during daylight, and 1 fix/hour at night (thus
182 giving a functioning unit lifespan of around 1.5-2 months). The 7 GPS transmitters were
183 initially programmed to record 1 fix/10 min during daylight, and 1 fix/30 min at night, and
184 were then remotely reprogrammed at a finer temporal resolution (up to 1 fix/5 min during
185 daylight, and 1 fix/15 min at night) when battery charge allowed.

186 Birds fitted with GPS were released in the areas of four different communal hunting
187 societies (Fig. 1). In 2015 and 2016, we fitted birds (174 and 138, respectively) that were
188 released for grey partridge shooting at Fors, Mougou and Prahecq (see Table 1 for the number
189 and sex ratio of birds released each year per site). All birds were released in flocks of 15 to 20
190 birds, between late August and early September, that is prior to hunting season
191 commencement. Around 60 birds were released per municipality, either placed in acclimation
192 pens (measuring ca. 5 m²) for 7 to 10 days (Fors and Mougou), or directly hand-released
193 without an acclimation phase (Prahecq; Table 1). Birds were either released all on the same
194 date (Prahecq, and in some release sites at Fors and Mougou), or sequentially at some pens
195 (releasing 2 birds per pen per day, as at some Fors and Mougou release sites). In Marigny,

196 where grey partridge shooting was suspended from 2016 to 2018, 131 birds were released in
197 mid-December 2016 and 179 in mid-September and in late October 2017. Birds were released
198 in flocks of 12-16 individuals (50% males and 50% females), with 6-8 tagged individuals per
199 flock. In each site, birds were all released at the same date after a 5-day acclimation phase (or
200 3-day when predator traces were observed around pens) in pens (of ca. 5 m²).

201

202 Data collection

203 Data loggers had to be recovered manually as they did not transmit the recorded fixes
204 remotely. In Fors, Mougou and Prahecq, devices were recovered by hunters mainly from
205 harvested partridges (hereafter called ‘hunted partridges’, see Appendix 1, Table S1). In
206 Marigny, since grey partridge shooting was suspended, few loggers were recovered by
207 hunters, and most recoveries came from recaptures carried out by the study team (hereafter
208 such birds are called ‘survivors’, Table S1). These birds were caught in cages (height 30 *
209 width 40 * depth 30 cm) baited with wheat and placed at known feeding sites and places
210 where opportunistic sightings of partridges had recently been reported by stakeholders (i.e.
211 hunters and farmers) or fieldworkers. If necessary, playback calls of territorial males were
212 also used to attract individuals. Finally, loggers opportunistically found (mainly by hunters
213 and farmers) on fresh carcasses of partridges showing predator traces (e.g. buried carcasses,
214 bite marks on carcasses or GPS devices, Parish & Sotherton, 2007) were considered as
215 predated (Rantanen *et al.*, 2010a) (Table S1). The time of death was estimated when possible
216 (with the precision of 1 hour), as the time of the fix record that preceded the bird movement to
217 the carcass location.

218 As GPS data inherently contains fixes with erroneous or inaccurate locations
219 (Bjørneraas *et al.*, 2010), we applied a filter on our data resulting in a reduction by ca. 4% of
220 the dataset (see Appendix 2 for filtering process details).

221
222 Statistical analyses
223 *Activity pattern*
224 Activity pattern was analyzed as distances between successive fixes (Bengtsson *et al.*, 2014).
225 As intervals between fixes were not consistent between night and day and between GPS types,
226 data were preliminarily standardized to 1 fix per hour. To do so, starting with the first location
227 for each bird after it left the pen, we filtered iteratively each fix recorded less than 57 min of
228 the previous one (mean time between successive fixes after filtering = 60.4 min \pm 1.6 SD). To
229 control for seasonal changes in daylight length from autumn to spring, we considered time as
230 deviation from times of dawn and dusk. Time deviations between GPS locations and
231 dawn/dusk were extracted using R package *suncalc* (Agafonkin & Thieurmél, 2018). We then
232 tested the effect of time on movement patterns using generalized additive mixed models
233 (GAMM, Gaussian response variable with a cubic regression spline smoothing, Wood, 2006)
234 with R package *gamm4* (Wood & Wood, 2015). *Individual identity (ID)* and *season* nested in
235 *year* were included as random factors.

236 Then, based on previous analysis of activity patterns, GPS fixes were divided into four
237 periods of homogeneous bird activity: dawn (from 45 min before to 75 min after dawn), day
238 (from 75 min after dawn to 45 min before dusk), dusk (from 45 min before to 75 min after
239 dusk), and night (from 75 min after dusk to 45 min before dawn). This periodicity was also
240 indicated by an activity study based on partridge vocal behaviour (Rotella & Ratti, 1988). To
241 test for differences in activity (i.e., distance travelled between successive fixes at 1-hour
242 intervals, log-transformed) according to these periods, we ran two linear mixed-effect models,
243 one for the morning and the other one for the evening. Time-period effect was assessed with a
244 likelihood ratio-test (i.e. χ^2). We used the R package *lme4*, and considered *individual ID* and
245 *season* nested in *year* as random factors.

246 Finally, to investigate whether birds conducted all daily activities in the same area or
247 whether they used different sites across the diel cycle, two complementary metrics
248 characterizing bird spatial activity were calculated. First, we assessed the mean distance
249 between the last diurnal and first nocturnal site at dusk. For each individual, and for each day,
250 the last diurnal site was determined as the location of the last grouped-fixes of the diurnal
251 period (at least three successive fixes mutually distant by less than 50 m). Similarly, the first
252 nocturnal site was considered as the location of the first grouped-fixes of the nocturnal period.
253 Finally, a mean distance between the centroids of both sites was calculated for each individual
254 per day. The same process was repeated for dawn, between the last nocturnal fixes and the
255 first fixes of the next day. Secondly, we characterized the overlap between diurnal and
256 nocturnal sites. For each individual, each day, each diurnal site was assessed using a 95%
257 Minimum Convex Polygon on fixes categorized within the “day” period (see above). Each
258 nocturnal site was assessed using the same method, based on fixes categorized within the
259 “night” period. Spatial overlap between both of these sites was then calculated. Finally, the
260 percentage of the nights spent in an area entirely distinct from the previous diurnal site (zero
261 overlap between both sites) was calculated for each individual.

262

263 *Habitat selection*

264 We used compositional analyses (Aebischer *et al.*, 1993) to quantify habitat preferences.
265 Because grey partridge is a gregarious species, we selected within each group of individuals,
266 the individual that was monitored the longest to guarantee individual independence. Records
267 from birds monitored for less than 7 days (i.e. 6 individuals) were discarded, as they remained
268 focused around the release site and the area they explored did not reflect the overall release
269 area habitat availability. Compositional analysis was computed for the autumn period only
270 (late-August to mid-November) to maintain homogeneity in land cover and hunting

271 disturbance. Data from 22 individuals during daytime and 13 individuals during nighttime
272 was used (no nocturnal data was available for birds monitored in 2015, see above). Analyses
273 were not possible in winter and spring as too few independent individuals remained (5 and 6,
274 respectively). Autumn land-cover was derived from land-cover surveyed in spring and stored
275 in a GIS database, according to crop phenology. Five habitat types were used: *harvested crops*
276 (mainly represented by winter cereals, rape and sunflower, already harvested in autumn),
277 *meadows*, *corn* (main unharvested crop in autumn), *woodlands* and *buildings*.

278 To investigate whether habitat selection varied across the circadian cycle, two
279 compositional analyses were performed: one on diurnal data and another on nocturnal data.
280 Fixes were classified as diurnal or nocturnal according to results of activity pattern analyses
281 (see above). To determine the proportion of each habitat type available for each individual,
282 the land-cover map was overlain with the 100% Minimum Convex Polygon (Aebischer *et al.*,
283 1993) of each individual, and the proportion of habitats lying within calculated. Then, the
284 proportion of each habitat used by individuals was assessed from the proportion of fixes
285 located in each habitat type (Aebischer *et al.*, 1993). Finally, compositional analyses testing
286 for habitat selection (i.e. significant differences between habitat use versus availability) were
287 performed using multivariate analysis of variance (MANOVA, Wilks' lambda (λ) statistic)
288 (Aebischer *et al.*, 1993) using the *adehabitatHS* package (Calenge, 2017). Habitats were then
289 ranked according to their relative selection.

290 To test for differences between diurnal and nocturnal habitat use, we performed a
291 compositional analysis using a MANOVA on the within-bird differences between diurnal and
292 nocturnal habitat use, based on paired data of individuals monitored in both periods ($n = 13$)
293 (Aebischer *et al.*, 1993; Novoa *et al.*, 2002).

