

RESEARCH ARTICLE

Do human infrastructures shape nest distribution in the landscape depending on individual personality in a farmland bird of prey?

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Abstract

1. Individuals' distribution across habitats may depend on their personality. Human activities and infrastructures are critical elements of the landscape that may impact the habitat selection process. However, depending on their personality, individuals may respond differently to these unnatural elements.
2. In the present study, we first investigated whether some human infrastructures (buildings, roads and paths) shaped Montagu's harrier nest spatial distribution in the landscape according to female personality (boldness). Second, we tested if the reproductive success of females depended on their boldness and nest location regarding infrastructures.
3. Using a long-term (19 years) dataset, we calculated, for each infrastructure type, the distance from each nest to the nearest infrastructure and the infrastructure density around the nest. We tested the effects of female boldness (bold vs. shy) and its interaction with egg-laying date on these six metrics.
4. Nest location in the landscape depended on female personality and on some human infrastructures: the building density was smaller around nests from shy females than from bold ones. Nest distribution related to other infrastructure metrics did not depend on female boldness. The pattern related to building density is consistent with some habitat choice hypotheses, which are discussed. Path density around nests negatively affected reproductive success regardless of female boldness, and late breeders nested further away from paths than early breeders. Human activities on paths (more common later in the season) could lead to disturbance and a decrease in parental care, reducing reproductive success.
5. Increasing human presence in farmlands implies a need to better understand its impact on population composition, in terms of personality. Our results suggest that individual behavioural differences should be taken into account in studies assessing the effects of human disturbance on animal populations, to propose more appropriate conservation measures.

KEYWORDS

boldness, *Circus pygargus*, human disturbance, nest site selection, reproductive success, spatial distribution

1 | INTRODUCTION

Understanding how animals select their breeding sites is crucial because environmental factors such as abiotic conditions, food resources and predator abundance may have direct and indirect effects on reproductive success (Barbaro et al., 2008; Chase, 2002; Hall et al., 1997; Jones, 2001; Warner et al., 2002). The distribution of breeding sites, thus, depends on the temporal and spatial arrangement of these environmental components within the landscape (Clark & Shutler, 1999; Stenhouse et al., 2005). Human activities and infrastructures are components increasingly present in the environment (Balmford et al., 2009; McKinney, 2002), which may negatively affect the reproductive success of animals through effects on their behaviour and physiology (Ellenberg et al., 2007; González et al., 2006; Hutflus & Dingemanse, 2019; Strasser & Heath, 2013; Zuberogoiitia et al., 2008). Nest attendance, including food provisioning to nestlings and time spent at the nest, has been shown to decrease with increasing human presence (e.g. fishermen, passers-by, hunters) and human activities (e.g. helicopters, motorbikes), resulting in reduced reproductive success, in species such as bearded vulture *Gypaetus barbatus* and marsh harrier *Circus aeruginosus* (Arroyo & Razin, 2006; Fernández & Azkona, 1993). Consequently, human activities and infrastructures could affect the breeding site selection process, and individuals may select breeding sites to avoid human disturbances (Hanane, 2014; Kolbe & Janzen, 2002; Martínez-Abraín et al., 2010; Pedrana et al., 2014; Remacha & Delgado, 2009; Yasué & Dearden, 2006). For instance, European nightjars *Caprimulgus europaeus* and great tits *Parus major* nest in areas with a lower density of walking and cycling tracks or nest further away from highly frequented tracks (Hutflus & Dingemanse, 2019; Lowe et al., 2014).

Within the same population, anthropogenic disturbances may, however, affect individuals differently. Some individuals could be more tolerant to human activities than others depending on their personality, that is the way individuals consistently differ in behaviour from each other across time and contexts (Biro & Stamps, 2008; Dingemanse et al., 2010; Réale et al., 2007). Personality traits such as boldness or exploration could be involved in individual abilities to disperse or colonise new habitats or even to tolerate human disturbance (Wolf & Weissing, 2012). Boldness may favour tolerance to humans and allow individuals to settle closer to human infrastructures, as shown in burrowing owl *Athene cunicularia* (Carrete & Tella, 2010; see also Evans et al., 2010; Atwell et al., 2012). For instance, the personality-matching habitat choice hypothesis (Cote et al., 2010; DiNuzzo & Griffen, 2020; Edelaar et al., 2008; Holtmann et al., 2017; Jacob et al., 2015) predicts that individuals should be selective in the way they use their environment depending on their personality. Individuals may select their habitat according to human disturbances, with shy individuals showing stronger avoidance of areas with more frequent human activities and infrastructures than bold ones (Holtmann et al., 2017; Sprau & Dingemanse, 2017; Wolf & Weissing, 2012). To date, few studies have investigated how human activities or infrastructures shape

