



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

Clément Harmange, Vincent Bretagnolle, Nathan Chabaud, Mathieu Sarasa,  
Olivier Pays

### ► To cite this version:

Clément Harmange, Vincent Bretagnolle, Nathan Chabaud, Mathieu Sarasa, Olivier Pays. Diel cycle in a farmland bird is shaped by contrasting predation and human pressures. *Biological Journal of the Linnean Society*, 2021, 134, pp.68-84. 10.1093/biolinnean/blab060 . hal-03266910

**HAL Id: hal-03266910**

**<https://hal.science/hal-03266910>**

Submitted on 7 Mar 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

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

Clément Harmange<sup>1,2,3</sup>, Vincent Bretagnolle<sup>2,4</sup>, Nathan Chabaud<sup>2</sup>, Mathieu Sarasa<sup>5,6</sup>, Olivier Pays<sup>1,3</sup>

<sup>1</sup>*LETG-Angers, UMR 6554 CNRS, Université d'Angers, 2 Bd Lavoisier, 49045 Angers France*

<sup>2</sup>*Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS and La Rochelle Université, F-79360 Beauvoir-sur-Niort, France*

<sup>3</sup>*REHABS International Research Laboratory, CNRS-Université Lyon 1-Nelson Mandela University, George Campus, Madiba drive 6531 George, South Africa.*

<sup>4</sup>*LTSER « Zone Atelier Plaine & Val de Sèvre », CNRS, 79360, Beauvoir sur Niort, France*

<sup>5</sup>*BEOPS, 1 Esplanade Compans Caffarelli, 31000 Toulouse, France*

<sup>6</sup>*Fédération Nationale des Chasseurs, 13 rue du Général Leclerc, 92136 Issy-les-Moulineaux cedex, France*

Corresponding author:

Clément Harmange, *LETG-Angers, UMR 6554 CNRS, Université d'Angers, 49000 Angers, France*, [c.harmange.pro@gmail.com](mailto:c.harmange.pro@gmail.com), +33(0)241735261, ORCID: 0000-0001-5207-021X

ORCID Olivier Pays: 0000-0001-8268-1804

ORCID Mathieu Sarasa: 0000-0001-9067-7522

## Abstract

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

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

## Introduction

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

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

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

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

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

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

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

## **Material and methods**

### **Study site**

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

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

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

#### GPS surveys

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



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

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

where grey partridge shooting was suspended from 2016 to 2018, 131 birds were released in mid-December 2016 and 179 in mid-September and in late October 2017. Birds were released in flocks of 12-16 individuals (50% males and 50% females), with 6-8 tagged individuals per flock. In each site, birds were all released at the same date after a 5-day acclimation phase (or 3-day when predator traces were observed around pens) in pens (of ca. 5 m<sup>2</sup>).

## Data collection

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

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

## Statistical analyses

### *Activity pattern*

Activity pattern was analyzed as distances between successive fixes (Bengtsson *et al.*, 2014). As intervals between fixes were not consistent between night and day and between GPS types, data were preliminarily standardized to 1 fix per hour. To do so, starting with the first location for each bird after it left the pen, we filtered iteratively each fix recorded less than 57 min of the previous one (mean time between successive fixes after filtering = 60.4 min  $\pm$  1.6 SD). To control for seasonal changes in daylight length from autumn to spring, we considered time as deviation from times of dawn and dusk. Time deviations between GPS locations and dawn/dusk were extracted using R package *suncalc* (Agafonkin & Thieurmél, 2018). We then tested the effect of time on movement patterns using generalized additive mixed models (GAMM, Gaussian response variable with a cubic regression spline smoothing, Wood, 2006) with R package *gam4* (Wood & Wood, 2015). *Individual identity (ID)* and *season* nested in *year* were included as random factors.

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

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

### *Habitat selection*

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

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

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

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

#### *Nocturnal movements*

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

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

#### *Differences in space use with survival status*

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

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

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

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

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

## 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 1 hr interval) being  $197 \text{ m} \pm 232$  and  $206 \text{ m} \pm 230$ , 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  $337 \text{ m} (\pm 203)$ . The mean morning distance travelled was very similar,  $324 \text{ m} (\pm 167)$ . 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  $\lambda = 0.145$ ,  $p = 0.016$ ). 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,  $n = 13$ ,  $\lambda = 0.109$ ,  $p < 0.001$ ): 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,  $n = 22$ ,  $\lambda = 0.514$ ,  $p = 0.524$ ).



*Daily movements, habitat preferences and effect on survivorship*

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

*Space use patterns of survivors versus non-survivors*

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

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

## Discussion

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

### Behavioural adjustment during the diel cycle

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

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

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

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

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

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

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

#### Space use behaviour and survival

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

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

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

## Effect of the origin of birds

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

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

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

## 568 Acknowledgements

569 Special thanks to Alexandre Villers for his very valuable help with the partridge releases and  
570 monitoring. We thank all the fieldworkers who contributed to the data collection, especially  
571 R. Bonnet, T. Rinaud, M. Souchet, P. Lagrange, J-B. Perrotin, G. Lemonnier, C. Palma, A.  
572 Gée, J. Léauté, P. Harmange, T. Joubin and M. Saillard. We also thank Nicholas Aebischer,  
573 Elisabeth Bro, Jérôme Moreau, Daniel Fortin, Romain Julliard, Mathieu Boos, Adrian



574 Barnett, and three anonymous reviewers for their valuable comments on the manuscript.  
575 Finally, we thank the Fédération Départementale 79 (G. Guédon, C. Jarriau, D. Vincendeau,  
576 F. Audurier, M. Garretier and B. Brunet) and the communal hunting societies of Marigny (M.  
577 and J. Caillaud), Mougou (M. Goudeau), Prahecq (L. Moinard) and Fors (P. Bernard) for their  
578 support. This work was supported by the Fédération Nationale des Chasseurs (grant number  
579 FNC-PSN-PR15-2014). Permission to handle birds was given by the authority Préfecture  
580 Départementale des Deux-Sèvres (Number: 2017/1). All applicable French guidelines for the  
581 ethical use of animals in research were followed. The project was conducted with permission  
582 from farmers who were made aware of the partridge monitoring.