294

295 *Nocturnal movements*

296 To define nocturnal movements, we assumed that at least 100 m should separate two clearly
297 identified roosting sites (defined as at least three successive nocturnal locations mutually
298 distant by less than 50 meters, see Appendix 3 for calculation details).

299 We tested for effects of distances to carnivore reservoirs (woodlands, built-up areas)
300 and corridors (hedgerows, roads) on the probability that grey partridge would undertake
301 nocturnal movements. First, distance between the centroid of the first nocturnally-used roost,
302 and each of the landscape features was assessed. Secondly, for each individual, each night
303 was allocated as 1 (if the individual undertook nocturnal movement from its first roost) or 0
304 (if no movement recorded). Then, generalized linear mixed-effect models (GLMM, binomial,
305 logit link) were used to test for the effect of distance to each landscape feature (square root
306 transformed) on the occurrence of a nocturnal movement, using *individual ID* as a random
307 factor. Effect of each variable was assessed with a likelihood ratio-test (i.e. χ^2). When a
308 significant effect was detected for a fitted GLMM, we used the R function *predict* to compute
309 predicted values of the probability for birds to move across a convenient range of distance to
310 the given risky feature.

311

312 *Differences in space use with survival status*

313 We explored the relationship between space use across the diel cycle and the survival status of
314 birds at 30 days after release. We used this particular cut-off since half of the monitored birds
315 (52%) died within the first 30 days after release. The first month after release has also been
316 identified as a pivotal period for partridge survival in other release programs (52% survived
317 the first month in Buner, 2006; see also Parish & Sotherton, 2007). We therefore determined
318 the survival status of birds at 30 days after release (hunted n = 25, predated n = 10, and
319 survivors n = 27), and standardized space use analyses by calculating, for all individuals,
320 space use variables over this period of 30 days. Individuals for which no GPS data were
321 recorded at night (i.e. birds monitored in 2015, n = 15, see Appendix 1, Table S1), those

322 categorized as “undetermined/other cause of death” (n = 9, Table S1), and those for which the
323 date of death was “unknown” (n = 7), were not considered in this analysis. Then, for each
324 individual, the mean distances to the nearest hedgerow, road/track, woodland and building
325 were calculated for the diurnal and nocturnal periods. Differences in space use according to
326 the survival status, the period (diurnal or nocturnal), and the two-way interaction between
327 both of them, were tested with linear mixed-effect models using likelihood ratio-tests.
328 *Individual ID* was considered as random factor to account for within-individual paired data of
329 space use between diurnal and nocturnal periods. When needed, Tukey’s multiple comparison
330 tests were performed using the R package *emmeans* (Lenth *et al.*, 2019).

331 We then used linear mixed-effect model to test for differences in the mean distance
332 travelled by individuals during nocturnal movements (see the previous section) according to
333 their survival status, with *Individual ID* as the random factor.

334 Finally, we tested whether survival of birds was influenced by their exploration
335 capacity during the 5 days after release. Fixes during the first 5 days of monitoring allowed us
336 to standardize all individuals independently from their lifespan, and to estimate their ability to
337 explore the surroundings from the release point. To investigate exploration capacity, we
338 assessed the diffusion coefficient given by the slope of the linear trend between time and the
339 squared distance between each fix and release site location (net-squared displacement, NSD)
340 (Kareiva & Shigesada, 1983). This slope was extracted from a linear mixed-effect model with
341 *Individual ID* as the random factor, and including time and the interaction time x survival
342 status as two fixed factors. Survival status was included in interaction with time only to
343 investigate variation of slope with time (Pays *et al.*, 2012).

344 All analyses were performed using R software (R Core Team, 2019). The data
345 underlying this article are available in Open Science Framework, at
346 <https://dx.doi.org/10.17605/OSF.IO/BC2P6>.

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Results

Activity patterns

Grey partridge activity changed markedly during the circadian cycle, with movements showing a clear bimodal pattern (Fig. 2). Distances travelled peaked at dawn, and similarly at dusk, with distances travelled (mean distance \pm SD between successive fixes at 1hr interval) being 197 m \pm 232 and 206 m \pm 230, respectively (Fig. 2A, B). Distance travelled between successive fixes were thus significantly higher at dawn and dusk, than during both daytime and nighttime (Table 2, Fig. 2A, B), and also higher at daytime compared to nighttime.

For each individual, the mean distance travelled between grouped-locations at the end of the day and first locations at night was 337 m (\pm 203). The mean morning distance travelled was very similar, 324 m (\pm 167). Furthermore, for each individual, in 78.9% (\pm 19.3) of the monitored days, the MCP of day and night were fully disjunct. There was, therefore, a clear spatial segregation between diurnal and nocturnal sites (see examples in Fig. 2C, D).

Habitat selection

At night, grey partridges did not use habitats as expected by chance (MANOVA, n = 13, Wilks's lambda λ = 0.145, p = 0.016). Harvested crops, representing stubble (i.e., short-vegetation cover) or ploughed fields in autumn, were most selected, while built-up areas and woodlands were avoided (Fig. 3, grey boxes, Appendix 1, Table S2). Meadows were also more selected than built-up areas at night (Table S2). Night and day habitat preferences, however, clearly shifted (MANOVA, n = 13, λ = 0.109, p<0.001): during the day, partridges used less stubble but more high-vegetation and refuge cover such as corn and woodlands (Fig. 3). During day, partridges appear to use habitats at random (MANOVA, n = 22, λ = 0.514, p = 0.524).

373 *Daily movements, habitat preferences and effect on survivorship*

374 Of those predated partridges for which the time of death could be estimated, 71% were killed
375 at night (10 out of 14). Movements between two roosting sites within a night (i.e. located at
376 more than 100 m), were detected at least once in 84% of night-monitored birds (65
377 individuals out of 77). Among them, such movements occurred on a mean of 23.7% (± 13.0)
378 of the monitored nights, and the mean distance travelled was 241 m (± 82). The probability for
379 a partridge to undertake such movement at night was negatively influenced by the distance to
380 the nearest woodland and building (Table 3). For example, based on model estimates (Table
381 3, see methods), partridges showed a twofold increase in probability (from 0.15 to 0.30) to
382 move at night when located in immediate proximity (distance of 0 m), compared to,
383 respectively, 675 m from woodlands and 1 km from built-up areas.

384

385 *Space use patterns of survivors versus non-survivors*

386 Space use differences varied according to survival status (Fig. 4, Table 4). Partridges killed by
387 hunters were located, on average, farther from hedgerows during daytime ($189 \text{ m} \pm 163$) than
388 surviving ones ($81 \text{ m} \pm 41$) (Fig. 4A, Table 4a). Furthermore, survivor and predated
389 partridges were located further from hedgerows at night than during the day (by, respectively,
390 73 m and 56 m), while there was no difference in nocturnal and diurnal to-hedgerow distances
391 for hunted partridges (Fig. 4A, Tables 4a and S3). Predated partridges were located on
392 average closer to roads/tracks ($73 \text{ m} \pm 39$) than either survivor ($118 \text{ m} \pm 32$) or hunted
393 partridges ($107 \text{ m} \pm 40$), regardless the period of the day (Fig. 4B, Table 4b). Finally, we did
394 not detect any difference in distances to woodland (Fig. 4C, Table 4c) or buildings between
395 survival statuses (Fig. 4D, Table 4d). However, differences in distance to woodlands for
396 diurnal and nocturnal periods were observed, regardless of bird survival status (Fig. 4C, Table
397 4c).

398 When they undertook nocturnal movements, survivors moved further ($281 \text{ m} \pm 16$)
399 than hunted birds ($186 \text{ m} \pm 31$) (Fig. 4E, Table 4e). Lastly, diffusion analysis (i.e. relation
400 between net-squared displacement and time) showed that non-survivor birds (predated or
401 hunted) had a lower diffusion rate from their release site during the first 5 days after release
402 (i.e. they moved away from the release site less), than survivors (Fig. 4F, Table 4f).

403

404 **Discussion**

405 Our results showed a clear shift in patterns of activity, space and habitat use between day and
406 night in grey partridge. This supports the hypothesis that either diurnal risks imposed by
407 human (hunting activity, agriculture, recreational outdoor activities) and/or diurnal predators
408 (mainly raptors), associated with nocturnal predation pressures (mainly from carnivores),
409 shape the diel cycle in this farmland landscape-living prey species (see also Moreno *et al.*,
410 1996; Lone *et al.*, 2014).

