Effects of conventional vs. organic farming practices on raptor nestling health: Neither black nor white

Elva Fuentes [a,*], Jérôme Moreau [a,b], Maria Teixeira [b], Vincent Bretagnolle [a,c], Karine Monceau [a]

[a] UMR 7372, Centre d'Études Biologiques de Chizé, La Rochelle Université & CNRS, 79360 Villiers en Bois, France
[b] Biogéosciences, UMR 6282 CNRS, Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France.
[c] LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, 79360 Villiers-en-Bois, France

ARTICLE INFO

ABSTRACT

Agricultural intensification is one of the main threats to biodiversity. Farmland bird specialists such as Montagu's harrier, *Circus pygargus,* are particularly at risk and declining. Conventional farming (CF) production systems usually involve landscape homogenisation, mechanisation, and the use of synthetic pesticides that may have direct and indirect effects on individuals. By contrast, organic farming (OF) systems typically promote agro-ecosystem health, which benefits biodiversity and the reproductive success of birds. However, the potential effects of agricultural systems on life history traits of Montagu's harrier chicks have not been investigated. Still, altered life history traits could impair chick survival and future reproductive success, which may in turn impact population dynamics. Here, we investigated the effects of OF (measured as a percentage around nests at different buffer sizes from 100 m to 2000 m) on a set of life history traits covering the behaviour, physiology (haematological, immune and nervous systems) and body condition of 380 chicks from 137 nests monitored between 2016 and 2021. At a local scale (<2000 m), only the H/L ratio (indicative of physiological stress) and carotenoid-based ornaments were clearly related to OF percentage. At 600 m around the nest, a higher OF percentage increased the H/L ratio, suggesting that chicks experienced greater stress due to either increased human disturbance or higher intra-/interspecific negative interactions around OF crop plots. Carotenoid-based ornaments were more strongly coloured with increasing OF around the nest at 1500 m. Considering the role of carotenoids in both detoxification processes and expression of secondary sexual traits, this result may indicate that CF would lead either to a difference in nestlings' diet and/or to a trade-off between organism's maintenance and sexual characters. These findings suggest that farming practices at a local scale surrounding nest locations may have subtle effects on chick development, but also on trade-offs between important physiological functions. This study highlights the importance of a multi-trait approach when assessing adverse and beneficial effects of both OF and CF on individuals.

1. Introduction

The biodiversity crisis, faced nowadays, spares no species. Among the most affected taxa, bird numbers decreased by 25% in Europe between 1980 and 2016 with farmland birds showing the steepest decline (Heldbjerg et al., 2018; Reif and Hanzelka, 2020; Rigal et al., 2023). At the same time, agricultural practices changed to increase yields, leading ecologists to hypothesise a causal link between agricultural intensification and farmland bird decline (Fuller et al., 1995; Krebs et al., 1999; Chamberlain et al., 2000). Among the features of this intensification, mechanisation appeared to have a direct negative impact on

ground-nesting birds (Crick et al., 1994; Tews et al., 2013; Santangeli et al., 2015). Landscape homogenisation and the use of pesticides also raised concerns because they can have insidious effects on farmland species (Matson et al., 1997; Benton et al., 2003; Mason et al., 2013; Sumasgutner et al., 2019; Moreau et al., 2022a). To counter the negative impacts of conventional farming (CF) involving intensive agricultural practices, organic farming (OF) emerged as an alternative in the late 1970s (Lockeretz, 2007). OF is defined as a production system excluding synthetic pesticides and fertilisers that uses nature-based solutions (Keesstra et al., 2018) to promote and enhance agro-ecosystem health (Lockeretz, 2007).

