Does anthropization affect physiology, behaviour and life-history traits of Montagu's harrier chicks?

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Abstract

The last century has seen a steep decline in biodiversity, and anthropization is considered one of the major drivers of this decline. Anthropogenic disturbances, due to human presence and/or activities, may be perceived as chronic stressors by wildlife and potentially lead to deleterious effects on traits related to fitness. The main objective of the present study was to highlight the effects of these anthropogenic elements on wild birds on sparsely urbanized farmland, far less studied than in urbanized areas. We investigated during four successive breeding seasons whether the anthropization level, assessed by infrastructure density around nests, and the harvesting conditions around nests may impact physiological, behavioural and life-history traits of Montagu's harrier *Circus pygargus* chicks. Higher anthropization levels were associated with higher basal corticosterone levels in nestlings during only one breeding season and a lower body condition at fledging for females, probably because they suffered from higher starvation than males. Nestlings reared in more anthropized areas or in harvested crops before their fledging harboured more fault bars on rectrices than those reared in less anthropized areas or in unharvested crops regardless of year and sex, which is suggestive of higher stress during development. Nestling behaviours were also impacted by anthropization level and harvesting conditions: chicks in harvested crops were more aggressive and in areas with higher anthropization levels more prone to escape than others. Because Montagu's harrier is a protected species, the impacts highlighted in the present study are a matter of concern, especially regarding farmland landscape modifications, and we advise limiting perturbations in areas where Montagu's harriers usually nest.

Introduction

In the last century, the rate of biodiversity loss has run at an unprecedented pace (Pievani, 2014; Ceballos *et al*., 2015). Birds are no exception, especially in agricultural areas (Inger *et al*., 2015; Stanton, Morrissey & Clark, 2018; Rosenberg *et al*., 2019). In Europe, 55% of farmland birds showed population declines between 1980 and 2006 (Voříšek *et al*., 2010). One of the major causes of this global biodiversity decline is the anthropization process due to the human population increase (Swanson, 1998; McKinney, 2002; Maxwell *et al*., 2016). Anthropization includes the reduction of natural areas and land use changes, that is the conversion of natural and semi-natural habitats into farmland (Ellis *et al*., 2010; Lai, Leone & Zoppi, 2017). It also includes disturbances due to human presence, human activities (e.g. cars, tractors), human-induced noises (e.g. road traffic) or human infrastructures (e.g. high-voltage powerlines), all of which may be perceived as

stressors by wildlife (Frid & Dill, 2002; Tarlow & Blumstein, 2007; Almasi *et al*., 2015), and are thus also causes of biodiversity loss (Maxwell *et al*., 2016).

Stressful stimulus activates the hypothalamic–pituitary–adrenal axis (HPA) with an increase in the level of plasma glucocorticoids (Ellis, McWhorter & Maron, 2012). In birds, this activation involves the secretion of corticosterone (hereafter CORT) into the blood by the adrenal gland, that is stress-induced CORT (Siegel, 1995; Sapolsky, Romero & Munck, 2000; Romero, 2004). In the case of acute stress, for example an individual facing a predator attack, the CORT level returns to its basal state after a few minutes to several hours, that is homeostasis (Wingfield *et al*., 1998). Such a pattern is considered adaptive because the short-term rise of CORT secretion allows individuals to reallocate energy and behaviour from normal activities to survival mode (Frid & Dill, 2002; Müller, Jenni-Eiermann & Jenni, 2009; Dantzer *et al*., 2014), by increasing blood glucose levels, regulating

immune system function or suppressing reproductive behaviour (Wingfield *et al*., 1998; Romero, 2004; Romero & Butler, 2007). Conversely, chronic stress results from persistent or repeated stressors where HPA remains overstimulated, which results in continuous CORT secretion leading to an increased basal CORT level (Wingfield *et al*., 1998). Desensitization of the receptors of the physiological response may be observed (e.g. dysregulation of negative feedback, down-regulation of hormone production) in which case the basal CORT level decreases (Cyr & Romero, 2009). However, chronic stress is likely to incur fitness costs such as physiological, behavioural and/or morphological alterations (Romero & Butler, 2007; Cyr & Romero, 2009).

Anthropogenic disturbance has been shown to increase stress-induced CORT and increase (in most cases) basal CORT in adult birds and chicks (Müllner, Linsenmair & Wikelski, 2004; Ellenberg *et al*., 2007; Schoech *et al*., 2007; Zhang *et al*., 2011; Strasser & Heath, 2013; Almasi *et al*., 2015; Kleist *et al*., 2018). Chronic stress due to direct anthropogenic disturbance can impact nestlings through three pathways: (1) through females affecting their offspring *via* increased maternal CORT concentration in egg albumen and subsequent negative post-natal consequences (Rubolini *et al*., 2005; Pitk *et al*., 2012), (2) through a decrease in parental care resulting from the parents spending a larger proportion of their energy and time on alarm calls and flying (Fernández & Azkona, 1993; Verhulst, Oosterbeek & Ens, 2001; Arroyo & Razin, 2006) and (3) through their own perception of anthropogenic noises (Flores *et al*., 2019; Zollinger *et al*., 2019). This may affect juvenile survival rate by altering chick growth rate (Fernández & Azkona, 1993; Wada & Breuner, 2008; Müller *et al*., 2009; Noguera, Kim & Velando, 2017; Zollinger *et al*., 2019) or inducing malformations in feathers during their growth, that is the so-called "fault bars" (Jovani & Rohwer, 2017). The latter is not triggered by malnutrition, as previously thought, but by punctual and psychological stressors (Murphy, King & Lu, 1988; Negro, Bildstein & Bird, 1994; Searcy, Peters & Nowicki, 2004) and may result in feather breaks (Jovani & Rohwer, 2017). These feather malformations may be critical for birds since reduced feather area can decrease flight performance (Navarro & González-Solís, 2007). Stress levels during the rearing period can thus have major impacts on nestlings (Magrath, 1991; Naef-Daenzer, Widmer & Nuber, 2001).