411

412 Behavioural adjustment during the diel cycle

413 Partridges shifted their habitat use between day and night. At night, they avoided high-
414 vegetation cover (corn, the main unharvested autumn crop), and carnivore reservoirs
415 (woodlands, buildings; Krauze-Gryz *et al.*, 2012), and selected short-vegetation cover
416 preferentially (harvested crops, i.e. stubble or ploughed fields), offering greater visibility,
417 enhanced detection capacity, and allowing greater facility for escaping predators
418 (Whittingham *et al.*, 2004). Birds located closer to carnivore reservoirs were also more likely
419 to make nocturnal movements, previously reported only as an escape behaviour in response to
420 intense disturbances (see Tillmann, 2009). Associated with the high number of predation-
421 based kills that occurred at night (71% of predated birds), and the high frequency of nocturnal
422 movements (1 night out of 4-5), these results suggest that nocturnal carnivores, as the main

423 predators of grey partridge (Bro *et al.*, 2001; Buner & Schaub, 2008), imposed a high level of
424 risk and a strong predation pressure. During the day, partridges shifted toward lower use of
425 short-vegetation covers and increased use of high-vegetation cover types (corn, woodlands),
426 which could provide shelters during peaks of human disturbance (such as hunting or other
427 outdoor recreational activities) and/or against diurnal birds of prey (Moreno *et al.*, 1996; Wolf
428 *et al.*, 2013).

429 However, it should be noted that diurnal habitat use in this species, previously
430 reported to forage on cereal grain within stubble fields during autumn (Moorcroft *et al.*,
431 2002), could also have been partly influenced by the distribution of seed-rich habitats (though
432 stubbles were not selected by day in the current study), and/or by artificial feeders (Guthery *et*
433 *al.*, 2004) used from autumn to spring for game management. Although it was not possible to
434 account for their effect in the current study, as feeder distribution and filling status (empty or
435 seed supplied) during the monitoring were unknown, we believe that artificial feeders did not
436 alter our results and conclusions for three reasons. First, even though habitat use may be
437 biased towards habitats surrounding feeders, the habitat selection processes are still likely to
438 operate in their presence. Sánchez-García *et al.* (2015) found that the numbers of grey
439 partridges and other gamebird species were higher at feeders located near hedgerows
440 compared to those located in open areas, because of the need to stay close to cover to reduce
441 predation risk during foraging (see also Watson *et al.*, 2007). Second, the increased daytime
442 use of high-vegetation cover by grey partridge is supported by similar patterns reported in
443 studies that do not report any supplementary feeding (e.g. Tillmann, 2009), and also in other
444 game species (Moreno *et al.*, 1996; Tolon *et al.*, 2009; Lone *et al.*, 2017). Finally, because
445 feeders were available both day and night, we do not believe they can explain the observed
446 behavioural shift in habitat use across the diel cycle. However, they may have contributed to
447 the nocturnal avoidance of supplementary feeding sites, as these may attract and concentrate

448 predators, so that the latter are sometimes even more present than the species targeted by food
449 supply themselves (Selva *et al.*, 2014; Sánchez-García *et al.*, 2015). Further studies
450 investigating the influence of feeders on wildlife would be helpful to clarify to what extent
451 their position within the landscape may drive spatial patterning in target species. This
452 necessarily implies controlling (or testing) for the type of feeders and their filling frequency,
453 as this may affect their probability of being visited.

454 The detected shifts in habitat use, likely occurring through routine crepuscular
455 movements between diurnal and nocturnal sites separated by around 330 m, strongly suggest
456 a form of commuting behaviour is operant (Duriez *et al.*, 2005; Masse *et al.*, 2013). This is
457 the first study providing empirical evidence of such behaviour in grey partridge using an
458 individual-based tracking approach (but see Tillmann, 2009; Potts, 2012), and one of the few
459 to have done so in farmland landscapes (but see Camacho *et al.*, 2014). The presence of a
460 bimodal activity pattern peaking at dawn and dusk suggests that crepuscular hours are pivotal
461 periods in prey behavioural adjustment, a pattern that may be tracking the nocturnal/diurnal
462 shift in predation regimes. Such high level of crepuscular activity (also coinciding with
463 patterns of vocal activity in this species Rotella & Ratti, 1988) could result from an adaptive
464 strategy to avoid both nocturnal and diurnal predators by concentrating activity in a time-
465 period when predation pressure relaxes (Halle, 2000). Indeed, Monterroso *et al.* (2013)
466 showed that the carnivore predation risk imposed on European rabbits, *Oryctolagus cuniculus*,
467 is twice as high at night than during crepuscular hours, and is associated with high raptor
468 predation risk during daytime, this would have shaped patterns of crepuscular activity likely
469 ensuring a higher rabbit survival probability (see also Duriez *et al.*, 2005; Tillmann, 2009).

470 Overall, our study provides evidence that individual grey partridges (even when
471 captive-reared and naïve, as in our study) perceive and adjust their behaviour to the temporal
472 variation in risks via a commuting strategy that allows a reduction in carnivore predation risk

473 at night and human-induced disturbance and/or raptor predation risk during the day (Lone *et*
474 *al.*, 2017). It further demonstrates that studies focusing on diurnal data may omit a non-
475 negligible part of the daily requirements, behaviour and ecology in this species and others,
476 and therefore emphasizes the importance of addressing ecological processes across the entire
477 diel cycle.

478

479 Space use behaviour and survival

480 Even though general patterns of response to risky situations were found, the strength of the
481 response may differ between individuals and thus affect differentially their survival (Sih *et al.*,
482 2012; Lone *et al.*, 2015). We found that non-survivors (either hunted or predated) and
483 survivors differed in their space use behaviour relative to risky landscape features. Compared
484 to survivors, predated birds were closer to roads, frequently used as corridors by nocturnal
485 carnivores (see also Rantanen *et al.*, 2010a for lower survival associated with proximity to
486 linear features). However, the survival status did not differ with distance to woodlands and
487 urban areas, which may be explained by the long distance at which all birds were located from
488 these two landscape features (around 400-500 m, Fig. 4). Hunted birds were farther from
489 hedgerows (potential shelter) during daytime than survivors, and had lower escape distances
490 (distance of nocturnal movements as a proxy of escape distance; Tillmann, 2009), possibly
491 making them more vulnerable to hunting in open terrains (Moreno *et al.*, 1996; Lone *et al.*,
492 2014). These results are consistent with those of Ciuti *et al.* (2012) who showed that Elk,
493 *Cervus elaphus*, are more likely to be harvested by hunters in open areas. However, in
494 contrast to their results showing that hunted individuals were more mobile, we found that non-
495 survivors (either hunted or predated) diffused less from the release site than survivors. The
496 proximity to release sites may favor an increased hunting pressure as gamebird density is
497 probably higher, but also a higher concentration of cues of prey presence (e.g. odours), thus

498 attracting scent-hunting predators and increasing mortality of those animals which moved
499 little (Banks *et al.*, 2002).

500 Overall, individual survival in partridges may depend on the space use behavioural
501 adjustment across the diel cycle, relative to risk-related features. Many studies have shown
502 that risk-taking and antipredator behaviours, respectively negatively and positively associated
503 with individual fitness (Réale *et al.*, 2007; Sih *et al.*, 2012; Hall *et al.*, 2015), are heritable and
504 thus have a genetic basis (Van Oers *et al.*, 2004; Bize *et al.*, 2012). Our results, based on such
505 behavioural traits, indicate that human hunters and nocturnal predators act as pressures that
506 select or favour individuals in opposing ways. Indeed, though most of the phenotypic changes
507 occurring in anthropogenic contexts would be associated with plasticity (Hendry *et al.*, 2008),
508 selection on heritable traits could also potentially, in time, lead to micro-evolution (Ciuti *et*
509 *al.*, 2012; Holtmann *et al.*, 2017). Such human-driven selection, acting on behavioural traits
510 and adding up to pre-existing selection pressures, has already been reported (Allendorf &
511 Hard, 2009), and could drive rapid evolutionary changes, particularly abrupt for harvested
512 organisms (Darimont *et al.*, 2009). These changes may be particularly worrying and damaging
513 if selection pressures are strong and contrasting (Lone *et al.*, 2017), since they may then
514 reduce the behavioural diversity expressed in populations (Sih *et al.*, 2012; Cordero-Rivera,
515 2017), affecting their ability to adapt to changing environments and thus their long-term
516 viability (Allendorf & Hard, 2009; Sih *et al.*, 2012). In this context, since it is very likely that
517 captive populations have been subjected to major evolutionary changes as a result of intense
518 selection in captivity, thus showing reduced behavioural diversity (see McDougall *et al.*,
519 2006), then further releases may not necessarily improve the fate of declining wild
520 populations.