Three main interrelated characteristics distinguish OF from CF: agricultural practices, natural and semi-natural habitat proportion and farm inputs. Agricultural practices can be harmful to farmland birds either directly or indirectly. A direct impact of agricultural machines used under intensive practices is the death of ground-nesting birds (Crick et al., 1994; Vickery et al., 2001; Tews et al., 2013). Incubating adults, broods and chicks are frequently destroyed during mechanical mowing, tilling and harvesting activities (Schekkerman et al., 2009; Santangeli et al., 2015; Bretagnolle et al., 2018a). Agricultural practices can also have indirect effects on birds, by increasing disturbance and decreasing available resources. For instance, manure spreading, manual and mechanical weed and pest control, tillage and multiple cultivations all together generally increase labour in OF systems (Karlen et al., 1995; Jansen, 2000; Orsini et al., 2018), and can be identified as a potential source of disturbance for farmland birds. Human presence and activity are known to affect bird feeding rates (Exposito-Granados et al., 2020), induce physiological stress (Mougeot and Arroyo, 2017; Rabdeau et al., 2023), and alter behaviour including parental care (Fernández and Azkona, 1993), sometimes leading to nest failures (Strasser and Heath, 2013). Farming activity has even been shown to increase nest abandonment in passerine birds and to cause up to 32% nest failure in river lapwing, *Vanellus duvaucelii* (Assandri et al., 2017; Mishra et al., 2020). Moreover, intensive agricultural practices that involve clearing of ditches, removal of hedgerows, and intensification of grassland management are associated with lower territory and breeding densities in yellowhammer, *Emberiza citrinella* (Bradbury et al., 2000) and barn owl, *Tyto alba* (de Bruijn, 1994). These intensive land-uses commonly found in CF lead to simplified landscapes where important habitats for birds are no longer available (Bradbury et al., 2000; Sumasgutner et al., 2019; Tarjuelo et al., 2020) and where their food supplies are reduced through fewer weed seeds and natural insect reservoirs (Matson et al., 1997; Chamberlain and Wilson, 2000; Benton et al., 2002). Insects rely on the availability of non-uniform patches of grass, weeds and hedgerows for food and shelter (Benton et al., 2002). These features are thus associated with higher insect diversity (Holland and Fahrig, 2000) and higher bird diversity and abundance (Chamberlain et al., 1999; Chamberlain and Wilson, 2000; Freemark and Kirk, 2001). Hedgerows and landscape complexity also maintain small mammal populations (Butet et al., 2006; Gelling et al., 2007) and consequently have a positive effect on populations of birds of prey (Koks et al., 2007; Butet et al., 2010), even if some find such a link only under favourable food conditions (Sumasgutner et al., 2019). OF has been shown to have a positive effect on biodiversity, an effect which is even greater in simplified landscapes (Roschewitz et al., 2005; Fischer et al., 2011; Henckel et al., 2015). In fact, OF practices that might imply non-cropped habitat management such as the establishment of hedgerows and field margins benefit insects and therefore insectivorous birds (Hole et al., 2005; Lockeretz, 2007). Under OF agricultural systems, natural and semi-natural areas are typically higher than under CF systems (Gibson et al., 2007; Norton et al., 2009), hence OF promotes resources for birds, especially food abundance (Fischer et al., 2011). Different meta-analyses support that view, showing that OF promotes higher overall biodiversity, from flora to insects and bird species richness and abundance (Tuck et al., 2014; Stein-Bachinger et al., 2021). Lastly, farm inputs are the main characteristic contrasting OF from CF. Although organic plant protection products can be used, no synthetic pesticides or fertilisers are employed for crop production in OF systems. Indeed, in Europe for farms to be considered organic the prohibition of use of synthetic pesticides and fertilisers is the only mandatory practice, other practices such as natural or semi-natural areas management being generally recommended but not systematic in OF systems (Regulation EU, 2018/848 of the European parliament and of the Council of 30 May, 2018). Recent reviews highlighted that synthetic pesticides are the main factor negatively affecting farmland birds (Stanton et al., 2018; Rigal et al., 2023). Pesticides can have indirect effects on birds through the elimination of crop pests and weeds, reducing food and habitat resources (Hole et al., 2005; Gibbons