the spatial distribution of breeding site depending on individual personality (Carrete & Tella, 2010; Holtmann et al., 2017; Martin & Réale, 2008; Sprau & Dingemanse, 2017) and particularly the consequences on their reproductive success (Zhao et al., 2016). Indeed, a decrease in the phenotypic diversity of a population related to personality traits may have negative consequences on its adaptability and viability, especially when facing perturbations (Smith & Blumstein, 2013; Wolf & Weissing, 2012). Understanding how individual personality and life-history traits of individuals may be affected by environmental conditions (including human disturbance) could provide more accurate information on population viability, and thus to set up management conservation measures to prevent population declines (McDougall et al., 2006; Merrick & Koprowski, 2017; Smith & Blumstein, 2013).

The Montagu's harrier *Circus pygargus* is a migratory species characteristic of farmland habitats that nests on the ground within cereal crops, making it vulnerable to human activities (including agricultural practices, activities around villages, recreative activities, traffic noise; see the synthesis by Arroyo et al., 2004). This raptor species is semi-colonial: pairs nest either isolated or in loose colonies depending on years and areas (maximum aggregation within c. 500 m in our study site, Cornulier & Bretagnolle, 2006). Females differ in their breeding phenology (egg-laying date occurred from the end of April until June in our study area), possibly resulting from differences in migratory patterns or individual quality. This could affect nest site selection depending on the availability of suitable breeding sites at different times during a breeding season. Links between nest site selection and reproductive timing could further differ according to individual personality if the relative quality of available breeding sites differs among females in relation to their personality. A long-term study highlighted the differences in boldness in Montagu's harrier females within the population and the consequences for their reproductive success (Arroyo et al., 2017).

In the present study, we investigated (a) if human infrastructures shaped nest spatial distribution in the landscape depending on female boldness and their egg-laying date and (b) if the reproductive success of females depended on their boldness and nest location regarding infrastructures. The study was carried out in intensive farmland and was based on the same long-term dataset (1995–2013) used by Arroyo et al. (2017) with additional information on infrastructures near study nests. Because our objective was to describe a spatial distribution pattern and to assess its consequences on reproductive success, the study was conducted *in natura* without experimental modifications of human disturbances. We considered the proximity and density of infrastructures such as buildings, roads (i.e. paved roads) or paths (i.e. dirt roads) and their influence on nest distribution depending on both main and interactive effects of female boldness and egg-laying date. We assessed the nest distribution in relation to each infrastructure metric separately because we hypothesized that they would be associated with different types of human disturbance. We expected shy females to nest in areas with lower infrastructures density and farther from them. We further expected

these patterns to be modulated by egg-laying date which may be linked to site availability: late reproduction may result in lower availability of suitable sites and may constrain females to settle in more disturbed areas. Lastly, we expected the proximity and density of infrastructures around the nest to reduce reproductive success for both shy and bold females because associated disturbances would lead to reduced parental care. These patterns were further expected to be modulated by female boldness, as the costs of choosing a more disturbed nesting site would be higher for shy than bold females. In areas with lower infrastructure density, we expected no differences in reproductive success between shy and bold females. Therefore, we tested for main and interactive effects of infrastructure metrics and female boldness on reproductive success. A significant interaction between these effects would highlight that females respond to infrastructures depending on their boldness and would suggest that females should choose nesting site depending on their boldness.

2 | MATERIALS AND METHODS

2.1 | Study site and model species

The study was conducted in the Long-Term Socio-Ecological Research (LTSER) Zone Atelier Plaine et Val de Sèvre (ZAPVS, western France, 46°110 N, 0°280 W), an intensive agricultural area mostly dedicated to cereal crop production. ZAPVS covers c. 435 km² of farmland (Bretagnolle et al., 2018), where land use in each crop field, as well as human infrastructures such as villages, industrial and agricultural buildings, motorway (one crosses the study site), roads and paths, have been monitored since 1995 and mapped onto a Geographical Information System (GIS; QUANTUMGIS 2.18; QGIS Development Team, 2017).

The Montagu's harrier population in the ZAPVS has been exhaustively monitored since 1995 (Bretagnolle et al., 2018), each nest being geo-localized using a Global Positioning System receiver (x, y coordinates) and surveyed over the whole reproductive season from late April (earliest egg-laying) to the end of July (incubation duration: 29 days on average; nestling rearing period duration: 30–35 days; Arroyo et al., 2007; García & Arroyo, 2001). Common vole *Microtus arvalis* abundance, the main prey of this raptor in the study area, greatly fluctuates among years (Bretagnolle et al., 2018) and has been shown to influence the number of Montagu's harrier breeders and their reproductive success (Arroyo et al., 2017; Millon & Bretagnolle, 2008). During years of high vole abundance, up to 100 pairs of Montagu's harriers can nest in the ZAPVS (Millon & Bretagnolle, 2008).