521

522 Effect of the origin of birds

523 The origin of birds (captive-reared and naïve) might also have, at least partly, affected the

524 observed patterns of behavioural adjustments in grey partridge space use. Artificial selection
525 in captivity associated with the lack of natural development of antipredator responses and
526 feeding behaviours, may lead captive-reared birds to exhibit survival-inappropriate
527 behaviours once released into the wild (e.g. low vigilance rates: Rantanen *et al.*, 2010b), or
528 inadequate habitat selection (e.g. inadequate roosting site: Whiteside *et al.*, 2016) so
529 increasing their exposure and vulnerability to predators. Captive-reared partridges usually also
530 demonstrate shorter dispersal distances than wild ones (Rymesova *et al.*, 2013). While we
531 found that non-survivors had a lower diffusion rate from the release site than survivors, the
532 captive-reared origin of birds may also have contributed to an increase in mortality within
533 released population, as well as GPS devices (Homburger *et al.*, 2021) though this does not
534 seem to be the case in our study (Appendix 4). Generations of captive breeding may also
535 affect bird morphology and physiology (e.g. shorter wings, higher bodymass, lower condition
536 index, lighter hearts: Putaala & Hissa, 1995; Rymesova *et al.*, 2013). Associated with the
537 predator-naivety, such alterations could have reduced their capacity to move (Rymesova *et*
538 *al.*, 2013), and so escape predators by increasing their latency of escape and/or reducing their
539 take-off velocity and distance flown (Putaala *et al.*, 1997; Pérez *et al.*, 2010). Finally, release
540 methods may also have partly influenced the settlement of birds within release sites (Letty *et*
541 *al.*, 2007), so influencing their exploration capacity and ultimately their survival (Lockwood
542 *et al.*, 2005).

543 To conclude, although released birds may show higher mortality risk (only 21% of
544 released birds were recovered, 5% alive) compared to natural populations, we detected
545 significant behavioural adjustments that are consistent with a reduction in carnivore predation
546 risk at night, and human-induced disturbance and/or raptor predation risk during the day.
547 However, further research is needed to quantify precisely the influence that release methods
548 may have on spatial patterning and survival in this species.

549

550 Conclusions

551 Our study provides empirical evidence of behavioural adjustment in a prey species in
552 response to contrasting risks in space and time imposed by multiple predators (human hunters,
553 non-human diurnal and nocturnal predators). In this species, a commuting strategy has been
554 the adopted spatio-temporal behavioural adjustment. However, it remains unclear whether the
555 benefits gained from such adjustments in terms of short-term reduction of predation risk allow
556 the maintenance of long-term fitness. Indeed, exposure to high-risk levels may bias the trade-
557 off resource acquisition/predation risk towards the maintenance of a high investment in costly
558 antipredator behaviour, so reducing the short-term predation risk, though imperiling long-term
559 individual fitness (Watson *et al.*, 2007). While humans have become a major evolutionary
560 force acting on wild animal populations (Allendorf & Hard, 2009), understanding the
561 ecological and evolutionary impacts from cumulative human and non-human pressures on
562 wild animal populations has become increasingly challenging. Our study suggests that future
563 research on how humans (e.g. hunting exploitation, captive-breeding programs, see
564 McDougall *et al.*, 2006) may add-up to selection pressures from non-human predators would
565 be critical to ensure population viability and increase wildlife management efficiency in
566 human-dominated landscapes.

567

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583

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SUPPORTING INFORMATION

836

Appendix 1. Additional results.

837

Appendix 2. Accuracy assessment and filtering of GPS data.

838

Appendix 3. Determination of nocturnal movements between different roosts.

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Appendix 4. Influence of GPS device on partridge condition and mortality.

Table 1 Summary of the number of GPS-equipped birds released each year per communal hunting society and the release practices employed. Total number of birds are given first, with number of males in brackets.

Hunting society	N of GPS-equipped birds (males)			Duration of acclimation	Simultaneous release
	2015	2016	2017		
Fors	57 (29)	46 (32)	-	Up to 10 days	Yes/No
Mougon	59 (37)	32 (18)	-	Up to 7 days	Yes/No
Prahecq	58 (?)	60 (35)	-	0 day	Yes
Marigny	-	63 (57)	66 (32)	3-5 days	Yes

Table 2 Statistics of the linear mixed-effect models testing for difference in log-transformed distance (m) between successive fixes (1-hour intervals) between periods of the day (morning periods: Night, Dawn, *Day*; evening periods: *Day*, Dusk, Night), with levels in italics used as reference. All models include individual identity, and season nested in year of monitoring as random factors.

Dependent variable	Independent variable	χ^2 value	df	P value	Estimate \pm SE (p)
Distance travelled between successive fixes	Morning periods	2020.9	2	<0.001	(intercept: 3.64 \pm 0.07)
					Dawn : 0.82 \pm 0.04 (<0.001)
					Night : -0.86 \pm 0.04(<0.001)
Distance travelled between successive fixes	Evening periods	1307.6	2	<0.001	(intercept: 3.61 \pm 0.12)
					Dusk : 0.95 \pm 0.04 (<0.001)
					Night : -0.71 \pm 0.05 (<0.001)

Table 3 Effects of the square root transformed distances to woodlands, buildings, hedgerows and roads/tracks on the probability of individual grey partridge moving at night, using a generalized linear mixed model (GLMM, binomial, logit link), including individual identity as random factor. Estimate \pm SE are indicated when variables are significant.

Variables	χ^2 value	Df	P value	Estimate \pm SE
				(intercept: -0.125 ± 0.347)
Distance to woodland	10.70	1	<0.01	-0.034 ± 0.010
Distance to building	5.64	1	0.02	-0.030 ± 0.013
Distance to hedgerow	0.39	1	0.53	
Distance to road or track	0.01	1	0.94	

Table 4 (a) distance to the nearest hedgerow, (b) road/track, (c) woodland, (d) building modelled as responses to the period of the day (*day*, *night*) and of the survival status at 30 days after release (Hunted, Predated or *Survivor*) through linear mixed-effect models using likelihood ratio-tests. For multiple comparisons, see Appendix 1, Table S3. (e) distance travelled during nocturnal movements, and (f) the strength of diffusion rate (i.e. relation between net-squared displacement and time) from the release site calculated on the first 5 days after release, modelled as responses to the survival status at 30 days after release, with linear mixed-effect models using likelihood ratio-tests. All models include individual identity as random factor. Levels used as reference are in italics. Estimate \pm SE are indicated when variables are significant.

Dependent variable	Independent variables	L.ratio	df	P value	Estimate \pm SE (p)
(a) Distance to hedgerow					(intercept: 81.46 \pm 20.90)
	Period	42.74	1	<0.01	
	Survival status	10.10	2	<0.01	
	Period x Survival status	11.79	2	<0.01	Night, Survivor: 73.04 \pm 9.26 (<0.01) Day, Hunted: 107.59 \pm 30.14 (<0.01) Day, Predated: -5.60 \pm 40.20 (0.89) Night, Hunted: -46.76 \pm 13.35 (<0.01) Night, Predated: -17.14 \pm 17.81 (<0.34) (see Table S3 for multiple comparison)
(b) Distance to road or track					(intercept: 117.84 \pm 8.37)
	Period	0.71	1	0.40	
	Survival status	7.54	2	0.02	Hunted: -11.14 \pm 12.07 (0.36) Predated: -45.00 \pm 16.10 (<0.01)
	Period x Survival status	0.45	2	0.80	
(c) Distance to woodland					(intercept: 406.49 \pm 34.99)
	Period	11.47	1	<0.01	Night: 35.40 \pm 10.06
	Survival status	1.26	2	0.53	
	Period x Survival status	1.79	2	0.41	
(d) Distance to buildings					
	Period	0.70	1	0.40	
	Survival status	5.58	2	0.06	
	Period x Survival status	0.29	2	0.86	
(e) Nocturnal travelled distance					(intercept: 281.10 \pm 15.60)
	Survival status	9.04	2	0.01	Predated: -17.06 \pm 33.34 (0.61) Hunted: -95.05 \pm 30.79 (<0.01)
(f) Diffusion coefficient					(intercept: 0 \pm 0)
	Time	206.58	1	<0.01	
	Time x Survival status	130.60	2	<0.01	Time: 57166 \pm 3137 (<0.01) Hunted: -45150 \pm 4372 (<0.01) Survivor: -51522 \pm 6029 (<0.01)

Figure captions:

Figure 1 Communal boundaries of each studied hunting association within the Long-Term Socio-Ecological Research (LTSER) platform “Zone Atelier Plaine & Val de Sèvre”, *Département des Deux-Sèvres*, France. Symbols represent release sites (●: 2015; ▲: 2016; ×: 2017).