et al., 2014). Furthermore, pesticides lack specificity and can affect non-target species (Sánchez-Bayo and Goka, 2014; Vyas, 2017). The use of pesticides can thus have direct effects on birds, either inducing lethal effects (immediate death after exposure) or delayed sublethal effects altering life history traits. In fact, different functions of a bird's organism can be affected by pesticides, from the cellular level to higher physiological functions and behaviours (Mitra et al., 2011; Moreau et al., 2021, 2022a; Gaffard et al., 2022). Many experimental studies have revealed altered life history traits due to pesticide toxicity, which may compromise bird survival, and consequently populations dynamics (Lopez-Antia et al., 2015a, 2015b; Ortiz-Santaliestra et al., 2020; see Moreau et al., 2022a for a recent review). *In natura*, birds are exposed to numerous molecules as multiple pesticides are usually applied to fields either at the same time or sequentially, inducing cocktail effects (Gaffard et al., 2022). Moreover, the persistence of some molecules in soil and water can lead to contamination without direct contact with the applied chemicals (Jagannath et al., 2008; Goulson, 2013; Fuentes et al., 2023). A recent study on wild passerines showed that birds nesting in hedges surrounded by CF were less vigorous than those nesting in hedges surrounded by OF, and that this might be due to pesticide contamination under CF (Moreau et al., 2022b).

Montagu's harriers, *Circus pygargus*, a migratory raptor species inhabiting agricultural lands in Europe, nest on the ground in cereal crops. In France, populations have declined by 10–30% over the past 30 years (Millon and Bretagnolle, 2004; Comolet-Tirman et al., 2015) and the principal cause is believed to be agricultural intensification (Butet and Leroux, 2001; Arroyo et al., 2002; Arroyo et al., 2004; Santangeli et al., 2015). Montagu's harriers mostly feed on common voles, *Microtus arvalis*, which display cyclic population dynamics in Western Europe, hence food availability and diet vary from year to year (Millon and Bretagnolle, 2008). In years of low vole abundance, Montagu's harriers compensate by feeding on Orthopterans (grasshoppers and crickets) (Salamolard et al., 2000). For this farmland specialist bird, the type of agricultural system at a local scale might be of great importance during the breeding season. Indeed, eggs and chicks are located on the ground in crop fields, and the altricial chicks stay in the nest during the whole rearing period (~35 days). Consequently, at all developmental stages, Montagu's harrier offspring might be affected by the composition and management of the habitats in the close surroundings. If the agricultural system in the vicinity leads to altered life history traits, survival may be compromised, reducing future recruitment of fledglings into the population of this declining species.

In the present study, we explored the patterns of life history traits variation in nestlings along a gradient of OF near their nests. Accordingly, we investigated the relative impacts of OF vs. CF on multiple life history traits of Montagu's harrier chicks at a local scale (up to 2000 m) around nests. Compared with OF, CF may decrease food availability (due to both lower quality habitats and intensive management practices) and increase exposure to pesticides (through contact or prey consumption). Therefore, we hypothesised that a higher percentage of CF around the nest may adversely affect fledglings. Since all life history traits involve complex interconnected functions, expectations for a single trait are complicated to raise. A multi-trait approach is therefore crucial to elucidate the effects of agricultural systems (OF vs. CF) on birds, and eventually to highlight potential trade-offs between life history traits. We expect chicks reared in nests surrounded by a lower percentage of OF (i.e., a higher percentage of CF) would have a poorer overall health status that might be reflected by inferior body condition, more markers (physical and biochemical) of chronic stress, a depressed immune system, and lower vigour than chicks surrounded by a higher percentage of OF.

2. Material and methods

2.1. Ethics statement

All experiments conformed to the French guidelines for the ethical use of animals in research (APAFIS#18557–2019010822312199v2). Bird handling was allowed and licensed by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO; Museum National d'Histoire Naturelle; licence #1308).