583

#### 584 **References**

- 585 **Aebischer NJ, Ewald JA. 2012.** The grey partridge in the UK: population status, research,  
586 policy and prospects. *Animal Biodiversity and Conservation* **35**: 353–362.
- 587 **Aebischer NJ, Robertson PA, Kenward RE. 1993.** Compositional analysis of habitat use  
588 from animal radio-tracking data. *Ecology* **74**: 1313–1325.
- 589 **Agafonkin V, Thieurmél B. 2018.** suncalc: Compute Sun Position, Sunlight Phases, Moon  
590 Position and Lunar Phases. - <<https://cran.r-project.org/web/packages/suncalc/index.html>>.
- 591 **Allendorf FW, Hard JJ. 2009.** Human-induced evolution caused by unnatural selection  
592 through harvest of wild animals. *Proceedings of the National Academy of Sciences* **106**:  
593 9987–9994.
- 594 **Aubry P, Anstett L, Ferrand Y, Reitz F, Klein F, Ruelle S, Sarasa M, Arnauduc JP,**  
595 **Migot P. 2016.** Enquête nationale sur les tableaux de chasse à tir. Saison 2013-2014.  
596 Résultats nationaux. *Faune Sauvage* **310**: 1–8.
- 597 **Banks PB, Norrdahl K, Korpimäki E. 2002.** Mobility decisions and the predation risks of  
598 reintroduction. *Biological Conservation* **103**: 133–138.

599 **Béchet A, Giroux JF, Gauthier G. 2004.** The effects of disturbance on behaviour, habitat  
600 use and energy of spring staging snow geese. *Journal of Applied Ecology* **41**: 689–700.

601 **Bengtsson D, Avril A, Gunnarsson G, Elmberg J, Söderquist P, Norevik G, Tolf C, Safi**  
602 **K, Fiedler W, Wikelski M. 2014.** Movements, home-range size and habitat selection of  
603 mallards during autumn migration. *PLoS ONE* **9**: e100764.

604 **Bischof R, Gjevestad JGO, Ordiz A, Eldegard K, Milleret C. 2019.** High frequency GPS  
605 bursts and path-level analysis reveal linear feature tracking by red foxes. *Scientific reports* **9**:  
606 1–13.

607 **Bize P, Diaz C, Lindström J. 2012.** Experimental evidence that adult antipredator behaviour  
608 is heritable and not influenced by behavioural copying in a wild bird. *Proceedings of the*  
609 *Royal Society B: Biological Sciences* **279**: 1380–1388.

610 **Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010.** Screening global  
611 positioning system location data for errors using animal movement characteristics. *The*  
612 *Journal of Wildlife Management* **74**: 1361–1366.

613 **Bonnot N, Couriot O, Berger A, Cagnacci F, Ciuti S, De Groeve J, Gehr B, Heurich M,**  
614 **Kjellander P, Kröschel M. 2020.** Fear of the dark? Contrasting impacts of humans vs lynx  
615 on diel activity of roe deer across Europe. *Journal of Animal Ecology* **89**: 132–145.

616 **Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KCJ. 2013.** A flexible GPS  
617 tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology* **154**:  
618 571–580.

619 **Bretagnolle V, Berthet E, Gross N, Gauffre B, Plumejeaud C, Houte S, Badenhauer I,**  
620 **Monceau K, Allier F, Monestiez P. 2018.** Towards sustainable and multifunctional  
621 agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER  
622 platform. *Science of The Total Environment* **627**: 822–834.

623 **Bro E, Reitz F, Clobert J, Migot P, Massot M. 2001.** Diagnosing the environmental causes  
624 of the decline in Grey Partridge *Perdix perdix* survival in France. *Ibis* **143**: 120–132.

625 **Bro E, Mayot P, Corda EVE, Reitz F. 2004.** Impact of habitat management on grey  
626 partridge populations: assessing wildlife cover using a multisite BACI experiment. *Journal of*  
627 *Applied Ecology* **41**: 846–857.

628 **Bro E, Millot F, Delorme R, Polvé C, Mangin E, Godard A, Tardif F, Gouache C, Sion I,**  
629 **Brault X. 2013.** PeGASE, bilan synthétique d’une étude perdrix grise «population-  
630 environnement». *Faune Sauvage* **298**: 17–48.

631 **Bro E. 2016.** *La Perdrix grise. Biologie, écologie, gestion et conservation*. Mèze.

632 **Bro E, Crosnier A. 2012.** Grey Partridges *Perdix perdix* in France in 2008: distribution,  
633 abundance, and population change. *Bird Study* **59**: 320–326.

634 **Buner FD. 2006.** Survival, habitat use and disturbance behaviour of re-introduced grey  
635 partridges "*Perdix perdix*" L. in an enhanced arable landscape in the Swiss Klettgau.

636 **Buner F, Schaub M. 2008.** How do different releasing techniques affect the survival of  
637 reintroduced grey partridges *Perdix perdix*? *Wildlife Biology* **14**: 26–35.

638 **Calenge C. 2017.** adehabitatHS: Analysis of Habitat Selection by Animals. - <[https://cran.r-](https://cran.r-project.org/web/packages/adehabitatHS/index.html)  
639 [project.org/web/packages/adehabitatHS/index.html](https://cran.r-project.org/web/packages/adehabitatHS/index.html)>.

640 **Camacho C, Palacios S, Sáez P, Sánchez S, Potti J. 2014.** Human-induced changes in  
641 landscape configuration influence individual movement routines: lessons from a versatile,  
642 highly mobile species. *PLoS One* **9**: e104974.

643 **Casas F, Mougeot F, Viñuela J, Bretagnolle V. 2009.** Effects of hunting on the behaviour  
644 and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural  
645 areas. *Animal Conservation* **12**: 346–354.

646 **Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS. 2012.** Human  
647 selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society of*  
648 *London B: Biological Sciences* **279**: 4407–4416.

649 **Cordero-Rivera A. 2017.** Behavioral diversity (ethodiversity): a neglected level in the study  
650 of biodiversity. *Frontiers in Ecology and Evolution* **5**: 1–7.

651 **Creel S, Winnie J, Maxwell B, Hamlin K, Creel M. 2005.** Elk alter habitat selection as an  
652 antipredator response to wolves. *Ecology* **86**: 3387–3397.

653 **Creel S, Christianson D. 2008.** Relationships between direct predation and risk effects.  
654 *Trends in Ecology & Evolution* **23**: 194–201.

655 **Cresswell W, Quinn JL. 2013.** Contrasting risks from different predators change the overall  
656 nonlethal effects of predation risk. *Behavioral Ecology* **24**: 871–876.