Figure 2 Activity patterns of grey partridge measured as the distance between successive fixes (1-hour intervals) as a function of time deviation from dawn (A), or dusk (B). Solid lines represent temporal trends in activity assessed by Generalized Additive Models (Gaussian, cubic regression spline smoothing). The red envelopes represent the standard error. C and D represent GPS locations of two different partridges monitored in different areas in 2017 and 2016, respectively. Black dots indicate nocturnal locations and white dots to diurnal locations.

Figure 3 Nocturnal (grey boxes, $n = 13$) and diurnal (white boxes, $n = 13$) ratios of proportion of habitat use/availability across 5 habitat types in autumn by grey partridge. The dashed line represents the threshold of 1, indicating the habitat use as expected by chance.

Figure 4 Mean individual distances from the nearest hedgerow (A), road/track (B), woodland (C) or building (D) between the diurnal and nocturnal period, and the survival status of birds at 30 days after release (Hunted $n = 25$; Predated $n = 10$; or Survivor $n = 27$). See Tables 3 and S3 for statistical details. (E) Differences in distance travelled during nocturnal movements. (F) Diffusion rate (slope between the net-squared displacement (m^2) and time (day)) from the release site based on the first 5 days after release between survival status of birds (Hunted, Predated, or Survivor at 30 days after release). See Table 4 for statistical details.