2.2. Study area and model species

The study site is located in southwestern France (46°11′N, 0°28′W), in the Long-Term Social-Ecological Research 'Zone Atelier Plaine & Val de Sèvre' (LTSER ZAPVS), a 450 km² area where annual crop identification is carried out, allowing mapping of organic crop plots in detail. In France, OF is regulated by the European legislation (Regulation EU, 2018/848 of the European parliament and of the Council of 30 May, 2018) on organic production, which details all practices to respect for farms to be considered organic, the main one being the complete ban on the use of synthetic pesticides and fertilizers. Other farming practices, including weeding or non-cropped habitat management, being at the discretion of each farmer. Nonetheless, Catarino et al. (2019) report general information on CF and OF systems of the study area; the main differences being smaller farm areas, more diversified crops and a lower nitrogen supply in OF systems. In this intensive agricultural area, cereal crops are the predominant cultures (average coverage of 41.5% between 2009 and 2016), followed by corn, sunflowers and oilseed rape (Bretagnolle et al., 2018b). Natural (or semi-natural) habitats and urbanized

areas represent only a small proportion of the study area (average coverage of 13.5% and 9.8% respectively between 2009 and 2016; Bretagnolle et al., 2018b) thus only organic crop plots were used for analyses (see Section 2.7 for further information). Montagu's harrier monitoring has taken place in this site since 1994 (Bretagnolle et al., 2018b). This species nests on the ground, mainly in cereal crops, and lays up to eight eggs (Arroyo et al., 1998; Millon et al., 2008). The incubation period lasts 29 days and the rearing period between 30 and 35 days (Arroyo et al., 2007). The mean productivity in this site is 2.05 fledglings per breeding attempt (Arroyo et al., 2004), breeding success depending mainly on the availability of common voles, their main prey in this area (Salamolard et al., 2000). Foraging range varies with location; in the study area males use home ranges of ~14 km² (Salamolard, 1997), but home ranges during the breeding season can stretch to 100 km² (Guixé and Arroyo, 2011).

2.3. Overall experimental design

From 2016 to 2021, the reproduction of Montagu's harriers was monitored from late April until late July. All nests were searched by professional ornithologists, and once located, visited and mapped using a global positioning system (GPS) receiver, they were stored on a geographical information system (GIS; QUANTUMGIS 3.16.5; QGIS Development Team, 2021, see Fig. 1). Nests were visited twice during the incubation period and every week after hatching (lag time between visits 7 ± 2 days). At 15 days old, chicks were sexed and banded with a unique coded aluminium ring from the Museum National d'Histoire Naturelle. Sex was determined by the colour of the iris (brown for females and grey for males) (Leroux and Bretagnolle, 1996).
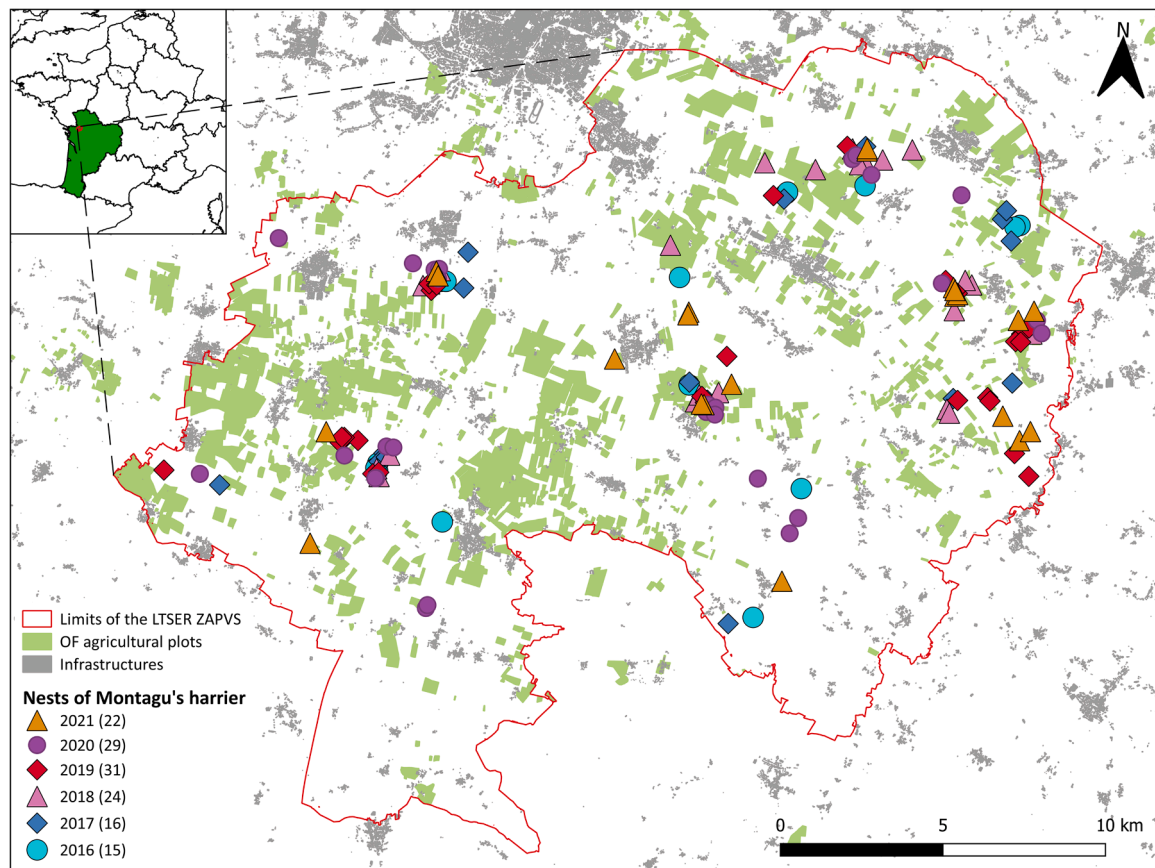