Studies assessing the effects of direct human disturbances on wild birds are usually conducted in moderate (suburbs) to highly urbanized areas (Halfwerk *et al*., 2011; Strasser & Heath, 2013; Glądalski *et al*., 2016) or in areas more prone to recreational activities (González *et al*., 2006; Ellenberg *et al*., 2007; Remacha *et al*., 2016). However, farmland which seems sparsely anthropized compared to cities and suburbs also experiences human activities, such as car traffic, walkers, joggers, cyclists, agricultural activities and anthropogenic noise from villages. Therefore, farmland specialist bird species, which could be less flexible and tolerant than generalists, may be more sensitive to these disturbances, even if they occur at low frequencies (Wretenberg *et al*., 2006;

Filippi-Codaccioni *et al*., 2008; Heldbjerg, Sunde & Fox, 2018; Giralt *et al*., 2021). The Montagu's harrier *Circus pygargus* is a ground-nesting raptor that may breed in semi-natural and extensive farmland habitats with low urban density (e.g. urban density <4% in the province of Lleida, Catalunya, north-east of Spain and in the meadows around Chelm, Poland respectively, Kitowski, 2003; Guixé & Arroyo, 2011). However, since the 20th century, this species breeds mainly in intensive farmland habitats, cereal crops, and areas surrounded by human infrastructures (e.g. 9.8% urban density in our study area, *Zone Atelier Plaine et Val de Sèvre*, France; Bretagnolle *et al*., 2018). Their chicks are thus exposed to anthropogenic disturbance, either directly or indirectly (Arroyo, García & Bretagnolle, 2004). Moreover, for the majority of nests, harvesting occurs during the rearing period before the chick fledge, though subjected to year-to-year variation. After harvesting, *c*. 4 m^2 of unharvested crops remain around the nest, and thereby the chicks become more visible from outside the plot and thus more exposed to human disturbance (Rabdeau *et al*., 2021) and predators such as foxes in our study area (Arroyo, Mougeot & Bretagnolle, 2001; Bravo *et al*., 2020, 2022). Our study followed an approach to capture the global effects of direct human disturbances on Montagu's harrier chicks. Assuming that infrastructure density around nests would be positively correlated with the intensity of direct human disturbances (see Benítez-López, Alkemade & Verweij, 2010), we specifically investigated whether this anthropization level, measured by the density of human infrastructure around the nest, affects the physiology, behaviour and body condition of Montagu's harrier fledglings. We also assessed whether harvesting conditions of the crop plot (i.e. crop harvested or not) where the nest was located, impacted the fledglings depending on the density of human infrastructure around the nest. We conducted a multi-trait approach and predicted that chicks from nests located in more anthropized areas would present higher basal CORT and stressor-induced CORT levels associated with a lower body condition and more fault bars than chicks reared in less anthropized areas. According to the results from a previous study in which repeated exposure and handling of chicks by the same experimenters caused a sensitization phenomenon (Rabdeau *et al*., 2019), we hypothesized that chicks reared in more highly anthropized areas and/or in harvested crops would be more stressed, and thereby more active and aggressive than others.

Materials and methods

Ethics statement

All the birds involved in the present study were released at their site of capture (i.e. their nests) after each handling. Bird manipulation was permitted and licensed by the CRBPO (*Centre de Recherches sur la Biologie des Populations d'Oiseaux – Museum National d'Histoire Naturelle*, licence #1308). The methods used for the capture, handling, banding and blood sampling of the birds comply with French guidelines for the ethical use of animals in research.

Study site and biological model

The study was conducted during four successive breeding seasons (2016–2019) in Western France, within a Long-Term Social-Ecological Research (LTSER) area; specifically, the *Zone Atelier Plaine & Val de Sèvre* (ZAPVS thereafter, GPS coordinates 46°110 N, 0°280 W, see nest distribution in Supporting Information Figure S1). This 435 km^2 area is managed principally for intensive farming but 9.8% of its surface is urbanized including villages, industrial and agricultural buildings, railways, a motorway, roads and paths (Bretagnolle *et al.*, 2018). Since 1994, the population of Montagu's harriers has been monitored each breeding season (Bretagnolle *et al.*, 2018). This migratory farmland raptor nests on the ground in tall vegetation, especially on cereal crops (Millon *et al.*, 2002; Gillis *et al.*, 2012). Females lay asynchronously up to eight eggs and *c.* four eggs on average in our studied population, with an average lag of 2 days between successive eggs, depending on food availability (Arroyo *et al.*, 2004; Millon, Arroyo & Bretagnolle, 2008). However, the eggs hatch with an average lag of 1 day. During the rearing period (30–35 days), the chicks depend on their parents for food, thermoregulation and predator protection. Montagu's harriers are local specialist predators; they prey mostly on a small cyclic rodent, the common vole *Microtus arvalis* in France and shift to insects, such as grasshoppers *Tettigonia viridissima*, in low-vole years (Arroyo, 1997).

Nest monitoring and measures

Nests were systematically searched for during the whole breeding season (Millon *et al.*, 2008). Each nest was recorded by its GPS coordinates. The nests were visited once during incubation to measure the eggs (length and width using a calliper, accuracy ±0.1 mm; mass using Pesola® electronic scale, accuracy ±0.1 g) and to calculate egg density (i.e. egg mass divided by volume; egg volume = $0.51 \times$ length $\times$ width^2/1000; Hoyt, 1979) in order to estimate the hatching date (egg density decreases linearly from laying to hatching date) and the laying date to plan nest visits during the rearing period (Arroyo *et al.*, 2004; Arroyo, Mougeot & Bretagnolle, 2017). From hatching to fledging, the nests were visited once a week. At 15 ± 2 days old, the chicks were ringed (metal numbered ring from the *Muséum National d'Histoire Naturelle*) and sexed according to iris colour: brown for females and grey for males (Leroux & Bretagnolle, 1996). Behavioural and physiological data were collected before fledging when the chicks were 26 ± 2 days old. A total of 86 nests were available ($N_{2016} = 15$, $N_{2017} = 16$, $N_{2018} = 24$, $N_{2019} = 31$) representing 243 chicks ($N_{2016} = 40$, $N_{2017} = 32$, $N_{2018} = 82$, $N_{2019} = 89$), 114 females and 129 males (no sex ratio bias). For four nests, it was not possible to estimate the laying date from egg measures because the nests were discovered after hatching. Therefore, for these four nests, we calculated retroactively the laying date from the date of nest visit with chick

measurements: we subtracted the chick age (26 days old) at this nest visit and the incubation duration (30 days; García & Arroyo, 2001) to estimate the laying date. At the end of the breeding period, a final nest visit was conducted to note the brood size at fledging.

Each nest visit when the chicks were 26 ± 2 days old followed the same procedure. After a quiet approach, the chicks were captured as soon as the experimenters arrived at the nest. The first blood sample was collected in the first 3 min of handling (Sample A). Then, the right and left tarsus lengths were measured twice using a digital calliper (accuracy ±0.1 mm) and the nestlings were weighed using a spring scale (Pesola® 500 g, accuracy: ±5 g) to estimate their body condition. The second blood sample (Sample B) was taken 15 min after the capture. The blood samples were kept refrigerated (0–5°C) for further analyses (see below). Before the release of the chicks at their nest, a photo of their tail was taken to count the number of fault bars on the rectrices (see Supporting Information Figure S2). The behaviour of each chick was recorded throughout the handling (see below). At this nest visit, we also noted whether the crop where the nest was located (harvest thereafter) was unharvested (0) or harvested (1).