657 **Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. 2009.**  
658 Human predators outpace other agents of trait change in the wild. *Proceedings of the National*  
659 *Academy of Sciences* **106**: 952–954.

660 **Duriez O, Fritz H, Said S, Ferrand Y. 2005.** Wintering behaviour and spatial ecology of  
661 Eurasian woodcock *Scolopax rusticola* in western France. *Ibis* **147**: 519–532.

662 **Frid A, Dill L. 2002.** Human-caused Disturbance Stimuli as a Form of Predation Risk.  
663 *Conservation Ecology* **6**: 11–26.

664 **Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018.** The influence of human  
665 disturbance on wildlife nocturnality. *Science* **360**: 1232–1235.

666 **Gée A, Sarasa M, Pays O. 2018.** Long-term variation of demographic parameters in four  
667 small game species in Europe: opportunities and limits to test for a global pattern. *Animal*  
668 *Biodiversity and Conservation* **41**: 33–60.

669 **Gehr B, Hofer EJ, Pewsner M, Ryser A, Vimercati E, Vogt K, Keller LF. 2018.** Hunting-  
670 mediated predator facilitation and superadditive mortality in a European ungulate. *Ecology*  
671 *and Evolution* **8**: 109–119.

672 **Guthery FS, Hiller TL, Puckett Jr WH, Baker RA, Smith SG, Rybak AR. 2004.** Effects  
673 of feeders on dispersion and mortality of bobwhites. *Wildlife Society Bulletin* **32**: 1248–1254.

674 **Hall ML, van Asten T, Katsis AC, Dingemanse NJ, Magrath MJL, Mulder RA. 2015.**  
675 Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young?  
676 *Frontiers in Ecology and Evolution* **3**: 1–14.

677 **Halle S. 2000.** Ecological relevance of daily activity patterns. In: Halle, S. and Stenseth, N. C.  
678 (eds), *Activity patterns in small mammals. An ecological approach*. Springer, pp. 67–90.

679 **Harmange C, Bretagnolle V, Sarasa M, Pays O. 2019.** Changes in habitat selection patterns  
680 of the gray partridge *Perdix perdix* in relation to agricultural landscape dynamics over the past  
681 two decades. *Ecology and Evolution* **9**: 5236–5247.

682 **Hendry AP, Farrugia TJ, Kinnison MT. 2008.** Human influences on rates of phenotypic  
683 change in wild animal populations. *Molecular ecology* **17**: 20–29.

684 **Holtmann B, Santos ES, Lara CE, Nakagawa S. 2017.** Personality-matching habitat choice,  
685 rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance.  
686 *Proceedings of the Royal Society B: Biological Sciences* **284**: 1–9.

687 **Homberger B, Jenni L, Duplain J, Lanz M, Schaub M. 2021.** Strong effects of radio-tags,  
688 social group and release date on survival of reintroduced grey partridges. *Animal*  
689 *Conservation*. (in press).

690 **Johnson AR, Wiens JA, Milne BT, Crist TO. 1992.** Animal movements and population  
691 dynamics in heterogeneous landscapes. *Landscape ecology* **7**: 63–75.

692 **Jucá T, Boyle S, Cavalcanti G, Cavalcante T, Tomanek P, Clemente S, de Oliveira T,**  
693 **Barnett AA. 2020.** Being hunted high and low: do differences in nocturnal sleeping and

694 diurnal resting sites of howler monkeys (*Alouatta nigerrima* and *Alouatta discolor*) reflect  
695 safety from attack by different types of predator? *Biological Journal of the Linnean Society*  
696 **131**: 203–219.

697 **Kareiva PM, Shigesada N. 1983.** Analyzing insect movement as a correlated random walk.  
698 *Oecologia* **56**: 234–238.

699 **Kenward RE. 2001.** *A manual for wildlife radio tagging*. Academic press, London, UK.

700 **Koolhaas JM, De Boer SF, Buwalda B, Van Reenen K. 2007.** Individual variation in  
701 coping with stress: a multidimensional approach of ultimate and proximate mechanisms.  
702 *Brain, behavior and evolution* **70**: 218–226.

703 **Krauze-Gryz D, Gryz JB, Goszczyński J, Chylarecki P, Zmihorski M. 2012.** The good,  
704 the bad, and the ugly: space use and intraguild interactions among three opportunistic  
705 predators—cat (*Felis catus*), dog (*Canis lupus familiaris*), and red fox (*Vulpes vulpes*)—under  
706 human pressure. *Canadian Journal of Zoology* **90**: 1402–1413.

707 **Kuijper DPJ, Oosterveld E, Wymenga E. 2009.** Decline and potential recovery of the  
708 European grey partridge (*Perdix perdix*) population—a review. *European Journal of Wildlife*  
709 *Research* **55**: 455–463.

710 **Laundré JW, Hernández L, Altendorf KB. 2001.** Wolves, elk, and bison: reestablishing  
711 the” landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* **79**:  
712 1401–1409.

713 **Lenth R, Singmann H, Love J, Buerkner P, Hervé M. 2019.** emmeans: Estimated Marginal  
714 Means, aka Least-Squares Means. - <[https://cran.r-](https://cran.r-project.org/web/packages/emmeans/index.html)  
715 [project.org/web/packages/emmeans/index.html](https://cran.r-project.org/web/packages/emmeans/index.html)>.

716 **Letty J, Marchandean S, Aubineau J. 2007.** Problems encountered by individuals in animal  
717 translocations: lessons from field studies. *Ecoscience* **14**: 420–431.

718 **Lima SL, Dill LM. 1990.** Behavioral decisions made under the risk of predation: a review  
719 and prospectus. *Canadian journal of zoology* **68**: 619–640.

720 **Lockwood MA, Griffin CP, Morrow ME, Randel CJ, Silvy NJ. 2005.** Survival,  
721 movements, and reproduction of released captive-reared Attwater's prairie-chicken. *The*  
722 *Journal of wildlife management* **69**: 1251–1258.

723 **Lone K, Loe LE, Gobakken T, Linnell JDC, Odden J, Remmen J, Mysterud A. 2014.**  
724 Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting  
725 pattern of predation risk imposed by lynx and humans. *Oikos* **123**: 641–651.

726 **Lone K, Loe LE, Meisingset EL, Stamnes I, Mysterud A. 2015.** An adaptive behavioural  
727 response to hunting: surviving male red deer shift habitat at the onset of the hunting season.  
728 *Animal Behaviour* **102**: 127–138.