Fig. 1. Spatial distribution of Montagu's harrier, *Circus pygargus*, nests across the Long-Term Socio-Ecological Research Zone Atelier Plaine & Val de Sèvres (LTSER ZAPVS). Only nests corresponding to data for fledglings included in the present study are shown (the number of nests monitored each year is given in brackets). Organic farming (OF) agricultural plots correspond to data available for 2021 from our GIS database. Infrastructures correspond to buildings, sport fields, cemeteries, locks and bridges present in the study area.

For the present study, we focused on data collected during the last visit before fledgling, when nestlings were 26 ± 2 days old. Briefly (see details below), chicks were caught in the nest and carefully handled to take morphometric measurements and breath rate and collect blood samples (Fig. 2). A phytohemagglutinin (PHA) skin injection was performed, and behaviour during handling was also recorded (Fig. 2). Chicks were handled and released at the nest, and the handling time was minimised to reduce potential stress. The following day of the visit, nests were again visited to record chicks' inflammatory response to the PHA skin injection (see details below). A total of 380 chicks were monitored ($N_{2016} = 40$, $N_{2017} = 32$, $N_{2018} = 81$, $N_{2019} = 84$, $N_{2020} = 85$, $N_{2021} = 58$) from 137 nests ($N_{2016} = 15$, $N_{2017} = 16$, $N_{2018} = 24$, $N_{2019} = 31$, $N_{2020} = 29$, $N_{2021} = 22$). No sex ratio bias was observed for the entire period (187 females and 193 males; Binomial test $p = 0.80$).

2.4. Morphometric measurements

2.4.1. Morphometrics for body condition assessment

Body condition is a morphometric estimate reflecting the overall health status of individuals, notably involved in post-fledgling survival of birds (Blums et al., 2005; Vitz and Rodewald, 2011; Duijns et al., 2017). Body condition for each nestling was estimated from the scale mass index following Peig and Green (2009):

$$SMI_i = Mass_i \times \left(\frac{Mean\ tarsus\ length\ of\ the\ group}{Mean\ tarsus\ length_i} \right)^{b_{sma}}$$

where b_{sma} is the slope of the major axis regression of log (body mass) on log (mean of the two measures of the left and right tarsus length) with the standard major axis method (package 'smatr') (Warton et al., 2012) for each chick i. The mass was obtained by weighing chicks with a Pesola 500 g spring scale (accuracy ± 5 g) (Schindellegi, Switzerland) and the left and right tarsus were measured twice with a digital calliper (accuracy ± 0.1 mm).