CORT analyses

Once back at the laboratory, the blood samples were centrifuged (10 min at 3880 g, Bio Lion XC-LED12K) to separate the plasma from the erythrocytes. The plasma samples were stored at −20°C until titrated by radioimmunoassay to obtain their CORT concentration (Lormée *et al.*, 2003). The intra-assay and inter-assay coefficients of variation were 10.57% and 13.72%, respectively, for the 3 years of the CORT analyses (2017–2019). The basal CORT level was obtained from Sample A. Two stress-induced CORT levels were used: the maximal CORT level, that is the CORT concentration from Sample B, and the change in CORT, that is subtracting the basal CORT level from the CORT level of Sample B (Rabdeau *et al.*, 2019). These two measures (maximal CORT level and change in CORT) provided different information on stress-induced CORT. The maximal CORT level represented the maximum value of CORT experienced by chicks during handling and the change in CORT represented individual plasticity in the stress-induced CORT. In 2016, no CORT analysis was done. This study was conducted under natural conditions within a 435 km^2 area, thus it was not possible to sample all chicks at the same time of the day because of the weather conditions and logistics. We tried to visit the nests in the morning: 106 chicks were sampled before 1 PM, 22 chicks were sampled after 3 PM and for 4 chicks, we did not have the time of the nest visit. The time of the nest visit had no effect (morning vs. afternoon) on the corticosterone levels (Linear Mixed effects Models [LMM], basal CORT: $\chi^2 = 2.25$, d.f. = 1, $P = 0.13$; maximal CORT: $\chi^2 = 0.18$, d.f. = 1, $P = 0.68$; change in CORT: $\chi^2 = 0.01$, d.f. = 1, $P = 0.91$).

Fault bars

The number of fault bars were counted from the chick tail pictures by the same experimenter to avoid potential measurement biases. This study is the first general approach to the global effects of human disturbances on different traits of nestlings, and therefore, we chose to count all kinds of fault bars. After a careful examination, all breaks in barbes and barbules from the finest to the widest (i.e. light, moderate and severe fault bars, see the review by Jovani & Rohwer, 2017) were counted on the most affected feather (Supporting Information Figure S2).

Behaviour

Chick behaviour was assessed by scoring specific behaviours (Rabdeau *et al.*, 2019). First, a general activity score was measured when the experimenter approached the nest and captured the chick (activity capture: act_{capt}): $0 =$ no reaction, $1 =$ it moved backwards or $2 =$ it ran away. During capture, whether the chick uttered a call (1) or not (0) was noted (vocalization capture: voc_{capt}). Subsequently, another activity score was tabulated during handling (activity handling: act_{hand}): $0 =$ motionless chick, $1 =$ low reaction chick, $2 =$ medium reaction chick or $3 =$ chick was continually in motion. The rate of claw attack (activity claw: act_{claw}), beak attack (activity beak: act_{beak}) and calls (vocalization handling: voc_{hand}) throughout the handling period were recorded (absolute frequency/handling time in min). The behaviours of the chicks were not recorded in 2016. Among and within each year, the chicks were not systematically handled by the same person, but all the experimenters were trained to measure and score the chick behaviours (see Rabdeau *et al.*, 2019).

Proportion of infrastructure around the nest

The GPS coordinates of the nests, as well as the different categories of human infrastructures georeferenced in the BD TOPO v.3® (derived from the internal database of the *Institut National de l'Information Géographique et Forestière*), were incorporated into the Geographic Information System (GIS) database of the LTSER, using QGIS (version 3.4.12). BD TOPO allowed us to distinguish between a highway, one-lane road, two-lane road, roundabout, gravel road, path and walkway. All kinds of buildings with a minimum footprint area of 50 m^2 were integrated, including sport fields and cemeteries, as well as transport infrastructures (trainlines, motorways, roads, paths) and high-voltage powerlines. Such linear elements were transformed into polygons with respect to the width of each element. If not referenced in the BD TOPO, an average width was estimated using Google Maps (five measurements were taken per group of elements characterized by the same attributes, e.g. highway, one-lane road, two-lane road, roundabout, gravel road, path, walkway).

We chose to quantify the anthropization level around each nest by calculating the cumulated surface area covered by all types of infrastructures instead of considering each infrastructure separately. Indeed, the effects of each infrastructure type cannot be disentangled from each other in a field study without any experimental modifications (which would have been questionable for our protected and declining model species). Our aim was not to identify the major components of disturbance but to realise an integrative assessment of the cumulative effects of all infrastructure types. The infrastructure density around the nest (IDN hereafter) was calculated within a 1000 m radius buffer (see Gormally *et al.*, 2021 for a similar quantification). At this study site, the median distance from the nests to their nearest infrastructure was 530 m (Rabdeau *et al.*, 2021). Thereby, by using twice this distance, we expected to obtain variability in IDN at the local scale. Additionally, a meta-analysis previously evidenced that infrastructures may impact a bird population up to 1000 m away (Benítez-López *et al.*, 2010), supporting our choice of buffer radius.

One nest (two female chicks) had a particular situation and was above 5% of IDN within the 1000 m radius buffer (Supporting Information Figure S3). As this nest (in 2016) would behave as a statistical outlier, it was excluded from all the analyses, but as a quality check, we also conducted the analyses with this nest included and show the results in the Supporting Information (Table S1). Calculated excluding this outlier, IDN ranged from 1.23 to 4.83%, with no statistical variation among the years (Supporting Information Figure S3; Kruskal–Wallis test: $\chi_3^2 = 2.45$, $P = 0.48$). Although the IDN may seem low, there was IDN variability among the nests for the next analyses: the maximum value of IDN (4.83%) was almost four times the minimum value of IDN (1.23%; see Supporting Information Figure S4). We provided pictures of the habitat within the 1000 m radius buffer around the nests with IDN of 1.23%, 3.0012% and 4.83% using our GIS database and the orthophoto of our study area in Supporting Information (Figure S5). The nests with 1.23% IDN could have less stressful anthropized surroundings than the nests with 4.83% IDN because of fewer surrounding human activities, such as car traffic, walkers, joggers, cyclists, agricultural activities and anthropogenic noise from the villages (Supporting Information Figure S5). Assessing the effects of human disturbances in sparsely urbanized landscapes was one of our objectives and defined the specificity of this study.

Statistical analysis

Morphology and behavioural indexes

Body condition was estimated based on mean tarsus length (right and left) and mass by calculating the Scaled Mass Index (SMI), following Peig & Green (2009), using the 'smatr' package (Warton *et al.*, 2012). Briefly, for each chick (i), SMI is defined as

$$\text{SMI}_i = \text{mass}_i \times \left(\frac{\text{overall mean tarsus length}}{\text{mean tarsus lenght}_i} \right)^{b_{sma}},$$

where b_{sma} is the slope of the major axis regression of log(mass) on log(mean tarsus length).