729 **Lone K, Mysterud A, Gobakken T, Odden J, Linnell J, Loe LE. 2017.** Temporal variation  
730 in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple  
731 predators. *Oikos* **126**: 624–632.

732 **Masse RJ, Tefft BC, Amador JA, McWilliams SR. 2013.** Why woodcock commute: testing  
733 the foraging-benefit and predation-risk hypotheses. *Behavioral Ecology* **24**: 1348–1355.

734 **McDougall PT, Réale D, Sol D, Reader SM. 2006.** Wildlife conservation and animal  
735 temperament: causes and consequences of evolutionary change for captive, reintroduced, and  
736 wild populations. *Animal Conservation* **9**: 39–48.

737 **Millon A, Bourrioux JL, Riols C, Bretagnolle V. 2002.** Comparative breeding biology of  
738 Hen Harrier and Montagu's Harrier: an 8-year study in north-eastern France. *Ibis* **144**: 94–  
739 105.

740 **Monterroso P, Alves PC, Ferreras P. 2013.** Catch me if you can: diel activity patterns of  
741 mammalian prey and predators. *Ethology* **119**: 1044–1056.

742 **Moorcroft D, Whittingham MJ, Bradbury RB, Wilson JD. 2002.** The selection of stubble  
 743 fields by wintering granivorous birds reflects vegetation cover and food abundance. *Journal*  
 744 *of Applied Ecology* **39**: 535–547.

745 **Moreno S, Delibes M, Villafuerte R. 1996.** Cover is safe during the day but dangerous at  
 746 night: the use of vegetation by European wild rabbits. *Canadian Journal of Zoology* **74**:  
 747 1656–1660.

748 **Novoa C, Aebischer NJ, Landry P. 2002.** Upland habitat use by Pyrenean grey partridges  
 749 *Perdix perdix hispaniensis* during the breeding season. *Wildlife Biology* **8**: 99–108.

750 **Parish DMB, Sotherton NW. 2007.** The fate of released captive-reared grey partridges  
 751 *Perdix perdix*: implications for reintroduction programmes. *Wildlife Biology* **13**: 140–149.

752 **Pays O, Fortin D, Gassani J, Duchesne J. 2012.** Group dynamics and landscape features  
 753 constrain the exploration of herds in fusion-fission societies: the case of European roe deer.  
 754 *PLoS ONE* **7**: e34678.

755 **Pereira M, Rodríguez A. 2010.** Conservation value of linear woody remnants for two forest  
 756 carnivores in a Mediterranean agricultural landscape. *Journal of Applied Ecology* **47**: 611–  
 757 620.

758 **Pérez JA, Alonso ME, Prieto R, Bartolomé D, Gaudioso DVR. 2010.** Influence of the  
 759 breeding system on the escape response of red-legged partridges (*Alectoris rufa*). *Poultry*  
 760 *Science* **89**: 5–12.

761 **Potts GD. 2012.** *Partridges: Countryside Barometer (Collins New Naturalist Library, Book*  
 762 *121)*. HarperCollins UK.

763 **Putaala A, Oksa J, Rintamaki H, Hissa R. 1997.** Effects of hand-rearing and  
 764 radiotransmitters on flight of gray partridge. *Journal of Wildlife Management* **61**: 1345–1351.

765 **Putaala A, Hissa R. 1995.** Effects of hand-rearing on physiology and anatomy in the grey  
 766 partridge. *Wildlife Biology* **1**: 27–31.



767 **R Core Team. 2019.** *R: A language and environment for statistical computing*. Vienna,  
768 Austria: R Foundation for Statistical Computing.

769 **Rantanen EM, Buner F, Riordan P, Sotherton NW, Macdonald DW. 2010a.** Habitat  
770 preferences and survival in wildlife reintroductions: an ecological trap in reintroduced grey  
771 partridges. *Journal of applied ecology* **47**: 1357–1364.

772 **Rantanen EM, Buner F, Riordan P, Sotherton NW, Macdonald DW. 2010b.** Vigilance,  
773 time budgets and predation risk in reintroduced captive-bred grey partridges *Perdix perdix*.  
774 *Applied Animal Behaviour Science* **127**: 43–50.

775 **Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007.** Integrating animal  
776 temperament within ecology and evolution. *Biological reviews* **82**: 291–318.

777 **Reitz F, Mayot P. 1999.** Effects of habitat characteristics on the predation risk of grey  
778 partridges. In: *XXIVth IUGB Congress, Greece.*, pp. 248–258.

779 **Reyna KS, Newman WL. 2018.** Comparative Analysis of Behavioural Response of Captive-  
780 Reared and Wild-Trapped Northern Bobwhites to Simulated Predator Attacks. *Avian Biology*  
781 *Research* **11**: 16–23.

782 **Rinaud T, Harmange C, Pays O, Sarasa M, Saillard M, Bretagnolle V. 2020.** Interspecific  
783 competition between two partridges in farmland landscapes. *Animal Behaviour* **165**: 23–34.

784 **Rotella JJ, Ratti JT. 1988.** Seasonal variation in gray partridge vocal behavior. *Condor* **90**:  
785 304–310.

786 **Rymesova D, Tomasek O, Salek M. 2013.** Differences in mortality rates, dispersal distances  
787 and breeding success of commercially reared and wild grey partridges in the Czech  
788 agricultural landscape. *European Journal of Wildlife Research* **59**: 147–158.

789 **Sánchez-García C, Buner FD, Aebischer NJ. 2015.** Supplementary winter food for  
790 gamebirds through feeders: Which species actually benefit? *The Journal of Wildlife*  
791 *Management* **79**: 832–845.

792 **Selva N, Berezowska-Cnota T, Elguero-Claramunt I. 2014.** Unforeseen effects of  
793 supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation. *PLoS*  
794 *One* **9**: e90740.

795 **Shamoon H, Maor R, Saltz D, Dayan T. 2018.** Increased mammal nocturnality in  
796 agricultural landscapes results in fragmentation due to cascading effects. *Biological*  
797 *Conservation* **226**: 32–41.

798 **Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS,**  
799 **Vonesh JR. 2010.** Predator–prey naïveté, antipredator behavior, and the ecology of predator  
800 invasions. *Oikos* **119**: 610–621.