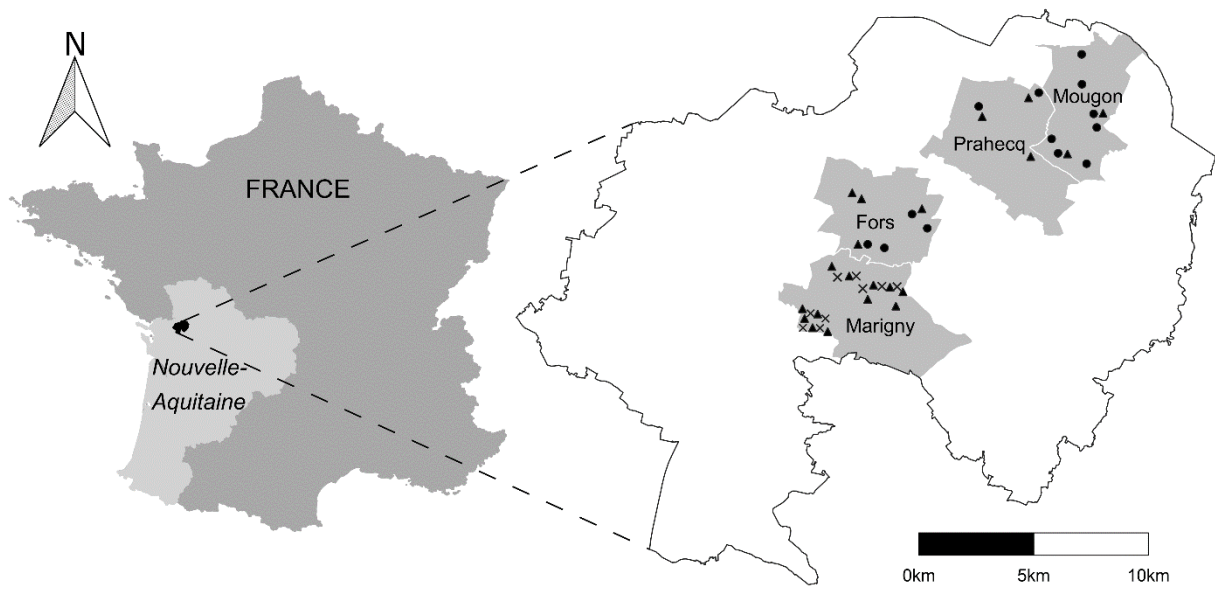


Figure 1

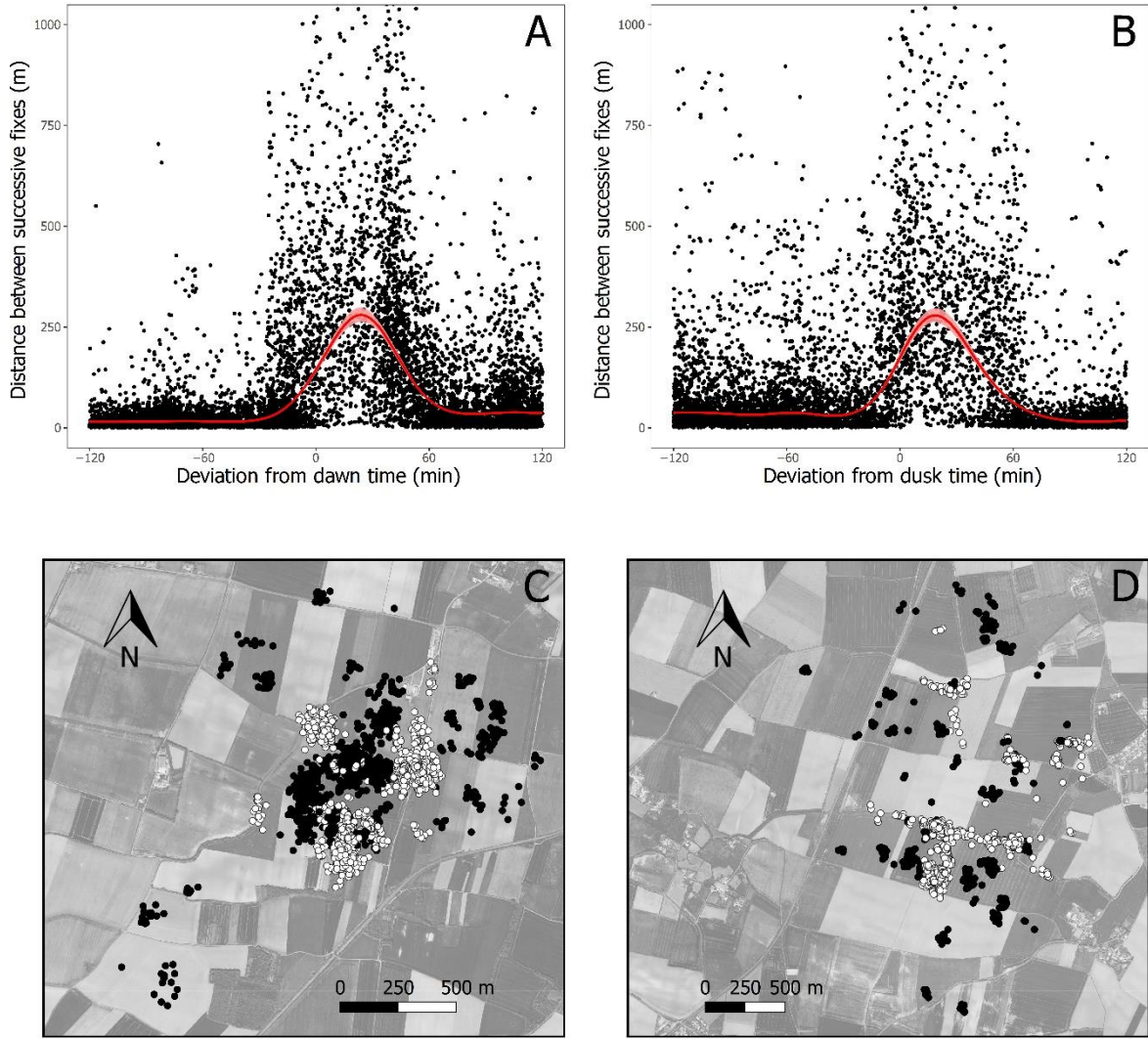


Figure 2

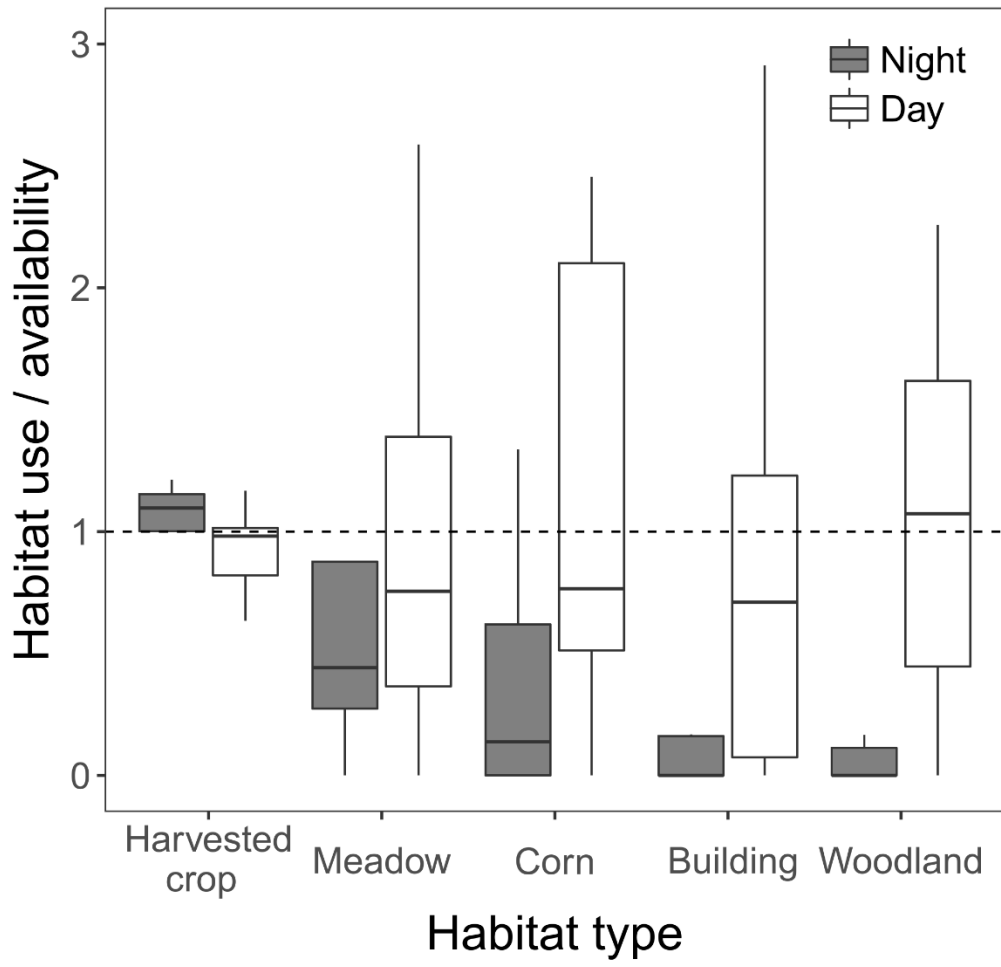


Figure 3

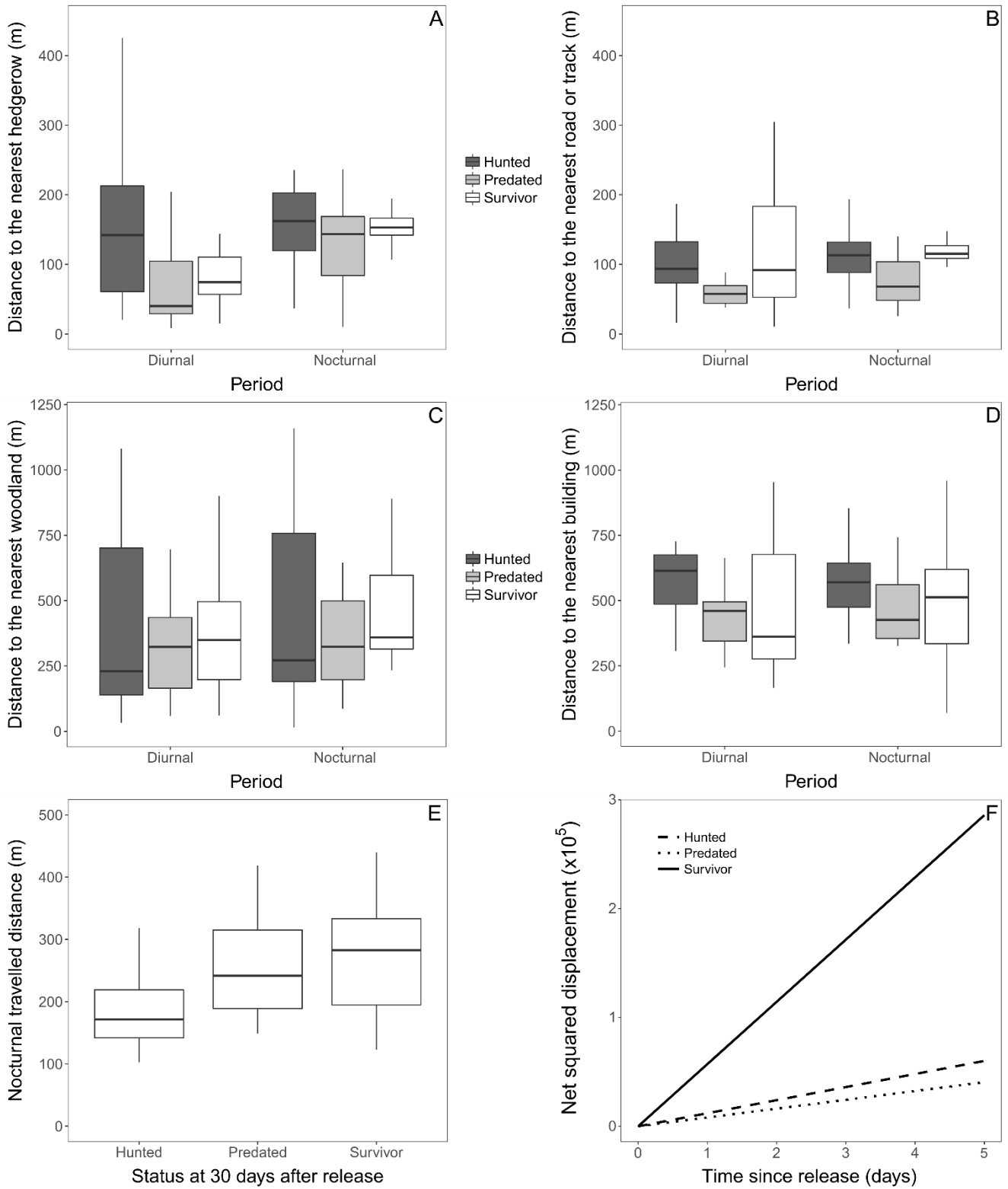


Figure 4

Appendix 1. Additional results

Table S1 Summary of the fate of birds (hunted, predated or survivor) at their last sighting, according to their year of release. The ‘unknown / other cause of death’ refers to six individuals found dead with no apparent cause (no predator nor lead shot traces), 1 individual killed by car collision, and 4 individuals equipped by GPS-transmitters whose signals were lost without any carcass recovery.

Fate of birds	2015	2016	2017	Total
Hunted	13	29	2	44
Predated	0	7	8	15
Survivor	0	13	10	23
Unknown / other cause of death	2	8	1	11
Total number of GPS-equipped birds	174	201	66	441

Table S2 Ranking matrix of habitat types on the nocturnal autumnal period (late August to mid-November), based on the proportional habitat use by grey partridge as proportion of fixes of each bird located in each habitat type, compared to the available proportion of each habitat type in the bird’s minimum convex polygon (MCP). A triple sign indicates a significant deviation from random ($p < 0.05$).

	Harvested crop	Meadow	Corn	Building	Woodland	Rank
Harvested crop	0	+	+	+++	+++	4
Meadow	-	0	+	+++	+	3
Corn	-	-	0	-	-	0
Building	---	---	+	0	+	2
Woodland	---	-	+	-	0	1

Table S3 Tukey’s multicomparison post-hoc tests calculated following computation of a linear mixed-effect model for grey partridge distance to hedgerows as a function of the interacting effect of the period (day, night) and the survival status of birds 30 days after release (Predated, Hunted, Survivor).

Contrasts	estimate	se	t-ratio	p-value
Day, Survivor – Night, Survivor	-73.04	9.26	-7.89	<0.01
Day, Survivor – Day, Hunted	-107.59	30.14	-3.57	<0.01
Day, Survivor – Night, Hunted	-133.87	30.14	-4.44	<0.01
Day, Survivor – Day, Predated	5.60	40.20	0.14	1.00
Day, Survivor – Night, Predated	-50.30	40.20	-1.25	0.76
Night, Survivor – Day, Hunted	-34.54	30.14	-1.15	0.82
Night, Survivor – Night, Hunted	-60.83	30.14	-2.02	0.28
Night, Survivor – Day, Predated	78.64	40.20	1.96	0.31
Night, Survivor – Night, Predated	22.74	40.20	0.57	0.99
Day, Hunted – Night, Hunted	-26.29	9.62	-2.73	0.06
Day, Hunted – Day, Predated	113.18	40.63	2.79	0.05
Day, Hunted – Night, Predated	57.28	40.63	1.41	0.66
Night, Hunted – Day, Predated	139.47	40.63	3.43	<0.01
Night, Hunted – Night, Predated	83.57	40.63	2.06	0.26
Day, Predated – Night, Predated	-55.90	15.22	-3.67	<0.01

Appendix 2. Accuracy assessment and filtering of GPS data

GPS data frequently contains inaccurate and unreliable fixes (Lewis *et al.*, 2007; Bjørneraas *et al.*, 2010). This emphasizes the need to assess the precision and then filter out fixes that are impairing the dataset. Further, Forin-Wiart *et al.* (2015) emphasize the need to test for the accuracy of GPS devices before deployment on wildlife, specifically those used in the current study (i.e. CatLog). They proposed to classify as an erroneous fix each location distant from the real position of the CatLog device by at least 3-fold the standard deviation of the location error (i.e. the distance between a recorded location and its real position). Therefore, in our study, 77 GPS were tested before deployment. Having been programmed to record data every 60 seconds, devices were placed in open area, where they then remained untouched for 2 hours. The mean location error (\pm SD) was evaluated at 16.71 m (\pm 18.85). However, even if informative about the GPS accuracy, tests in control conditions are of limited applicability during to the actual monitoring situation, when real position of animals is unknown. Therefore, the distance between two successive locations is often used as another metric to assess device accuracy (Bjørneraas *et al.*, 2010). Even though optimally expected to be close to zero (as the GPS is static during the test), this distance was estimated on average at 15.84 m (\pm 21.49).