A principal component analysis (PCA) was performed on all behavioural data (act_{capt}, act_{hand}, act_{claw}, act_{beak}, voc_{capt} and voc_{hand}) to avoid multiple tests (and also because the behavioural variables were moderately to highly correlated with each other, see Supporting Information Figure S6). Of the six axes, we retained the first three as their standard deviations were above 1 for a total of the cumulative proportion of variance of 74.50% (Table 1). On the first axis of the PCA (PC1), act_{hand}, act_{beak} and act_{claw} were the major contributors and represented the behaviour of the chicks during handling on the second axis (PC2), voc_{capt} and voc_{hand} represented overall vocalization activity and on the third axis (PC3), act_{capt} contributed mostly negatively (Table 1).

Effects of anthropization

The effect of IDN was tested on basal CORT and the two stress-induced CORT levels (both square root-transformed to meet normality and homoscedasticity assumptions), body condition (log-transformed), PC1, PC2 and PC3 with LMMs (from lmerTest package, Kuznetsova *et al.*, 2017). The two stress-induced CORT levels (maximal CORT level and change in CORT) were highly correlated (Spearman's rank correlation coefficient: $\rho = 0.82$ and $P < 0.0001$; see Supporting Information Figure S6); therefore, we chose to present the results on the maximal CORT level in the main text and the change in CORT in Supporting Information (Table S2). Generalised LMM (GLMM) fitted with Poisson distribution was used for the fault bars. In all models (LMMs and GLMM fitted with Poisson distribution), IDN, year, sex, harvest, laying date (Julian calendar), brood size at fledging, IDN × year interaction, IDN × sex interaction and IDN × harvest interaction were included as fixed effects. Nest identity was always included as a random effect to control for the non-independency of chicks from the same nest. Model comparisons were performed using likelihood ratio-based χ^2 statistics to estimate the statistical significance of the explicative variables (from the 'car' package, Fox *et al.*, 2012). We chose to present full models with all fixed effects following Forstmeier & Schielzeth (2011). Significant

Table 1 Factor loadings for the principal component analysis and the three first axes kept for further analyses. Values in bold indicate the behavioural variables that are mostly represented for each axis

	PC1	PC2	PC3
act_{capt}	−0.29	0.16	**−0.76**
act_{hand}	**−0.52**	0.03	0.02
act_{claws}	**−0.55**	−0.003	0.28
act_{beak}	**−0.58**	−0.05	0.15
voc_{capt}	−0.01	**0.73**	−0.26
voc_{hand}	0.06	**0.66**	0.49
SD	1.48	1.13	1.00
Cumulative variance explained (%)	36.44	57.64	74.50

effects were tested using posthoc tests based on least-squares means if necessary (using the 'emmeans' package, Lenth, Singmann & Love, 2018). The sample sizes varied depending on the traits because some data were unavailable. On the individuals for which all variables were available, we also performed Spearman's rank correlation tests to assess the potential links among the variables (Supporting Information Figure S6). All statistical analyses were run using R software (v 4.0.4, R Core Team, 2021).

Results

The basal CORT level of nestlings increased with increasing IDN in 2019 (estimate ± standard error assorted with [95% CI]: 0.66 ± 0.35 [−0.038; 1.36]), whereas no significant relationship was found for 2017 (−0.51 ± 0.33 [−1.16; 0.15]) and 2018 (0.15 ± 0.19 [−0.24; 0.53]; Table 2; Fig. 1a). The interaction between IDN and sex, the interaction between IDN and harvest and the main effects of sex, harvest, laying date and brood size at fledging did not influence the basal CORT (Table 2). Maximal CORT level did not vary depending on the interaction between IDN and year, the interaction between IDN and harvest and the main effects of the year, harvest, laying date and brood size but tended to vary depending on IDN interacting with sex (Table 2). In males, the maximal CORT level tended to decrease with increasing IDN (−0.37 ± 0.25 [−0.86; 0.13]), whereas it was stable in females (0.081 ± 0.21 [−0.35; 0.51]; Table 2; Fig. 1b). The interaction between IDN and sex influenced the body condition of the chicks (Table 2). Female body condition slightly decreased with IDN (−0.023 ± 0.015 [−0.053; 0.0067]), whereas no effect was detected for males (0.0089 ± 0.016 [−0.023; 0.041]; Fig. 2). The body condition of the chicks was neither influenced by the interactive effect of IDN and year, nor by the interaction between IDN and harvest, or by the main effects of the year, harvest, laying date and brood size (Table 2). The number of fault bars observed on chicks' rectrices increased with increasing IDN (0.15 ± 0.067 [0.019; 0.28]) whatever the year, the sex and the harvest (Table 2; Fig. 3a). A higher number of fault bars was found in 2018 compared to 2017 and 2019 (mean fault bars assorted with [95% CI], 2016: 3.71 [3.11; 4.32], 2017: 3.12 [2.59; 3.66], 2018: 4.51 [4.061; 4.95] and 2019: 2.84 [2.46; 3.22]), despite that, in 2018, IDN was on average lower but not statistically different compared to the other years (Supporting Information Figures S3 and S7). Chicks from nests in harvested crops had more fault bars (mean fault bars assorted with [95% CI], 3.73 [3.40; 4.06]) than chicks in nests in unharvested crops (3.54 [3.11; 3.97]) whatever the IDN (Table 2; Fig. 3b). Laying date and brood size did not influence the number of fault bars observed on chicks' rectrices (Table 2). Concerning chicks' behaviour, neither their behaviour during handling (PC1) nor their vocalization (PC2) or escape behaviour at nest approach (PC3) were influenced by the three interactive terms of IDN with year, IDN with sex and IDN with harvest (Table 2). Chicks from nests in harvested crops were more active and attacked more during handling (−0.16 [−0.41; 0.093]) than

Table 2 Summary of models investigating variation in different chick traits ([a]Linear Mixed Models, LMMs; [b]Generalised Liner Mixed Models, GLMMs, with Poisson distribution). Sample sizes are in parentheses and vary according to life-history traits (according to the data available). The significance of each independent variable was tested using model comparison with likelihood-based χ^2 statistics (statistic values, degrees of freedom and *P* values). Significant effects are in bold