801 **Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012.** Ecological implications of behavioural  
802 syndromes. *Ecology letters* **15**: 278–289.

803 **Sih A, Englund G, Wooster D. 1998.** Emergent impacts of multiple predators on prey.  
804 *Trends in ecology & evolution* **13**: 350–355.

805 **Tillmann JE. 2009.** Fear of the dark: night-time roosting and anti-predation behaviour in the  
806 grey partridge (*Perdix perdix* L.). *Behaviour* **146**: 999–1023.

807 **Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E. 2009.** Responding to spatial  
808 and temporal variations in predation risk: space use of a game species in a changing landscape  
809 of fear. *Canadian Journal of Zoology* **87**: 1129–1137.

810 **Valkama J, Korpimäki E, Arroyo B, Beja P, Bretagnolle V, Bro E, Kenward R, Mañosa**  
811 **S, Redpath SM, Thirgood S, Viñuela J. 2005.** Birds of prey as limiting factors of gamebird  
812 populations in Europe: a review. *Biological Reviews* **80**: 171–203.

813 **Van Oers K, Drent PJ, Goede P de, Noordwijk AJ van. 2004b.** Realized heritability and  
814 repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the*  
815 *Royal Society of London B: Biological Sciences* **271**: 65–73.

816 **Watson M Aebischer NJ, Cresswell W. 2007.** Vigilance and fitness in grey partridges  
817 *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation  
818 mortality. *Journal of Animal Ecology* **76**: 211–221.

819 **Whiteside MA, Sage R, Madden JR. 2016.** Multiple behavioural, morphological and  
820 cognitive developmental changes arise from a single alteration to early life spatial  
821 environment, resulting in fitness consequences for released pheasants. *Royal Society Open*  
822 *Science* **3**: 160008.

823 **Whittingham MJ, Butler SJ, Quinn JL, Cresswell W. 2004.** The effect of limited visibility  
824 on vigilance behaviour and speed of predator detection: implications for the conservation of  
825 granivorous passerines. *Oikos* **106**: 377–385.

826 **Wolf ID, Hagenloh G, Croft DB. 2013.** Vegetation moderates impacts of tourism usage on  
827 bird communities along roads and hiking trails. *Journal of Environmental Management* **129**:  
828 224–234.

829 **Wood SN. 2006.** *Generalized additive models: an introduction with R*. Boca Raton: CRC-  
830 Chapman and Hall.

831 **Wood S, Wood MS. 2015.** mgcv: Mixed GAM Computation Vehicle with Automatic  
832 Smoothness Estimation. - <<https://cran.r-project.org/web/packages/mgcv/index.html>>.

833

834

## 835 **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.

839 **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	$\chi^2$ 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	$\chi^2$ value	Df	P value	Estimate $\pm$ SE
				(intercept: $-0.125 \pm 0.347$ )
Distance to woodland	10.70	1	<0.01	$-0.034 \pm 0.010$
Distance to building	5.64	1	0.02	$-0.030 \pm 0.013$
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:

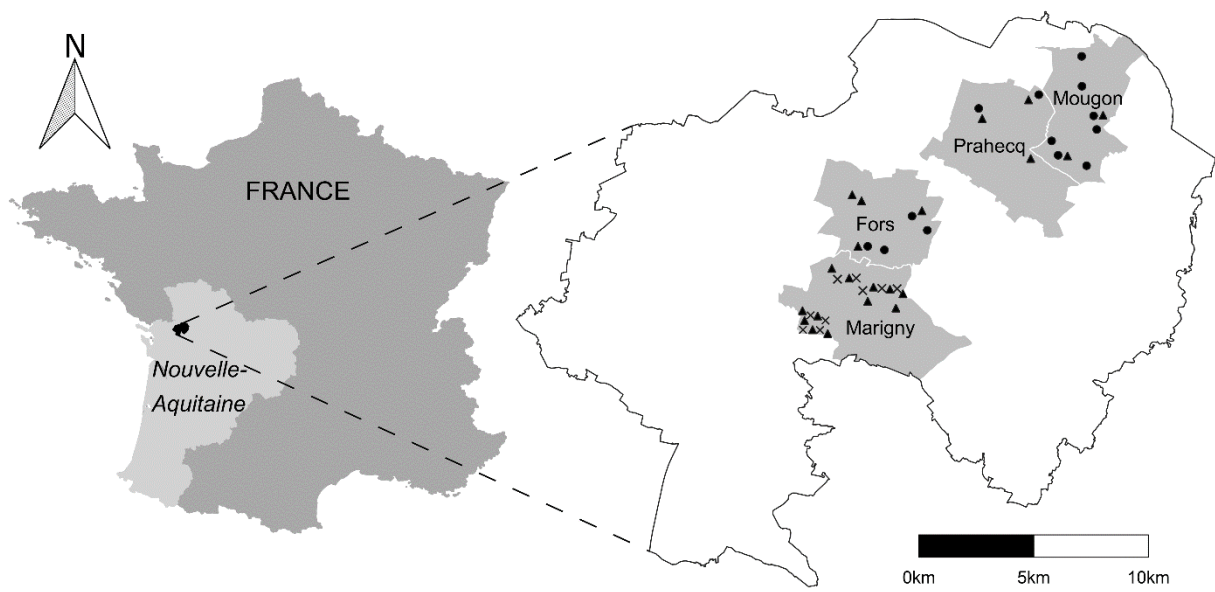
**Figure 1** Communal boundaries of each studied hunting association within the Long-Term Socio-Ecological Research (LTSER) platform “Zone Atelier Plaine & Val de Sèvre”, *Département des Deux-Sèvres*, France. Symbols represent release sites (●: 2015; ▲: 2016; ×: 2017).