2.2 | Montagu's harrier female boldness and reproduction monitoring

Once nests were localized, they were visited by researchers once (rarely twice) during incubation and once a week during the rearing

period on average. At each nest visit, the fleeing probability of female was recorded as follows: 0 = the female stayed around the nest during the visit or 1 = disappeared. The male presence (0 = absent; 1 = present) during each nest visit was also recorded and the visit date transformed relative to the laying onset from each female (day 0 = day of first-egg laying). Female boldness was estimated from a generalized linear mixed-effects model fitted to a binomial-error distribution with a logit link function (BGLMM) analysing the fleeing probability regarding the nesting stage estimate (and its quadratic term) and the male presence/absence (binomial variable), including nest identity as a random term (see Arroyo et al., 2017). The random intercept extracted from the BGLMM was used as an estimate of female boldness (indicative of the female response at the beginning of the laying period - day 0, and in the absence of the male). This variable ranged between -5.16 and +5.78 but had a bimodal distribution (see Figure S1). For this study, boldness was categorized into two groups: bold females (0, those with random intercepts lower than or equal to -4.55, indicating low fleeing probability) and shy females (1, those with random intercepts higher than or equal to -1.08, indicating high fleeing probability; Figure S1).

Nest visits during incubation allowed recording clutch size and measuring eggs. Egg length and width were measured using a caliper (accuracy: ±0.1 mm) and egg mass using Pesola® electronic scale (accuracy: ±0.1 g) to estimate the laying date following Arroyo et al. (2017). Visits at the end of the rearing period allowed assessing the number of fledglings. Two factors, the relative laying date and the nest visit frequency were included in the present study because they are known to influence the reproductive success (Arroyo et al., 2017). The relative laying date for a given nest was calculated as the difference between its laying date and the mean laying date from all nests for that particular year. The relative laying date was used as a continuous variable in all models (see below). For each nest, the visit frequency represented the number of visits divided by the total length of nest monitoring (i.e. number of days from laying to fledging for successful nests, or to the estimated date of the failure otherwise).

2.3 | Vole abundance

In April and June, live-trapping was conducted in five different crop types to estimate vole abundance (vole captures/100 trap-nights; see Arroyo et al., 2017; Bretagnolle et al., 2018). Annual vole abundance estimates at the scale of the whole ZAPVS were calculated as the average abundance from all crop types in each trapping session (April and June) and then the average from the two trapping seasons each year (Arroyo et al., 2017; Barraquand et al., 2014).

2.4 | Nest distribution in the landscape

Three different human infrastructures were considered in this study: buildings whatever their use (i.e. houses, industrial and

agricultural buildings), roads (motorway, national, departmental and communal roads) and paths (dirt roads, agricultural and bike paths). In our GIS database, buildings were quantified by their surface, whereas linear elements (roads and paths) were quantified by their length. Then, two metrics were extracted from the GIS database for each nest. We first calculated the distance from the nest to the nearest infrastructure of each type (building, road, path): $Dist_{build}$, $Dist_{road}$, $Dist_{path}$. Second, we calculated the density of each infrastructure type around each nest, using a 1,000 m radius buffer. We chose this distance because it was twice the median distance from any nest to the nearest building (median = 530 m). Additionally, this radius is congruent with the distance of infrastructure effects reported by Benítez-López et al. (2010) in their meta-analysis. For each nest, we calculated the density of the buildings, hereafter $Dens_{build}$, as their percentage surface within the 1,000 m radius around the nest. The densities of roads or paths ($Dens_{road}$ and $Dens_{path}$) were calculated as their total length within the buffer per km². Links between all infrastructure metrics ($Dist_{build}$, $Dist_{road}$, $Dist_{path}$, $Dens_{build}$, $Dens_{road}$ and $Dens_{path}$) were checked with Spearman's rank correlation tests and the coefficients were small (Table S1).

Landscape metrics were calculated using R software (v. 3.5.1, R Development Core Team, 2018) and `RGDAL`, `RGEOS` and `RASTER` packages (Bivand et al., 2015; Bivand et al., 2019; Hijmans et al., 2015, respectively).