Measured parameter (sample size)	Independent variables	X^2	d.f.	*P*
Basal CORT (square root-transformed)[a]				
132 chicks	IDN	1.10	1	0.29
63 nests	**Years**	**6.31**	**2**	**0.04**
	Sex	0.01	1	0.92
	Harvest	0.00	1	0.97
	Laying date	0.04	1	0.85
	Brood size	0.18	1	0.67
	IDN × year	**7.85**	**2**	**0.02**
	IDN × sex	0.25	1	0.61
	IDN × harvest	0.00	1	0.99
Maximal CORT level (square root-transformed)[a]				
132 chicks	IDN	0.02	1	0.89
63 nests	Years	0.06	2	0.97
	Sex	2.47	1	0.12
	Harvest	0.00	1	0.95
	Laying date	0.47	1	0.49
	Brood size	0.22	1	0.64
	IDN × year	0.31	2	0.86
	IDN × sex	**3.99**	**1**	**0.05**
	IDN × harvest	0.08	1	0.77
Body condition (log-transformed)[a]				
239 chicks	IDN	0.02	1	0.90
85 nests	Year	3.50	3	0.32
	Sex	**6.10**	**1**	**0.01**
	Harvest	2.14	1	0.14
	Laying date	0.05	1	0.82
	Brood size	0.03	1	0.86
	IDN × year	3.29	3	0.35
	IDN × sex	**4.60**	**1**	**0.03**
	IDN × harvest	1.70	1	0.19
Fault bars[b]				
210 chicks	**IDN**	**6.78**	**1**	**0.009**
80 nests	**Year**	**28.19**	**3**	**<0.0001**
	Sex	1.77	1	0.18
	Harvest	**4.24**	**1**	**0.04**
	Laying date	0.75	1	0.39
	Brood size	1.42	1	0.23
	IDN × year	2.14	3	0.54
	IDN × sex	0.95	1	0.33
	IDN × harvest	1.60	1	0.21
PC1[a]				
196 chicks	IDN	0.05	1	0.82
70 nests	Year	3.43	2	0.18
	Sex	0.21	1	0.65
	Harvest	**7.18**	**1**	**0.007**
	Laying date	0.003	1	0.96
	Brood size	**12.16**	**1**	**0.0005**
	IDN × year	4.29	2	0.12
	IDN × sex	0.68	1	0.41
	IDN × harvest	0.98	1	0.32

Table 2 Continued.

Measured parameter (sample size)	Independent variables	X^2	d.f.	*P*
PC2[a]				
196 chicks	IDN	1.95	1	0.16
70 nests	Year	0.68	2	0.71
	Sex	2.78	1	0.10
	Harvest	0.001	1	0.98
	Laying date	0.18	1	0.67
	Brood size	1.86	1	0.17
	IDN × year	1.18	2	0.56
	IDN × sex	0.06	1	0.81
	IDN × harvest	0.65	1	0.42
PC3[a]				
196 chicks	**IDN**	**5.13**	**1**	**0.02**
70 nests	**Year**	**23.74**	**2**	**<0.0001**
	Sex	0.29	1	0.59
	Harvest	2.49	1	0.11
	Laying date	0.12	1	0.73
	Brood size	0.35	1	0.55
	IDN × year	2.30	2	0.32
	IDN × sex	0.001	1	0.97
	IDN × harvest	0.16	1	0.69

chicks from nests in unharvested crops (0.42 [0.086; 0.75]; Table 2; Fig. 4). PC1 varied depending on brood size: chicks from nests with lower brood size were more active and attacked more (estimate ± standard error with [95% CI]: 0.50 ± 0.14 [0.21; −0.79]; Table 2). The main effects of IDN, year, sex and laying date did not influence PC1 and PC2 (Table 2). PC2 did not vary depending on the harvest and the brood size (Table 2). PC3 differed with IDN: chicks were more prone to escape with increasing IDN (estimate ± standard error with [95% CI]: −0.27 ± 0.13 [−0.53; −0.0012]; Table 2; Fig. 5). Additionally, escape behaviour at nest approach (PC3) decreased from year to year (mean PC3 score assorted with [95% CI], 2017: −0.83 [−1.095; −0.56], 2018: −0.13 [−0.31; 0.045] and 2019: 0.42 [0.20; 0.64]; Table 2; Supporting Information Figure S8).

Discussion

Conservation physiology has recently emerged, emphasizing the urgent need to understand the multidimensional processes and effects of human-induced perturbations and animal population declines through processes altering the fitness of individuals (Cooke *et al.*, 2013, 2020). In the present study, we investigated whether even low anthropization levels in rural landscapes, estimated by IDN around the nests, may impact the development of Montagu's harrier chicks which also suffer an additional effect of harvesting. Based on different indexes related to physiology, morphology and behaviour that were measured for chicks just before fledging, we found some links between anthropization levels, harvesting conditions and chick development.
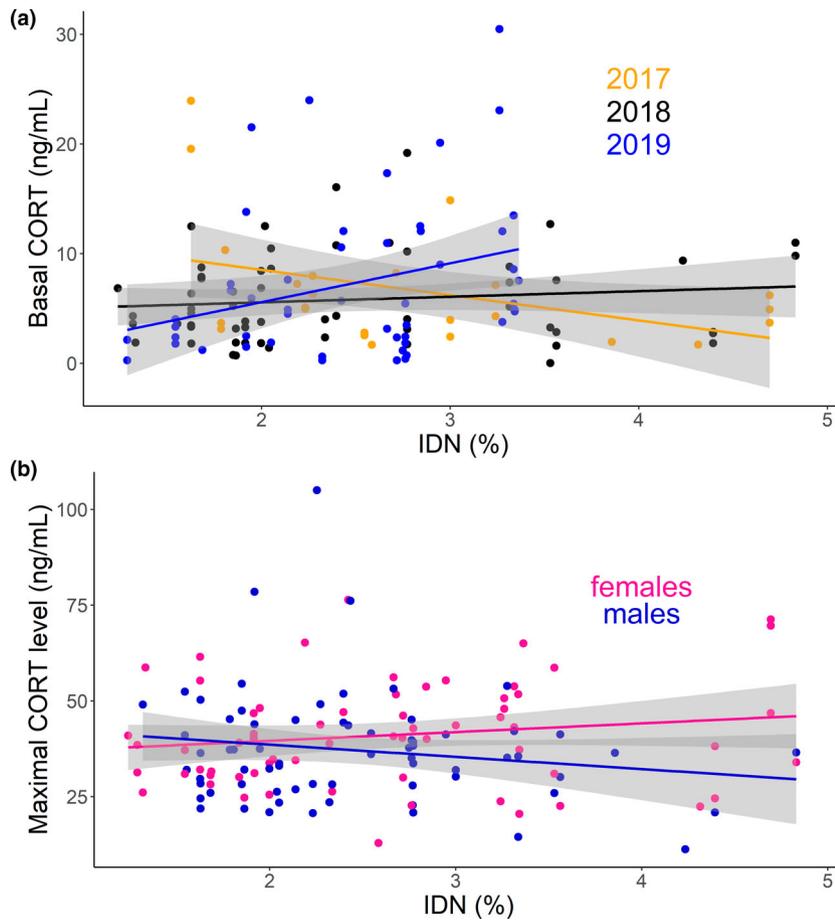
Figure 1 Effect of IDN on (a) basal CORT according to the year (b) maximal CORT level in females and males. Dots represent the observed values for each chick. Line predicts CORT level depending on IDN, and shading represents the 95% confidence interval. IDN, infrastructure density around the nest.
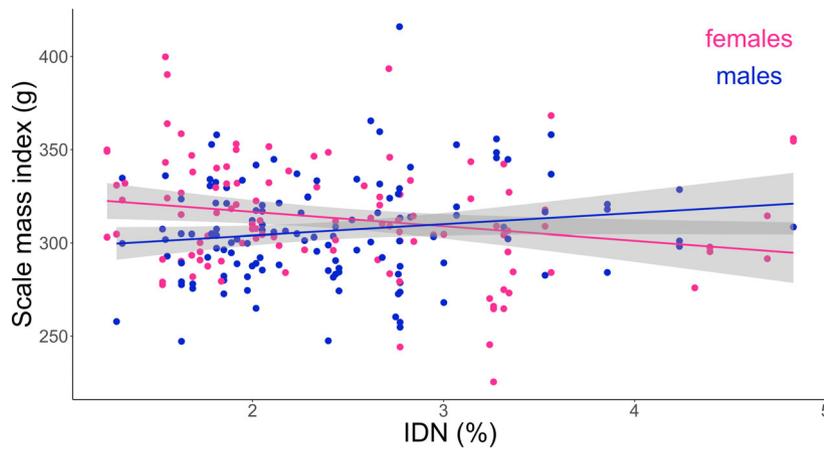