Additionally, a variety of techniques exist to filter out unreliable locations. The first type of filters is based on positioning error given the satellites position (e.g. position dilution of precision), and provided by the GPS devices for each location recorded (Lewis *et al.*, 2007; Jiang *et al.*, 2008). Therefore, filters frequently use the number of satellites and/or level of precision dilution to identify unreliable locations (Jiang *et al.*, 2008; Bjørneraas *et al.*, 2010). However, the use of such filters is debated, as they may strongly reduce animal location dataset size, while still leaving large location errors unfiltered (Bjørneraas *et al.*, 2010). In the current study, such criteria were not appropriate since, while in general location error decreases as the number of available satellites increases at recording time (Fig. S1A), most of the most accurate fixes (from a sub-selection of fixes whose location error < 20 m) were recorded when few satellites were available (Fig. S1B). Similarly, while a high HDOP index is usually associated with low accuracy, revealed a great accuracy (Fig. S1C), here the majority of most accurate fixes (from a sub-selection of fixes whose location error < 20 m) had low HDOP indexes. Such mismatching between accuracy index and location error has already been observed by McGregor *et al.* (2014), therefore indicating the need for a second filter type.

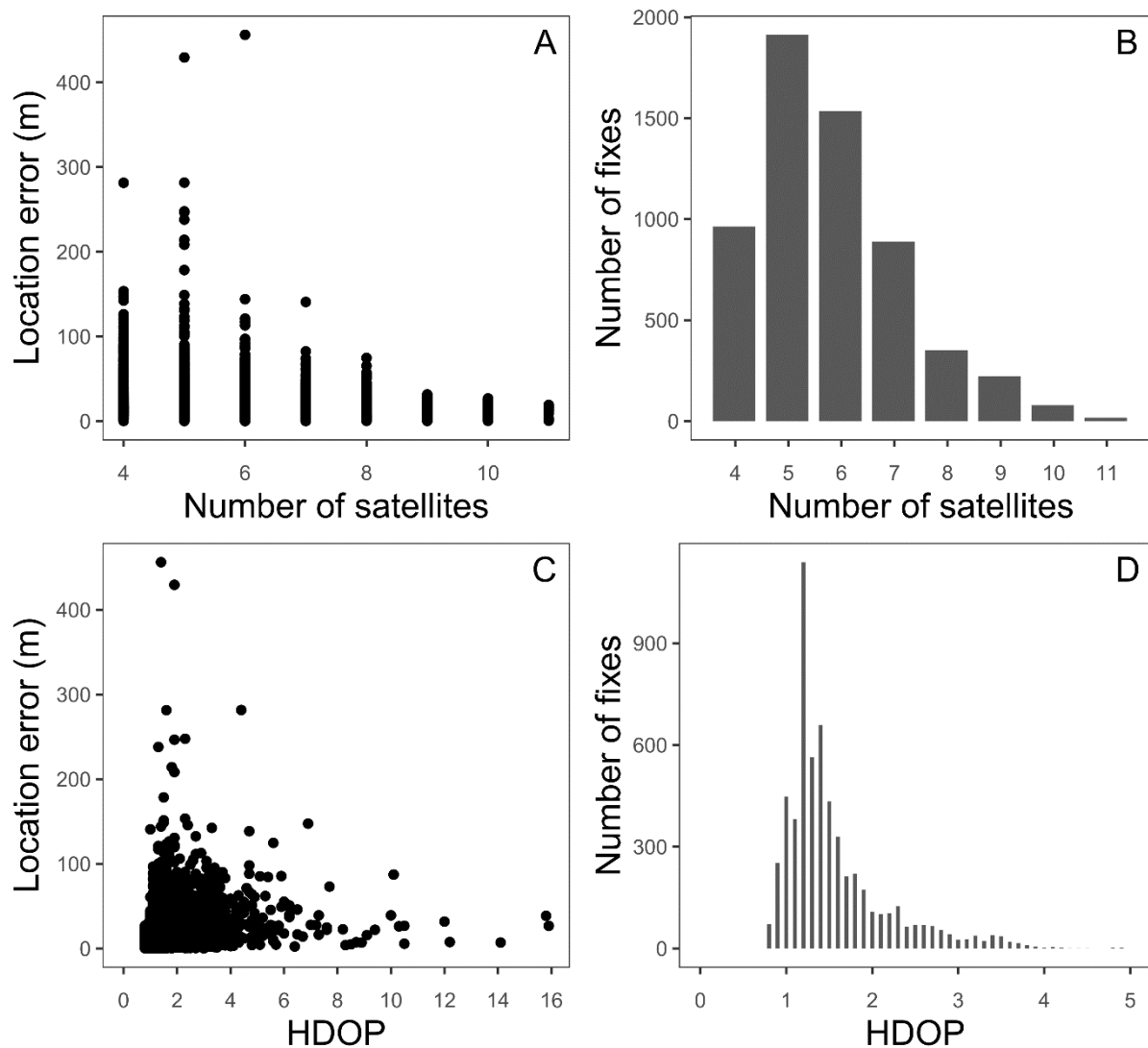


Figure S1 Location error (i.e. distance between the recorded fix and the real position of the GPS device) as a function of the number of satellites available at recording time (A), and of the Horizontal Dilution of Precision (C). Graphs B and D represent the distribution of the most precise fixes (sub-selection of fixes with location error < 20 m), based on number of satellites and HDOP index.

A second filter type, based on biologically relevant criteria is often used (e.g. Bjørneraas *et al.*, 2010). Such filters aim to identify implausible movement spikes and discard any erroneous fixes involved. To this end, filters focus on three successive locations, and use different indicators as distances from the previous and next fixes, speed, and angle between the three successive locations indicating unreliable movement spikes (Bjørneraas *et al.*, 2010; McGregor *et al.*, 2014). For instance, in birds, using devices identical to those used in the current study (CatLog), Kleyheeg *et al.* (2017) identified erroneous fixes as spikes in movement greater than 100 m and immediately followed by a return of at least halfway to the direction of the original position (with a 15-min interval).

For the current study, we applied two filters to three successive locations simultaneously. For each fix, a first, coarse, filter was applied: a fix (F_t) recorded at the time t , is considered erroneous when the turning angle is $> 165^\circ$, and the distance from the last fix and to the next fix are both > 100 m, indicating an unreliable spike in the movement trajectory. Simultaneously, a second, and finer, filter was applied; in this, the fix F_t is considered erroneous when the distance between the previous and the next fixes $d_{F_{t-1}, F_{t+1}}$ is less than to both distance $d_{F_t, F_{t-1}}$ (between the current fix and the previous one), and the distance $d_{F_t, F_{t+1}}$ (between the current fix and the next one), thereby showing any unreliable spike movement at the time t . However, given the biology and size of the species, a minimal condition of 50 m was applied to the distances of $d_{F_t, F_{t-1}}$ and $d_{F_t, F_{t+1}}$ to avoid filtering out the valid movements associated with foraging bouts. After filtering, precision was reassessed, under controlled conditions and on data recorded *in natura* (Table S4). For controlled conditions, 1.40% of fixes were filtered out and the mean location error (\pm SD) varied from 16.71 m (\pm 18.85) to 15.66 m (\pm 14.51) (Table S4). Mean distances between two successive locations varied from 15.84 m (\pm 21.49) to 13.63 m (\pm 13.19), so improving control of fix dispersion variance (Table S4). *In natura*, 4.37% of fixes were filtered out, and the mean distance between 2 successive locations varied from 49.57 m (\pm 96.70) to 41.06 m (\pm 78.11) (Table S4). This process was replicated on the few other GPS devices, with 0.71% of fixes filtered out bringing the mean distance between two successive locations from 23.87 m (\pm 80.85) to 22.12 m (\pm 78.15) for UvA-BiTS devices, and 4.19% of fixes filtered out resulting in the mean distance between two successive fixes to be reduced from 45.88 m (\pm 76.57) to 40.27 m (\pm 73.95) for Milsar devices.