**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.

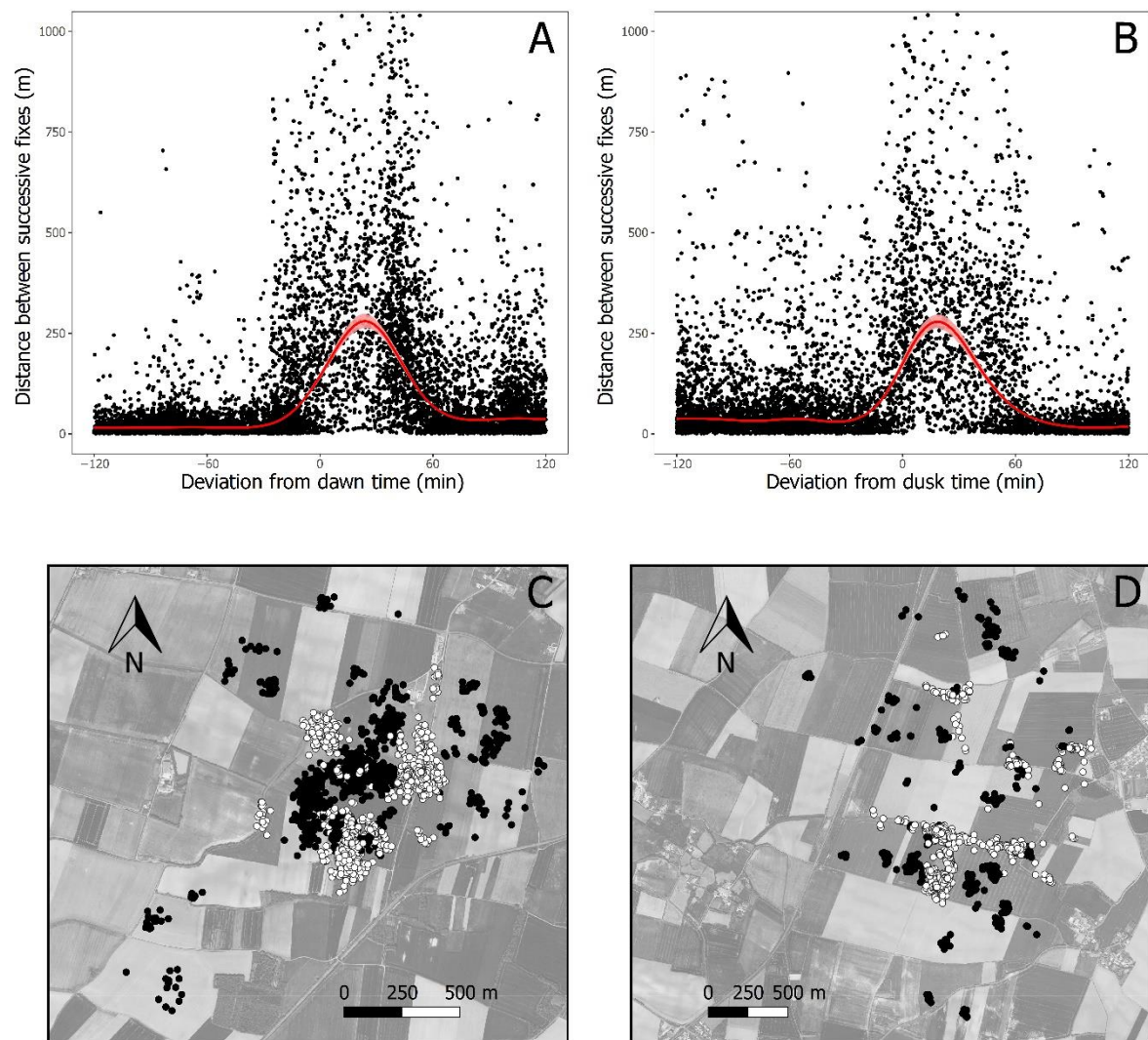
**Figure 3** Nocturnal (grey boxes,  $n = 13$ ) and diurnal (white boxes,  $n = 13$ ) ratios of proportion of habitat use/availability across 5 habitat types in autumn by grey partridge. The dashed line represents the threshold of 1, indicating the habitat use as expected by chance.