2.5 | Statistical analyses

The effect of human infrastructures on nest distribution was tested by modelling (a) the distances from the nest to the nearest infrastructure and (b) the infrastructure density within 1,000 m radius buffer around each nest depending on female boldness, relative laying date and their interaction as fixed effects. These analyses were performed using information from 787 nests. The consequences of infrastructure proximity and density on the reproductive success depending on female boldness were tested using 749 nests (information on reproductive success was lacking for 38 nests). We chose to test the effect of each infrastructure metric separately to avoid overfitting and collinearity problems (Table S1). We, however, provide results using one principal component analysis from the six infrastructure metrics in Supporting Information (see Tables S2, S3 and S4).

2.5.1 | Nest distribution related to human infrastructures: Effects of female boldness and relative laying date

Linear mixed-effects models (LMMs) were used to model the nest distances to the nearest different infrastructures ($Dist_{build}$, $Dist_{road}$, $Dist_{path}$), and the density of the different infrastructures around the nests ($Dens_{build}$, $Dens_{road}$, $Dens_{path}$) as dependent variables (using

`LMERTEST` package, Kuznetsova et al., 2014). The normality and the homoscedasticity of each infrastructure variable were checked using Shapiro-Wilk and Levene tests, respectively, and they were compliant except for $Dist_{road}$, $Dist_{path}$ and $Dens_{build}$. $Dist_{road}$ and $Dist_{path}$ were log-transformed and $Dens_{build}$ was square-root-transformed to meet normality and homoscedasticity assumptions. Thus, six separate models were tested, including female boldness, relative laying date and their interaction as fixed effects. The relative laying date was a continuous variable and was centred and scaled. We checked that fixed effects were not collinear. The proportion of the variance in each of these variables that is explained by the other independent variable (R^2) was estimated: $R^2 = 24\%$ for boldness explained by relative laying date, thus equivalent to VIF value of 1.32. We considered that collinearity was not an issue for VIF values below the threshold value of 2, following Zuur et al. (2010).

2.5.2 | Reproductive success

The reproductive success of females was assessed using BGLMM with a two-vector response variable that integrated both the number of fledglings and the clutch size for each female. We used the `cbind` function in R: `cbind(number of fledglings, clutch size - number of fledglings)`. Six separate BGLMMs were used, and each tested the effect of each of the six infrastructure metrics ($Dist_{build}$, $Dist_{road}$, $Dist_{path}$, $Dens_{build}$, $Dens_{road}$ and $Dens_{path}$) on reproductive success. Female boldness, relative laying date and vole abundance in the ZAPVS were included as fixed effects in the models. Visit frequency was included in the models to account for additional human disturbance due to research activities. Two interaction terms were considered in the models: the interaction between female boldness and infrastructure metrics and the interaction between female boldness and visit frequency. Each continuous variable (relative laying date, vole abundance, visit frequency and infrastructure metrics) was centred and scaled.

In all LMMs and BGLMMs, we included 'year' as a random effect to take into account environmental variations (other than those already evaluated) among years. Few females were individually tagged and could be identified from a year to the next (30 tagged females out of 797 nests nested at least 2 years in our study area from 1995 to 2013). It was therefore not possible to include female identity as a random effect. Within each model (LMMs and BGLMMs), significant effects of the interactions were tested using post hoc tests based on least-squares means associated to Benjamini-Hochberg's correction for multiple comparisons to control for false discovery rate (using 'multcomp' and 'lsmeans' packages, Hothorn et al., 2008; Lenth, 2016, respectively, Benjamini & Hochberg, 1995). Following Forstmeier and Schielzeth (2011), we chose to present full models (LMMs and BGLMMs) with all main and interactive effects of explanatory variables. Statistics were performed with R software (v. 3.5.1, R Development Core Team, 2018).

3 | RESULTS

3.1 | Nest distribution related to human infrastructures: Effects of female boldness and relative laying date

A summary of the infrastructure metrics of nests depending on female boldness is given in Table S5. There was no effect of the interaction between female boldness and relative laying date on the different infrastructure metrics (95% confidence intervals (CI), $Dist_{build}$: [-51.018; 31.75]; $Dist_{road}$: [-0.11; 0.12]; $Dist_{path}$: [-0.18; 0.070]; $Dens_{build}$: [-0.0074; 0.0054]; $Dens_{road}$: [-0.0017; 0.00078]; $Dens_{path}$: [-0.0011; 0.0011]; Figure 1). $Dist_{build}$ did not vary with female boldness (95% CI = [-4.44; 82.85]) nor relative laying date (95% CI = [-23.37; 19.46]; Figure 1a). Female boldness (95% CI = [-0.084; 0.15]) and relative laying date (95% CI = [-0.076; 0.041]) did not explain variation in $Dist_{road}$ (Figure 1b). $Dist_{path}$ did not vary depending on female boldness (95% CI = [-0.052; 0.21]) but increased with increasing relative laying date (95% CI = [0.0095; 0.14]; Figure 1c). $Dens_{build}$ was lower around nests of shy females than around nests of bold females (95% CI = [-0.015; -0.0012]) but did not vary with the relative laying date (95% CI = [-0.0014; 0.0052]; Figure 1d). Neither female boldness (95% CI = [-0.0018; 0.00073]) nor relative laying date (95% CI = [-0.00026; 0.0010]) explained variation in $Dens_{road}$ (Figure 1e). $Dens_{path}$ tended to decrease with increasing relative laying date (95% CI = [-0.0010; 0.00013]) but was not influenced by female boldness (95% CI = [-0.0014; 0.00098]; Figure 1f).