Figure 2 Effect of IDN on the scale mass index (body condition) of females and males. Dots represent the observed values of body condition for each chick. Line predicts body condition depending on IDN, and shading represents the 95% confidence interval. IDN, infrastructure density around the nest.

Anthropization and associated activities, such as human presence, noises and traffic, are considered chronic stress as chicks reared in more or less perturbated areas are constantly exposed to these unnatural stimuli (Dantzer *et al.*, 2014). Individuals exposed to chronic stress are expected to exhibit higher basal CORT and increased stress-
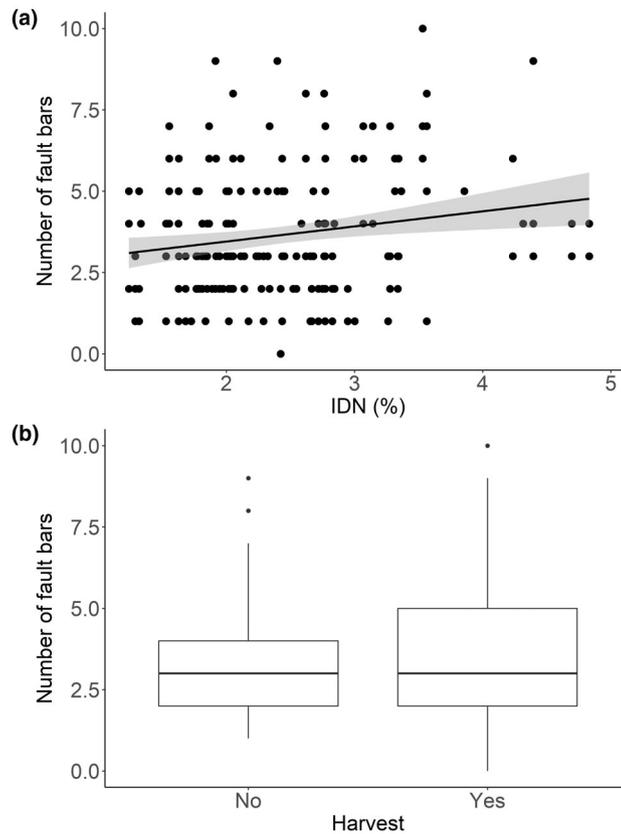
Figure 3 Variations of the number of fault bars on chicks' rectrices depending on (a) IDN (b) harvest (No = unharvested crop; Yes = harvested crop around the nest). (a) Dots represent the observed values of the number of fault bars for each chick. Line predicts the number of fault bars depending on IDN, and shading represents the 95% confidence interval. (b) Box plot represents the median (heavy lines), 25% and 75% quartiles (boxes), 1.5 times the interquartile line (whiskers) and data points outside, for the number of fault bars depending on harvest. IDN, infrastructure density around the nest.
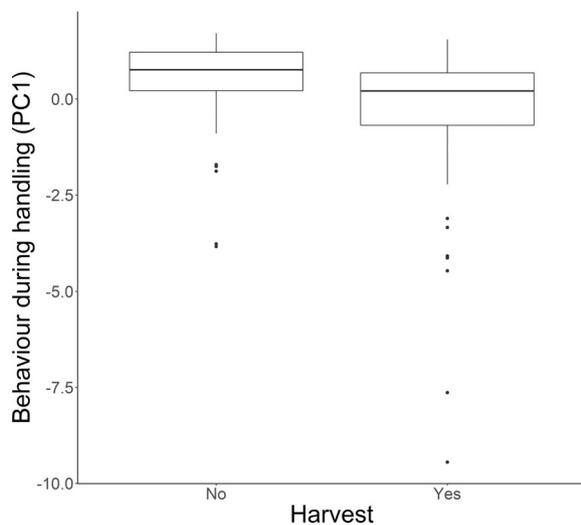
Figure 4 Effect of harvest (No = unharvested crop; Yes = harvested crop around the nest) on behaviour during handling (PC1). Box plot represents the median (heavy lines), 25% and 75% quartiles (boxes), 1.5 times the interquartile line (whiskers) and data points outside, for PC1 depending on harvest.