**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.

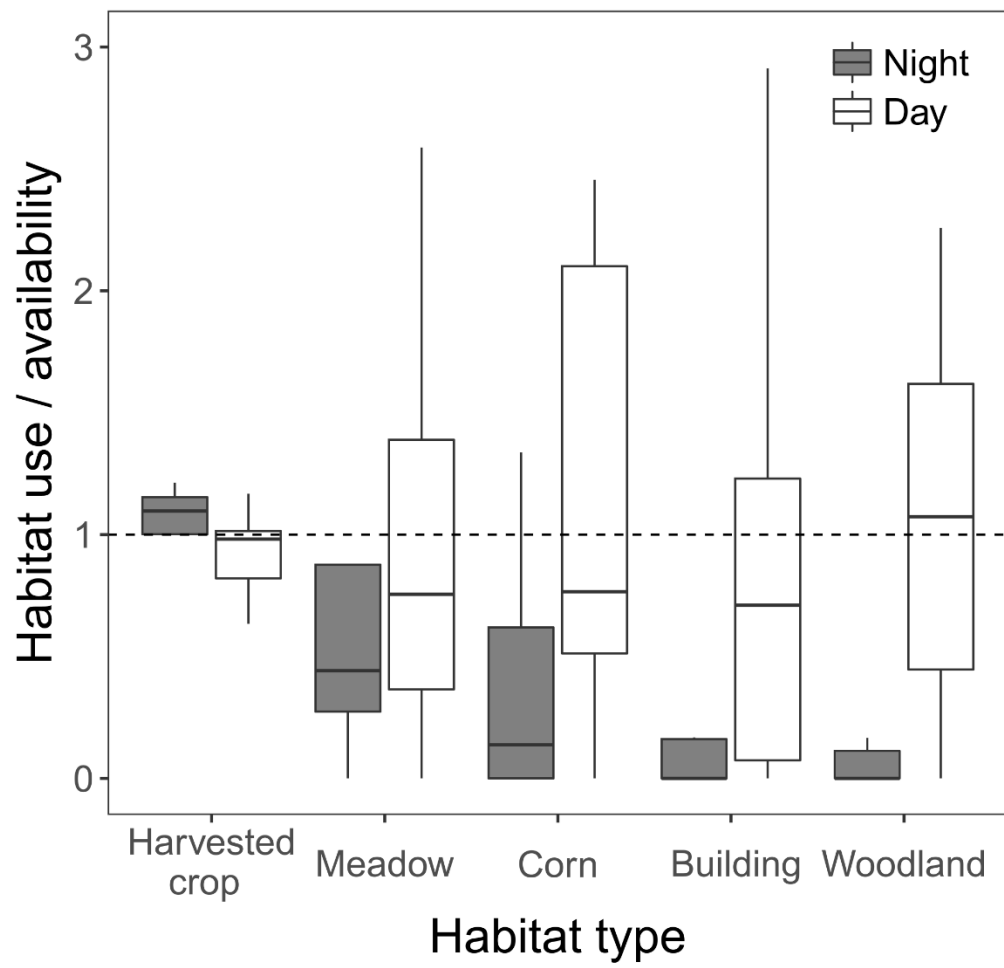




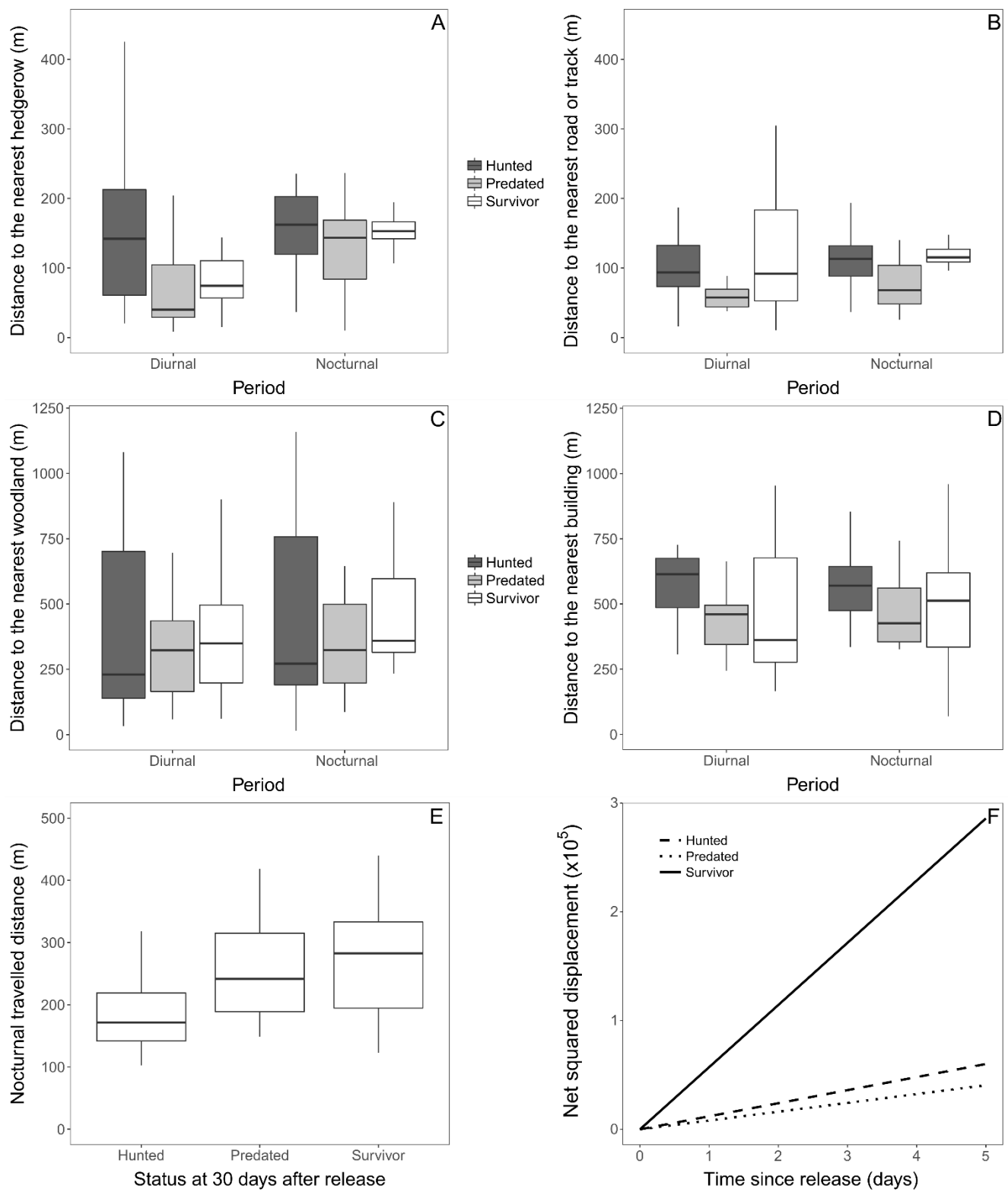
**Figure 1**



**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.

<b>Fate of birds</b>	<b>2015</b>	<b>2016</b>	<b>2017</b>	<b>Total</b>
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

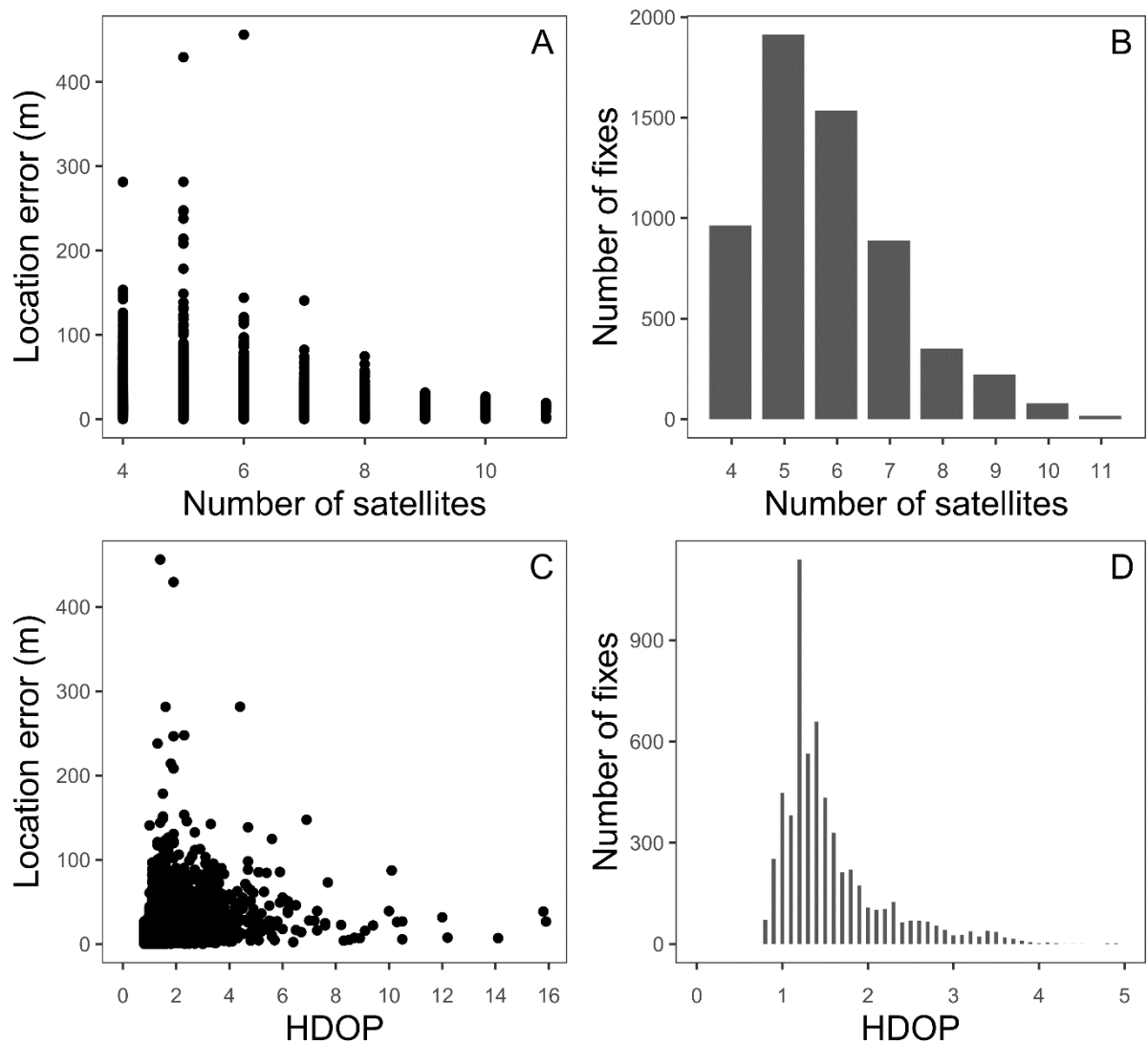
**Table S3** Tukey's multicomparison post-hoc tests calculated following computation of a linear mixed-effect model for grey partridge distance to hedgerows as a function of the interacting effect of the period (day, night) and the survival status of birds 30 days after release (Predated, Hunted, Survivor).