2.4.2. Fault bars

Fault bars are malformations in feathers induced by punctual stressors during chick growth, which may result in feather and even rachis breaks (Jovani and Rohwer, 2016; see Rabdeau et al., 2023 for an example of recent usage). Chick tails were photographed and the number of fault bars (all breaks in barbs and barbules) was counted on the most affected rectrix feather by the same experimenter to avoid observer bias. The number of fault bars on each chick ranged between 0 and 10.

2.4.3. Colouration

Colouration of nestling bare parts, a carotenoid-related trait, can be limited through the diet and mediated by different physiological effects (Garcia-Heras et al., 2017). The colour of the cere and tarsus (bare parts) were scored by direct comparison with a colorimetric chart from Yolk Colour Fan (Roche, Neuilly-sur-Seine, France). Scores ranged from 0 (almost white / pale yellow) to 15 (orange) and were highly correlated with colour parameters obtained using a spectroradiometer (Faivre et al., 2001). Cere scores ranged from 0 to 5 and tarsi ranged from 0 to 6. Both scores were highly correlated (Spearman's rank correlation test, $\rho > 0.77$, $p < 0.0001$, 95% confidence interval CI = [0.72, 0.81], n = 380), and only cere scores were used for statistical analyses.

2.5. Physiological measures

2.5.1. Breath rate score

Breath rate usually refers to a proxy of physiological stress (Carere and van Oers, 2004; Torné-Noguera et al., 2014; Rabdeau et al., 2019). Breath rate was measured using chicks handled in back position, and corresponded to the number of thoracic movements counted during 15 s for three consecutive replicates. The breath rate score was then obtained by averaging the three replicates.

2.5.2. Physiological parameters assessed from blood

2.5.2.1. Blood collection.
Blood sampling was made on the brachial vein through a puncture using a sterile needle and heparinised capillaries. A single microcapillary of 10 µL was used for both sedimentation rate and haematocrit, a droplet of blood was used for blood smear (see below), and two capillaries of 100 µL each were placed in Eppendorf tubes and kept refrigerated (0–5 °C) for 2–3 h while transporting to the lab, where they were stored at − 20 °C until further analyses (carotenoid titration and acetylcholinesterase activity; see below).

2.5.2.2. Sedimentation rate and haematocrit.
Erythrocyte sedimentation rate (ESR) corresponds to the proportion of red blood cells sedimented per hour, and it increases in response to various inflammatory or infectious processes (Saino and Møller, 1996). Microcapillaries were kept vertical for 5 h in a refrigerated container (0–5 °C), lengths were measured with an electronic calliper to the nearest 0.1 mm, and ESR in millimetres per h (mm/h) was estimated as follows:
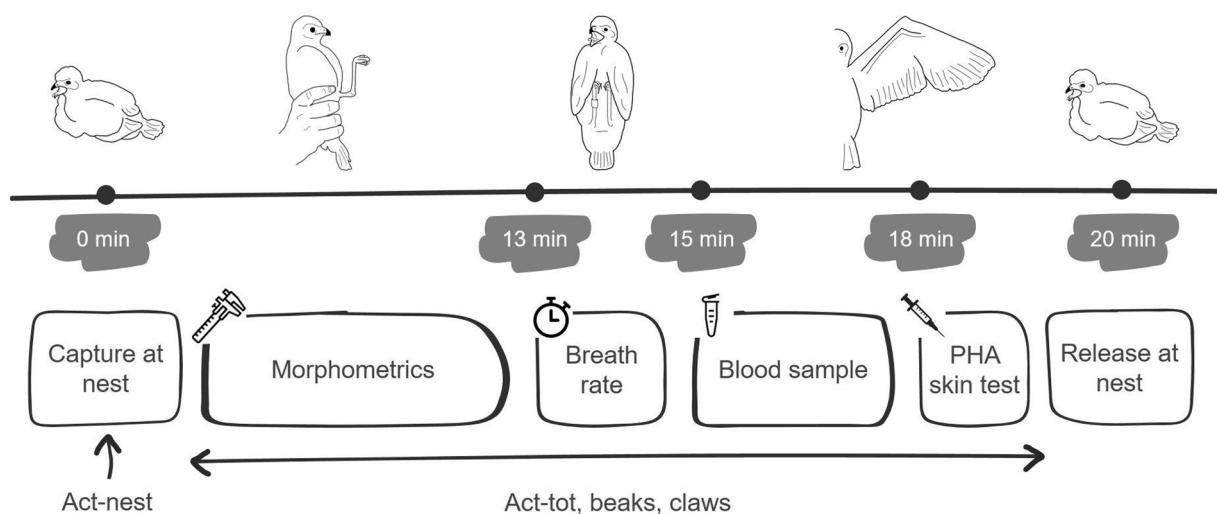