Table S4 Precision of GPS data assessed before (unfiltered) and after (filtered) filter application on data collected under controlled conditions and *in natura*. Dataset reduction corresponds to the proportion of fixes filtered out. Location error corresponds to the distance between a fix and the real position of the GPS device at the time of the record (only for controlled conditions). Q95 correspond to the 95% quantiles of distances.

	Controlled conditions		<i>In natura</i>	
	Unfiltered	Filtered	Unfiltered	Filtered
Dataset reduction (%)	0	1.40	0	4.37
Location error (mean in m \pm SD)	16.71 \pm 18.85	15.66 \pm 14.51	-	-
Q95 of the location error (m)	47.51	42.98	-	-
Distance between two successive locations (mean in m \pm SD)	15.84 \pm 21.49	13.63 \pm 13.19	49.57 \pm 96.70	41.06 \pm 78.11
Q95 of the distance between two successive locations (m)	49.17	39.98	198.65	162.13

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Appendix 3. Determination of nocturnal movements between different roosts

The discrimination of intrapatch movements (or encamped modes) and interpatch movements (or exploratory modes) has been rather well conceptualized in movement ecology, and often relies on turning angles, step length or speed criteria (Benhamou, 1992; Barraquand & Benhamou, 2008). However, this discrimination factors needs to be based on highly accurate and high-resolution temporal data. In the present study, the temporal resolution of GPS devices was about one fix per hour at night. As this resolution level did not provide reliable measures of turning angles or speed, we developed a process to do this, which can be broken down into three steps. It was applied to nocturnal data (from 75 min after the dusk to 45 min before the dawn to prevent the inclusion of movement data which peaks around dawn and dusk, see Results).

First, for each night and each individual, we determined the first roosting site at a minimum of three successive locations all separated from each other by less than 50 meters (which correspond to the mean distance between successive *in natura* fixes, see Appendix 1). Once an initial roost had been identified, the same process was repeated with the 2nd to 4th fixes to check if the next fix was also included in the roost. If fixes were mutually separated by less than 50 meters, the 4th fix was aggregated with the three previous ones. This process was repeated until the condition of mutual distance of less than 50 meters within the trio of fixes was no longer met. For all locations, the centroid included in the first roost was calculated as a synthetic location of the roost, using the R package *rgeos* (Bivand & Rundel, 2017).

Next, the second step was implemented which aimed to identify any departure from the first roosting site to settle in a second one. An exit was defined as at least two successive fixes located more than 100 meters (twice the mean distance observed between successive fixes, see Appendix 1) far from the centroid of the first roost, but also mutually distant by less than 50 meters.

The latter part of this linked process formed the third step and simulated the settlement of the bird in a second roost during the night. When these coupled conditions were not satisfied, the last two steps were repeated with the two next fixes sequentially until the end of the night. When a second roost was detected, we repeated, as in the first step, the process with the next fixes to check the next fix satisfied the mutual distance condition criteria and could be included in the analysis. The centroid of the second roost was calculated.

As a result, a nocturnal change of roosting site was considered only when all three of the operational steps were satisfied. Then, the moved distance between both roosts was calculated as the straight-line distance between centroids.

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Appendix 4. Influence of GPS device on partridge condition and mortality

GPS device influence on bird mortality

A total of 310 grey partridges were released at Marigny in 2016 and 2017, with respectively 129 (41.6%) GPS-equipped birds and 181 (58.4%) non-equipped (but ringed) birds (see methods, Table 1).

Then, a total of 56 partridges were recaptured, among which 23 (41.1%) were GPS-equipped and still alive at their last sighting (see Appendix 1, Table S1), while 33 (58.9%) were non-equipped birds.

We found that proportions of GPS-equipped and non-equipped birds at recapture were conform to their respective proportions at release (chi-square test: $\chi = 0.007$; $n = 56$; $df = 1$; $p = 0.93$), suggesting that partridge mortality was not influenced by GPS devices in this released population.

GPS device influence on bird condition

At Marigny, all birds were weighted, ringed, and a part of them equipped by a GPS device (see methods). Then, all birds (GPS-equipped and non-equipped) were weighted again at recapture (mean delay \pm SD between both measures = 69.5 days \pm 43.8 SD).

In order to test whether GPS devices affect the condition of bird, difference in body mass (g) according to the equipment of birds (GPS-equipped or non-equipped), the measurement period (before equipment, i.e. at release, and after equipment, i.e. at recapture), and the interaction between both of them, was tested with a linear mixed-effect model using likelihood ratio-tests. Individual identity was considered as random factor to account for within-individual paired data of body mass between measurement periods.

Results showed that all birds had increased mass at recapture (Figure S2), whether they were equipped or not with a GPS device (see Table S5), hence indicating that no influence of GPS devices was detected on the partridge gain of mass or condition.

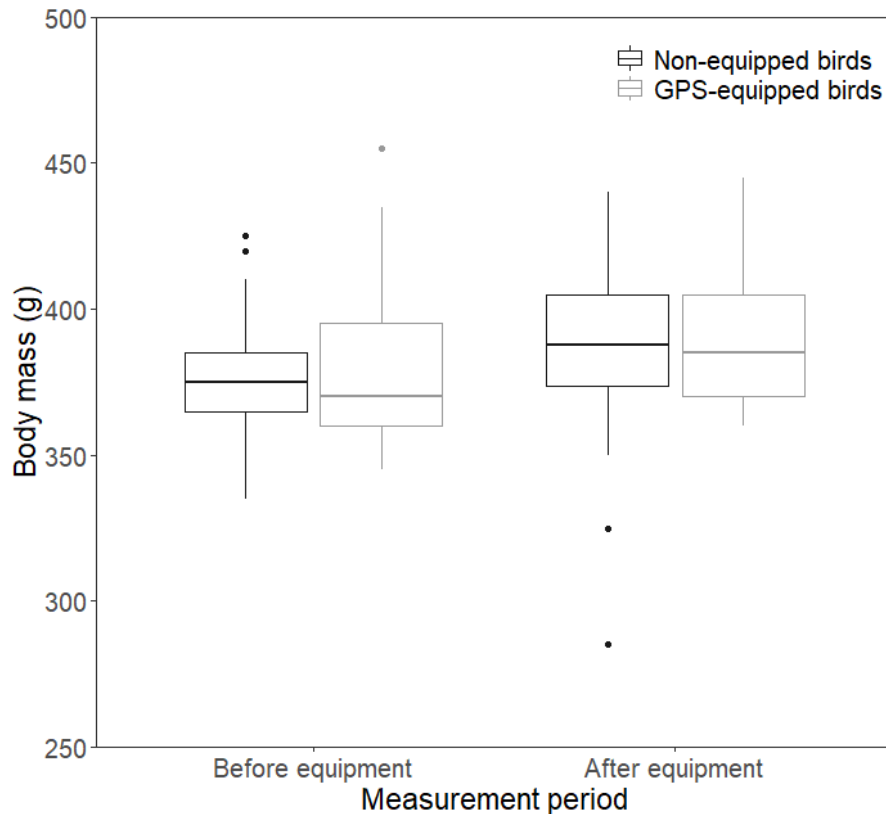


Figure S2 Body mass of non-equipped (black boxes) and GPS-equipped (grey boxes) birds as a function of the measurement period (before equipment, i.e. at release, and after equipment, i.e. at recapture).

Table S5 Body mass modelled as response to the equipment of birds (non-equipped, GPS-equipped), the measurement period (before equipment, after equipment) and the interaction between these two variables, through linear mixed-effect model using likelihood ratio-tests. Individual identity ($n = 56$) was included as random factor. Levels used as reference are in italics. Estimate \pm SE are indicated when variables are significant.

Independent variables	L.ratio	df	P value	Estimate \pm SE (p)
				(intercept: 377.41 \pm 3.54)
Equipment x Measurement Period	0.01	1	0.925	
Equipment	0.87	1	0.350	
Measurement period	8.43	1	0.004	After equipment: 11.36 \pm 3.80

However, it should be noted that the same analyses were not possible for the three other study sites (Fors, Mougou and Prahecq), at which only GPS-equipped birds were released (no solely ringed birds), and no recapture was made as GPS devices were recovered by hunters (see methods).