3.2 | Reproductive success: Effects of human infrastructures and female boldness

There was no effect of the interaction between female boldness and any infrastructure metric on reproductive success (95% CI related to Odds Ratios, interaction between boldness and $Dist_{build}$: [0.83; 1.16]; $Dist_{road}$: [0.94; 1.37]; $Dist_{path}$: [0.87; 1.24]; $Dens_{build}$: [0.89; 1.30]; $Dens_{road}$: [0.72; 1.01]; $Dens_{path}$: [0.95; 1.35]; Figure 2). Proximity to or density of human infrastructures around nests did not have any effect on reproductive success (95% CI, $Dist_{build}$: [0.94; 1.13]; $Dist_{road}$: [0.84; 1.0]; $Dist_{path}$: [0.96; 1.16]; $Dens_{build}$: [0.89; 1.06]; $Dens_{road}$: [0.97; 1.17]), except path density around nests, $Dens_{path}$ (95% CI = [0.81; 0.97]; Figure 2). Reproductive success was lower for both shy and bold females with increasing $Dens_{path}$ (Figures 2f and 3). Reproductive success decreased with increasing visit frequency and this relationship was more marked for shy females (Figure 2). Relative laying date influenced significantly reproductive success: females that reproduced later in the season had a lower reproductive success than early breeding females (Figure 2). Reproductive success tended to be higher with increasing vole abundance (Figure 2).

4 | DISCUSSION

Nest distribution of Montagu's harriers within anthropized farmlands was influenced by some infrastructure metrics and depended on female personality: building density was lower around shy than bold female nests. However, no difference in spatial distribution between shy and bold females was found in

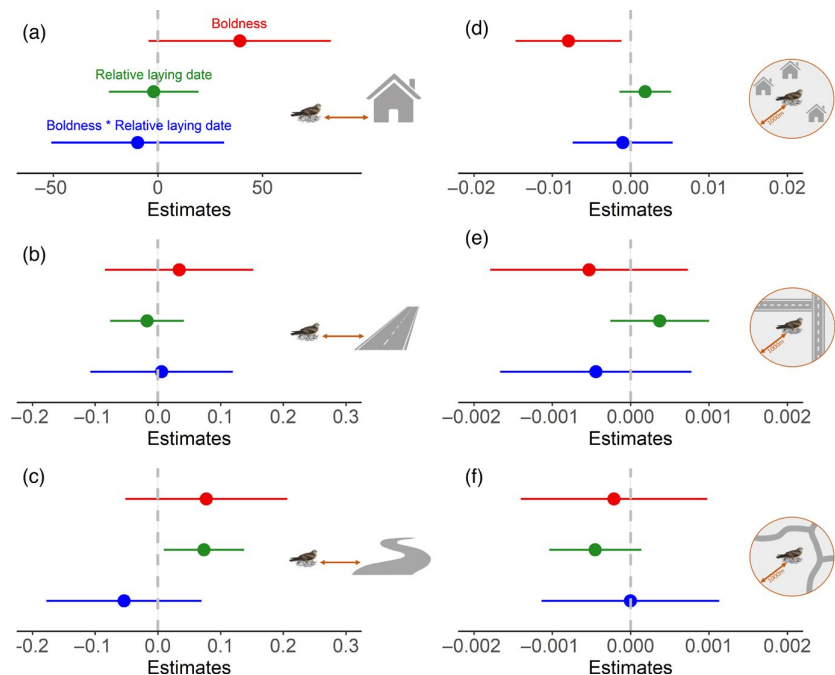


FIGURE 1 Overall estimates for the effects of female boldness, relative laying date and their interactive effect on the nest location relative to human infrastructures: (a) $Dist_{build}$, (b) $Dist_{road}$, (c) $Dist_{path}$, (d) $Dens_{build}$, (e) $Dens_{road}$ and (f) $Dens_{path}$ around nests, using LMMs with a random intercept on years. Dots and bars stand for estimates and their 95% confidence intervals (CI), respectively (see text for details). Estimates with confidence intervals that did not overlap zero (dashed line) were considered significant