induced CORT although this common thought is challenged, thus questioning this general rule and suggesting potential publication bias (see the review by Dickens & Romero, 2013). In the present study, we found only slight evidence for increased basal CORT levels and only for the year 2019. Other studies also report an increase in basal CORT levels in different species (Ellenberg *et al.*, 2007; Busch & Hayward, 2009; Wingfield & Romero, 2001; Dickens & Romero, 2013; Almasi *et al.*, 2015). This higher basal CORT level in 2019 could be explained by IDN differences among the years with higher IDN found in 2019, but there were no statistical differences in IDN between the years. Therefore, it is difficult to draw conclusions on the relationship between basal CORT and anthropization. On one hand, the favourable and therefore less competitive conditions experienced by this harrier population during 2019 (higher vole abundance) may have allowed all pairs, even lower quality pairs, to raise their chicks to fledge irrespective of their sensitivity to disturbances, resulting in lower nesting failures that year (52% of the nests failed in 2016, 63% in 2017, 40% in 2018, 8% in 2019, data not shown). Moreover, these lower quality pairs could have settled in
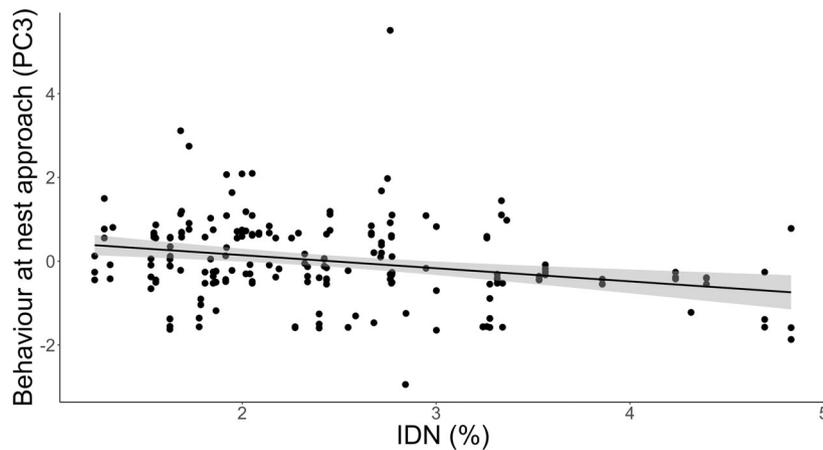
Figure 5 Effect of IDN on chick behaviour. Dots represent the observed values of PC3 for each chick. Line predicts PC3 depending on IDN, and shading represents the 95% confidence interval. Note that behaviour at nest approach is the major contributing variable on this axis and is negatively correlated (see Table 1). IDN, infrastructure density around the nest.

lower quality areas with higher IDN, by default of space and/or experience, thereby explaining the increased basal CORT of the chicks in areas with higher IDN. These conditions and hypotheses may have contributed to conserving large variability in basal CORT levels and thereby detecting the subtle physiological effects of anthropization – although this was also the year with the lowest variability for IDN. This hypothesis is plausible since the probability of nesting failure may increase with increasing anthropogenic stressors perceived by the parents (White & Thurow, 1985; Arroyo & Razin, 2006; Strasser & Heath, 2013). A previous study, conducted on the same population of Montagu's harriers, showed that shy females were less tolerant of disturbances than bold females (Rabdeau *et al.*, 2021). Therefore, in most anthropized areas, the nests of less tolerant parents could fail before fledging during less favourable years in terms of food resources. The chicks measured at fledging in the more anthropized areas may consequently represent chicks raised by tolerant parents and who are themselves also relatively tolerant of human disturbances as personality traits are partly heritable (Cockrem, 2007; Dochtermann, Schwab & Sih, 2015). Accordingly, a reduction in variance associated with low statistical power due to the small sample size may have led to the absence of a detectable relationship observed in 2017 and 2018. On the other hand, finding no increase in basal CORT related to increasing anthropization levels is consistent with the literature (see the meta-analysis by Injaian *et al.*, 2020). Additionally, the variation in basal CORT may depend on the matrix used to titrate glucocorticoid metabolite. Results from meta-analysis showed different trends between faecal and plasma samples: an increase is observed in faecal but not in plasma samples (Dantzer *et al.*, 2014). Therefore, basal CORT from plasma is probably not affected by chronic anthropogenic stress (Dantzer *et al.*, 2014; Injaian *et al.*, 2020) and this finding could explain the small effect of the anthropization level depending on the year.

While basal CORT levels were similar between sexes, the maximal CORT level tended to only be influenced by the anthropization level in males. In a previous study on Montagu's harrier nestlings, we did not find any difference in stress-induced CORT between sexes over repetitive manipulations by experimenters during nest visits (Rabdeau *et al.*, 2019). This small anthropization level effect depending on the sex could be explained by a lack of statistical power due to low sample size for basal CORT. These low sex differences may be either suggestive of differential exposure to the stressor and/or of differing physiological constraints between sexes. The first hypothesis is unlikely because all chicks within a nest were exposed to the same perturbations whatever their sex. Interestingly, our results differ from the general trends that show a more important response to human perturbation in males than in females (Dantzer *et al.*, 2014). Contrary to what was expected (see Kleist *et al.*, 2018; Expósito-Granados, 2020 for a few recent examples), stress-induced CORT levels slightly decreased with increasing IDN in males. The ontogeny of stress is still poorly understood but it is known that it may, for instance, shape pre-migratory movements (Pakkala *et al.*, 2016) and to a further extent adult physiology, behaviour and fitness (Schoech, Rensel & Heiss, 2011; Crespi *et al.*, 2013). Additionally, CORT level differences between sexes in nestlings are rarely integrated into analyses (Tilgar, Saag & Moks, 2009; Wada *et al.*, 2009; Rensel, Wilcoxen & Schoech, 2010; Tilgar *et al.*, 2010; Kidawa *et al.*, 2014; Pakkala *et al.*, 2016; Newman *et al.*, 2017; Injaian, Taff & Patricelli, 2018; Injaian *et al.*, 2019; Bebus, Jones & Anderson, 2020; Expósito-Granados *et al.*, 2020), or evidenced either no difference (Sockman & Schwabl, 2001; Beaugeard *et al.*, 2019; Grunst *et al.*, 2020) or low sex effects (Rensel, Wilcoxen & Schoech, 2011). This slight decrease in stress-induced response in males may arise from habituation (i.e. repetitive exposures lead to a change in the perception of the stimulus from noxious to innocuous),

physiological desensitization of CORT receptors (decrease in the physiological response although the stimulus is still considered noxious) or exhaustion (decrease in energy allocated to the stress physiological system) (reviewed in Cyr & Romero, 2009). However, our data and study design do not allow identifying the processes explaining this slight difference in stress-induced CORT among sexes.

Interestingly, female body condition was slightly negatively impacted by anthropization, whereas no effect in males was detected. Body condition at fledging is a fundamental life-history trait in migratory species as it determines later survival during migration (Duijns *et al.*, 2017). This small decrease is congruent with the literature on chronic stress consequences (Dickens & Romero, 2013). However, no evident link with stress hormone can be made since basal and stress-induced CORT levels did not seem to be impacted by anthropization (see above), and only a slight correlation can be made between CORT levels and body condition. Alternatively, this result may be explained by a decrease in parental investment as human disturbances can decrease food item delivery by parents to both female and male nestlings (Fernández & Azkona, 1993). The diminution in the body condition of chicks as a result of human disturbances is already known in blue tits *Cyanistes caeruleus* (Remacha *et al.*, 2016) but without difference between sexes. Contrary to blue tits, Montagu's harriers are sexually dimorphic, males being 15% lighter than females (Millon & Bretagnolle, 2008). This implies that females may require more energy to fledge (Teather & Weatherhead, 1988), similar to female American kestrels which consume 7% more food than their brothers (Anderson *et al.*, 1993). It may also imply that females suffer higher starvation when food is scarce than male nestlings (Clutton-Brock, Albon & Guinness, 1985; Teather & Weatherhead, 1988). However, our hypothesis contrasts with the results from a previous study showing that the smaller sex (the male) has a higher probability of starvation in Montagu's harriers; because females are the bigger sex, they could be more competitive than males when consuming food items delivered by the parents (Arroyo, 2002). Taking into account this contrast among studies, the process explaining the lower body condition of female nestlings in areas with higher IDN could be independent of food delivery by the parents but due to other unexplored processes.