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

## References

- Bjørneraas K, Van Moorter B, Rolandsen CM & Herfindal I. 2010.** Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management* **74**: 1361–1366.
- Forin-Wiart MA, Hubert P, Sirguey P & Poulle ML. 2015.** Performance and accuracy of lightweight and low-cost GPS data loggers according to antenna positions, fix intervals, habitats and animal movements. *PLoS ONE* **10**: e0129271.
- Jiang Z, Sugita M, Kitahara M, Takatsuki S, Goto T & Yoshida Y. 2008.** Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. *Ecological Research* **23**: 581–588.
- Kleyheeg E, van Dijk JGB, Tsopoglou-Gkina D, Woud TY, Boonstra DK, Nolet BA & Soons MB. 2017.** Movement patterns of a keystone waterbird species are highly predictable from landscape configuration. *Movement Ecology* **5**: 2.
- Lewis JS, Rachlow JL, Garton EO & Vierling LA. 2007.** Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology* **44**: 663–671.
- McGregor HW, Legge S, Jones ME & Johnson CN. 2014.** Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* **9**: e109097.

### 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 2<sup>nd</sup> to 4<sup>th</sup> fixes to check if the next fix was also included in the roost. If fixes were mutually separated by less than 50 meters, the 4<sup>th</sup> 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.

## References

**Barraquand F & Benhamou S. 2008.** Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology* **89**: 3336–3348.

**Benhamou S. 1992.** Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology* **159**: 67–81.

**Bivand, R. and Rundel, C. 2017.** rgeos: Interface to Geometry Engine-Open Source (GEOS). - <<https://cran.r-project.org/web/packages/rgeos/index.html>>.

## **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.

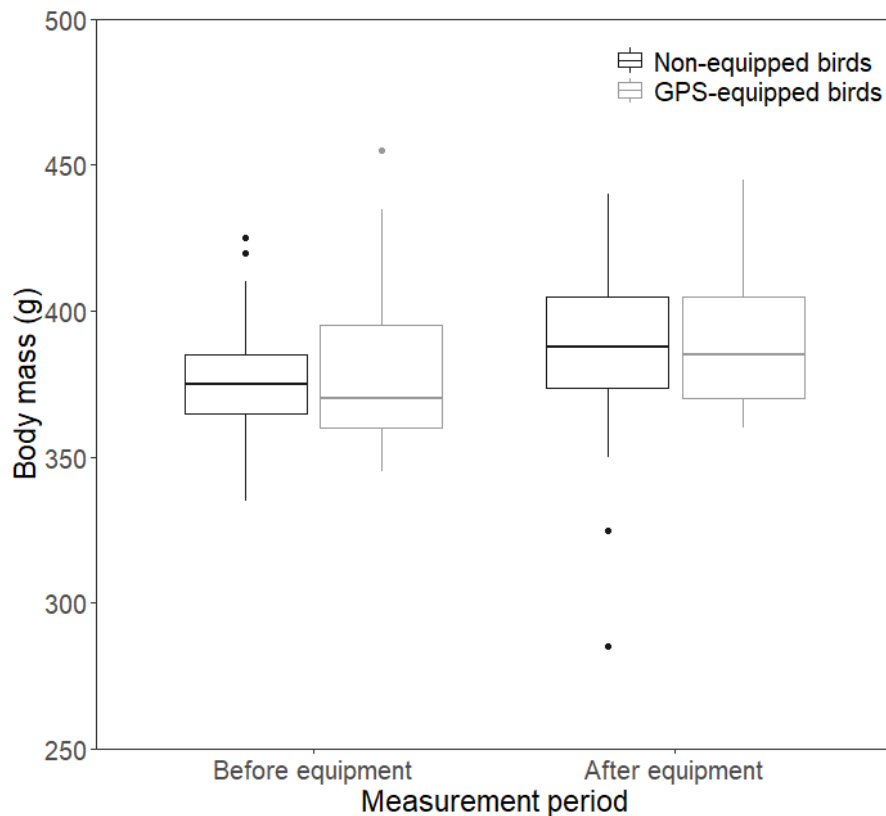
We found that proportions of GPS-equipped and non-equipped birds at recapture were conform to their respective proportions at release (chi-square test:  $\chi = 0.007$ ;  $n = 56$ ;  $df = 1$ ;  $p = 0.93$ ), suggesting that partridge mortality was not influenced by GPS devices in this released population.

### *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).