FIGURE 2 Overall odds ratios for the effects of relative laying date, vole abundance, visit frequency, infrastructure metric, female boldness, the interaction between boldness and visit frequency and the interaction between boldness and infrastructure metrics on the reproductive success of Montagu's harriers, using BGLMMs with a random intercept on years. Infrastructure metrics represented (a) $Dist_{build}$, (b) $Dist_{road}$, (c) $Dist_{path}$, (d) $Dens_{build}$, (e) $Dens_{road}$ and (f) $Dens_{path}$ around nests. Dots and bars stand for odds ratios and their 95% confidence intervals (CI), respectively (see text for details). Odds ratios with confidence intervals that did not overlap one (dashed line) were considered significant

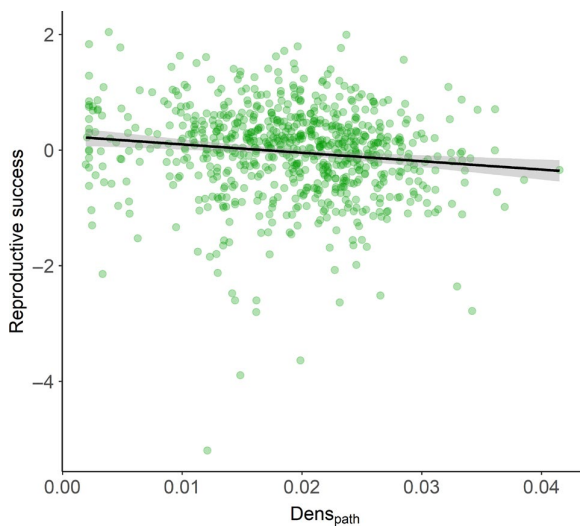
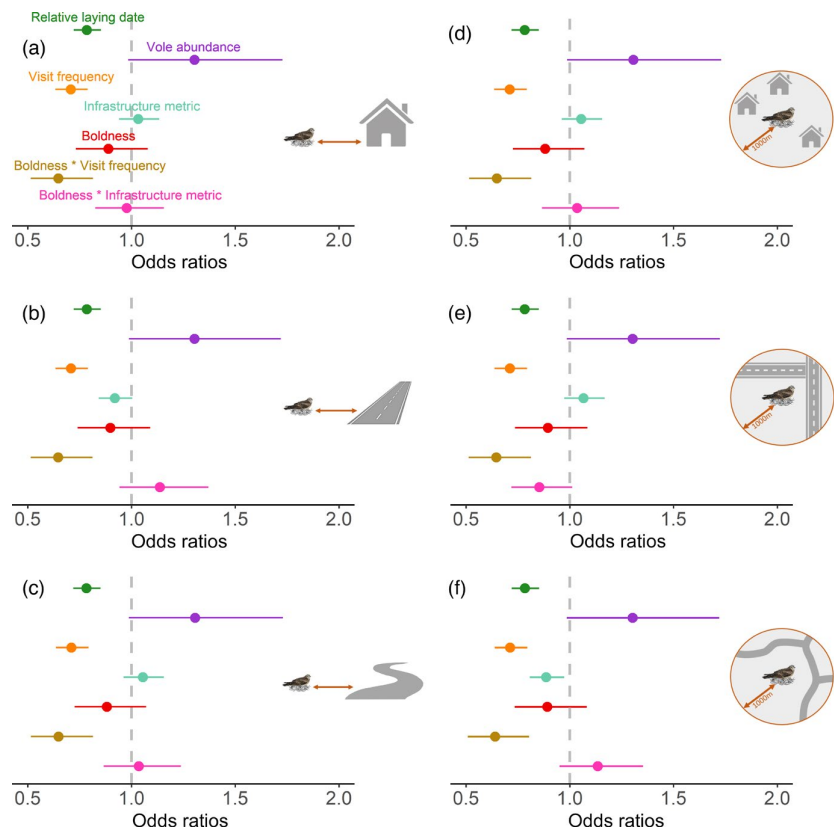


FIGURE 3 Effects of the $Dens_{path}$ (km/km^2) around nests on reproductive success. Green dots represented the predicted values of reproductive success from the BGLMM for each female depending on $Dens_{path}$. The black line represents predicted reproductive success depending on $Dens_{path}$ and shading represented 95% confidence interval

relation to any other infrastructure metrics (roads or paths). Paths also shaped nest distribution in the landscape depending on the relative laying date, but regardless of female personality. Late

breeders nested further away from paths than early breeders and path density around the nest had a negative effect on reproductive success regardless of female boldness. Relative laying date, vole abundance and the interaction between female boldness and visit frequency also influenced reproductive success as shown in Arroyo et al. (2017).