In our study area, most of the chicks had fault bars on their rectrices; our results showed that chicks in the most anthropized areas had more fault bars than chicks in less anthropized areas. Moreover, a higher number of fault bars was found on chicks in harvested crop plots than on those in unharvested plots. Fault bars may appear consecutively to chronic or acute stress related to CORT secretion (Jovani & Rohwer, 2017). In European starlings *Sturnus vulgaris* for instance, individuals experimentally stressed (chronically or punctually) had more fault bars than unstressed individuals (Strochlic & Romero, 2008). Potentially, the increase in fault bars development in our area could be caused by a variety of stressors related to human disturbances. Moreover, after harvesting, only 4 m^2 of crops around the nest remain unharvested. Therefore, nests become more visible and we cannot exclude that neighbouring inhabitants and/or farmers may visit nests. This increase in fault bars could directly result from human disturbances (e.g. nest visits by intruders such as walkers or farmers) but also indirectly due to random punctuated reduction/absence in parental care due to disturbances. For instance, a smaller and less predictable food supply and/or decrease in time spent by the parents around the nest are stressors that can be caused by human disturbances and can trigger fault bar formation in nestlings (Strochlic & Romero, 2008; Rensel *et al.*, 2010; Fokidis *et al.*, 2012). The development of fault bars seems closely related to the stress experienced by the chicks. Our results highlight that their presence could be a good indicative marker of perturbations induced by human activities although further investigations are needed to properly test the hypothesis of the cascading effects of human disturbances on parental care and thus on fault bars of chicks (Jovani & Rohwer, 2017).

Finally, the infrastructure density around the nest and the harvesting conditions also affected chick behaviour. Chicks from nests in harvested crops were more active and aggressive towards the experimenter during handling than those in unharvested crops. Moreover, chicks from nests located in areas with higher anthropization levels displayed more escape behaviour than those in areas with lower infrastructure density around the nest. As for fault bars, higher anthropization levels and harvested crops could increase human disturbances and its perception around the nest and thus increase stress for chicks. Disturbed and stressed chicks could be more aggressive and agitated. These results are consistent with a previous study in which a sensitization phenomenon increases the stress, activity and aggression of chicks over repeated handlings by the same experimenters (Rabdeau *et al.*, 2019). These effects on chick behaviour suggest that higher levels of anthropization and harvesting conditions may be linked to repetitive exposure to the same stimulus (e.g. traffic noise, human visitation). Further studies are needed to properly measure these different stressor stimuli, such as human visitation around the nest, and to test the hypothesis of sensitization.

Conclusion

The present study showed the interest in considering several indexes for establishing how anthropization in the rural landscape may trigger chronic stress for wild fauna. Different physiological, behavioural and life-history traits of Montagu's harrier nestlings were affected by the harvesting conditions and the IDN around the nest and related human activities, although the observed anthropization level was low. Nests with 4.83% IDN seemed to have more stressful anthropized surroundings than nests with 1.23% IDN, because it implied more car traffic, walkers, joggers, cyclists, anthropogenic noise from villages and possibly more nest visits by neighbouring inhabitants. Moreover, nests in harvested crops were more visible from outside the crop plots, that is from paths and roads, and thus could be more exposed to human

disturbances. These effects may compromise the recruitment of fledglings in the population through altered survival during migration, due to a decrease in flight ability (fault bars) or low body condition. CORT secretions are known to produce long-term effects on bird quality in adulthood (Blas *et al.*, 2007; Wada & Breuner, 2008; Schoech *et al.*, 2011; Blas, 2015) and may compromise the persistence of some harrier populations. Because Montagu's harrier is a protected farmland raptor, the impacts of the anthropization level and harvesting conditions on nestlings are a matter of concern for the conservation of this species and possibly also for other ground-nesting farmland birds. Further studies are needed to accurately measure the human visitation (type and frequency) around nests and their impacts on chick development: agricultural activities on fields, walkers, joggers, nest visitation by neighbouring inhabitants, by using camera traps, for example. These camera traps would also allow for the measurements of nest visitation by predators. Conservation measures could be thus proposed to farmers and include a delay of the harvest until the fledging as already recommended by Arroyo, García & Bretagnolle (2002), and/or a larger area of unharvested crops around the nest. These measures should be considered a matter of urgency because harvesting occurs earlier and earlier every year due to global warming (see Fatima *et al.*, 2020). Considering that even low levels of anthropization on farmland may have various consequences on birds and could contribute to their decline is vital information and should therefore be considered in the management of all areas where competing uses between ground-nesting birds and humans intersect (Cooke *et al.*, 2020).

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Authors' contributions

JR, KM, VB and JM conceived the ideas and designed the methodology; JR, MD, JM and KM collected the data; JR, MD, VB, JM and KM analysed the data; JR, JM and KM led the writing of the paper. All the authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Spatial distribution of nests in our study area, *Zone Atelier Plaine et Val de Sèvre*.

Figure S2. Fault bars on rectrices of Montagu's harrier chicks: (a) light to moderate fault bars and (b) moderate to severe fault bars (see review by Jovani & Rohwer, 2017).

Figure S3. Infrastructure density around the nest by year.

Figure S4. Distribution of nests in relation to IDN ranging from 1.23% to 4.83%.

Figure S5. Different IDN scenarios within the 1000 m radius buffer (red) around nests (blue): (a) 1.23%, (b) 3.0012% and (c) 4.83%.

Figure S6. Spearman's rank correlation coefficients for all behavioural, physiological and life-history traits included in the present study (115 chicks, 58 nests).

Figure S7. Number of fault bars by years.

Figure S8. Differences in behaviour between years for PC3 are mostly represented by the behaviour at nest approach.

Table S1. Summary of models ([a]Linear Mixed Models, [b]Generalised Liner Mixed Models, with Poisson distribution) investigating variation for body conditions and fault bars including the nest excluded from the analyses in 2016 for the 1000 m-radius.

Table S2. Summary LMM investigating variation for changes in CORT.