4.1 | Nest distribution related to female boldness

Location of Montagu's harrier nests in the study area varied according to female boldness and building density in the landscape. As expected, avoidance of areas with buildings seemed to be stronger in shy than bold females because building density around their nests was lower. Our study thus highlighted a spatial distribution pattern related to female boldness, and different non-exclusive processes may explain this result. A first explanation could be that the distribution of boldness types regarding buildings results from a habituation process, as shown in king penguins *Aptenodytes patagonicus* (Viblanç et al., 2012, see the synthesis by Blumstein, 2016). Females nesting in areas with higher building density could habituate to human disturbance and become increasingly bold throughout the breeding season. However, boldness was measured once nesting had begun, a short time after their return from the wintering areas, leaving little time to habituate. Moreover, females did not show habituation in their fleeing probability (boldness estimate) over the breeding season

(Arroyo et al., 2017). Different habitat choice hypotheses may also lead to this nest distribution pattern depending on personality.

First, according to the personality-matching habitat choice hypothesis, as suggested in other studies (Carrete & Tella, 2010, 2011; Cote et al., 2010; DiNuzzo & Griffen, 2020; Edelaar et al., 2008; Holtmann et al., 2017; Jacob et al., 2015; Sprau & Dingemanse, 2017), the choice of nest site in relation to the building density in an area could be different among Montagu's harrier females according to their personality. Buildings are likely associated with human frequentation and anthropogenic noise (Barber et al., 2010; McKinney, 2002) and shy females could be less tolerant to this source of disturbances. Individuals may select the most suitable habitat according to their personality (Chalfoun & Schmidt, 2012; Holtmann et al., 2017), which would lead to a decrease in individual stress and a reduction in fitness costs (Holtmann et al., 2017). Following this hypothesis, a cost of mischoosing should be observed for shy females nesting in areas with higher building density. However, in our study, the building density did not affect the reproductive success depending on female boldness. Therefore, our results do not seem to support the personality-matching habitat choice hypothesis. Second, the pattern we observed could also be explained by a genetic habitat choice or a plastic habitat choice (see Akcali & Porter, 2017). For example, natal habitat preference induction or habitat imprinting may operate and the offspring of shy females born in areas with lower building density may select natal-like nesting areas (i.e. with lower building density). In any case, all habitat choice processes are complicated to disentangle, and our study allowed to highlight a spatial distribution pattern depending on personality but not to precisely conclude on the underlying processes. Experimental studies manipulating the distance between nests and building or using a cross-fostering design could allow to properly test and separate them, but they are logistically difficult to implement and, most importantly, questionable in terms of potential disturbance for a protected and declining species such as the Montagu's harrier.

4.2 | Paths shape the nest distribution and the reproductive success

In contrast to buildings, female boldness did not affect nest distribution according to paths. Paths are not systematically associated with human frequentation, and human disturbance in these infrastructures may be ephemeral (agricultural vehicles, walkers, joggers, cyclists). Additionally, human frequentation in paths may be much lower when females chose their nest site (April–May) than later in the breeding season (June–July) when both recreative and agricultural activities become more frequent with more favourable weather conditions and/or crop harvesting. This could explain variations in the distance from the nest to the nearest path depending on the relative laying date: an increased human frequentation on paths later in the breeding season could be used as a cue by late breeding females in their nest site selection process, which, therefore, avoid paths. By contrast, ephemeral disturbance might be more difficult to measure

and integrate into the selection process of a nest site by early breeding females. Nevertheless, this kind of ephemeral disturbance may have negative impacts on fitness.

Indeed, path density affected negatively the reproductive success of Montagu's harriers. Thus, there were costs of mischoosing related to paths for females, but regardless of their personality. Two non-exclusive hypotheses may explain this result. First, nests with higher path density around them could be more exposed to predation, as terrestrial predators may use paths for foraging (Bischof et al., 2019; Geyle et al., 2020), resulting in lower reproductive success. Second, paths may involve human frequentation for leisure (e.g. walkers, joggers, cyclists) and agricultural activities, which are more frequent and intense in June and July, during the rearing period, and that could cause disturbance and stress for Montagu's harriers. Harvesting occurs increasingly early in the season and a majority of chicks are not fledged before harvesting. Nests are protected and c. 4 m² of crop around the nest are not harvested. Consequently, nests become more visible from paths after harvesting and human disturbance (motivated by curiosity) may increase. Disturbed females could spend more time flying or being vigilant and decrease their food provisioning, as shown in bearded vultures and marsh harrier (Arroyo & Razin, 2006; Fernández & Azkona, 1993). Consequently, offspring could be more prone to starvation, stress and/or predation thus resulting in lower reproductive success.

Further investigations are needed to identify the nature of disturbances related to paths to limit them. The various and complex origins of disturbances could explain our contrasted results for the different infrastructure metrics. Roads are associated with car traffic, which does not necessarily correlate with on-foot human frequentation. Montagu's harriers could be more sensitive to slow-pace nearby human presence than high-speed car occurrence, the former being more readily associated with a potential predator. This could explain the lack of effect of roads on Montagu's harrier reproductive success, although this would need further confirmation. Our study was conducted *in natura*; thus, some infrastructure metrics were slightly correlated. Testing experimentally the various components of these disturbances (i.e. with experimental modifications of the disturbances) on the female selection process would be challenging for this vulnerable species, and therefore, the relative importance of different infrastructures cannot be determined.

4.3 | Evolutionary and conservation implications for the population

The different distribution of boldness types influenced by the building density may have evolutionary implications for the Montagu's harrier population. A previous study in the same population showed a positive assortative pairing according to boldness (Rabdeau, Badenhauer, et al., 2021). However, no fitness benefit was detected from this pairing pattern, suggesting that it probably results from ecological constraints rather than only sexual selection. Similarly to Spanish imperial eagles *Aquila adalberti*, which

show an age-dependent spatial distribution leading to a positive age-assortative pairing (Ferrer & Penteriani, 2003), the distribution of Montagu's harrier females depending on their boldness may partly explain the boldness-dependent assortative pairing. In addition, Montagu's harriers could display different migratory patterns among individuals leading to variations in the egg-laying date that could be linked to individual boldness, as shown in blue tits *Cyanistes caeruleus* (Nilsson et al., 2010). Differences in migratory patterns related to boldness could involve boldness-dependent temporal distribution, thus contributing to the pairing pattern. Further investigations are needed to clarify the effects of human infrastructures and activities on the population structure and explore the hypothesis of boldness-dependent temporal distribution.

The impacts of human infrastructures on nest distribution and of human activities (nest visits) on reproductive success depending on female boldness (Arroyo et al., 2017) could lead to changes in the phenotypic composition of the Montagu's harrier population over time or among areas, following urban encroachment. Such a temporal trend has been shown in our study population, where the proportion of bold females in the population has markedly increased over time, concomitantly with the increase in nest visits for research and conservation (Arroyo et al., 2017). In other species such as dark-eyed junco *Junco hyemalis hyemalis* and song sparrow *Melospiza melodia*, spatial differences in the phenotypic composition of urban and rural populations have been shown, as urban habitat does not favour the colonisation by shy individuals (Atwell et al., 2012; Evans et al., 2010). However, a low phenotypic diversity within a population may have negative consequences on its viability (McDougall et al., 2006; Smith & Blumstein, 2013; Wolf & Weissing, 2012). Consequently, monitoring of individual personality over time and space is needed to better understand the impacts of anthropogenic activities on animal population dynamics and to propose conservation measures to mitigate the negative effects.

Finally, the Montagu's harrier is a conservation dependent species and its populations are declining in France but also elsewhere in Europe (Arroyo et al., 2002; IUCN, 2020; Santangeli et al., 2014, 2015). Therefore, the negative effects of path density around nests on reproductive success is a matter of concern for the conservation of this species. The nature of the disturbance from paths should be identified, so its effects on individuals and populations could be precisely tested, and management measures could be established. Conservation measures could be focused on Montagu's harrier colonies and in the Special Protected Area (Natura 2000) in our study site, where farmers are sensitive to agro-environmental measures. Such measures could include a delay in harvesting until most chicks have fledged as already suggested by Arroyo et al. (2002). If the relationship between nest visibility and disturbance from paths was proven, these conservation measures could reduce the negative effect of path density on reproductive success in Montagu's harriers and also benefit other species nesting in crops (Bretagnolle et al., 2018; Kuijper et al., 2009; Voříšek et al., 2010).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

J.R., B.A., F.M., I.B., V.B. and K.M. conceived the study; J.R., B.A., F.M., I.B. and K.M. analysed the data; J.R., I.B. and K.M. wrote the original draft, and all authors contributed substantially to the final manuscript; V.B. designed and coordinated long-term data collection and secured associated funding.

DATA AVAILABILITY STATEMENT

The dataset is available at Dryad Digital Repository <https://doi.org/10.5061/dryad.wm37pvmns> (Rabdeau, Arroyo, et al., 2021).

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