Fig. 2. Summary of the experimental design measuring different morphological, physiological and behavioural traits of Montagu's harrier, *Circus pygargus*, chicks before fledging. For each chick, act-nest = activity at nest approach, act-tot = total activity during handling, and beaks and claws = the rates of beak and claw attacks during handling.

$$ESR = \frac{volume\ not\ filled\ by\ erythrocytes}{total\ blood\ volume\ in\ the\ tube \times time\ of\ sedimentation}$$

Once ESR was measured, microcapillary tubes were centrifuged at 5000 rpm for 5 min to measure haematocrit. Haematocrit is used as an index of anaemia and corresponds to the proportion of the tube filled with erythrocytes divided by the total volume of blood sample in the tube, given as a percentage (Saino and Møller, 1996; see also Biard et al., 2015; Moreau et al., 2021).

2.5.2.3. Carotenoid titration. Carotenoids are involved in different functions of birds, including as antioxidants, and a high concentration in blood can reflect physiological stress (McGraw and Ardia, 2003). Eppendorf tubes containing ~150 μL of blood were centrifuged (10 min at 9000 rpm) and plasma was collected and kept at − 20 °C until laboratory analyses. Plasma carotenoid concentration was subsequently obtained in micrograms per millilitre (μg/mL) using a standardised colorimetric technique (see Biard et al., 2010 for additional information).

2.5.2.4. Acetylcholinesterase activity. Acetylcholinesterase (AChE) activity is negatively affected by some neurotoxic pesticide molecules altering neural functions, which in turn has disruptive consequences on diverse behaviours and complex functions (Grue et al., 1997; Eng et al., 2017; Moreau et al., 2022a). AChE activity in milliunits per minute (mU/min) was obtained by a method derived from Ellman et al. (1961) using 5 μL of blood diluted in 100 μL of a 1% Triton X-100 solution and measured using a SpectraMax iD3 microplate reader (Molecular Devices Inc., Sunnyvale, CA, USA) over 40 min at 324 nm and 37 °C. AChE activity was calculated using SoftMax Pro7 software (Molecular Devices, San Jose, CA, USA) as the maximum change in absorbance per minute during kinetics analysis.

2.5.2.5. Blood smear. For each bird, a blood smear was performed with a droplet of blood sample. Slides were air-dried and fixed in absolute methanol before being stained with Giemsa solution (Sigma Chemical, St. Louis, MO, USA). Blood smears were examined with an oil immersion microscope under 1000x magnification. Total white blood cells (WBC) count was estimated from the number of leucocytes found among 8000 erythrocytes. A high number of leucocytes reflects stress and inflammatory processes (Ots et al., 1998). Different types of leucocytes were counted and used to estimate the relative proportion of heterophils to lymphocytes (H/L ratio). The H/L ratio is used as an index of physiological stress, as it is supposed to increase in response to various stressors (Maxwell, 1993; Ots et al., 1998; Moreau et al., 2021; see Biard et al., 2015 for details).

2.5.3. Immune challenge

Before release into the nest, the immune system of nestlings was challenged using phytohemagglutinin (PHA) skin tests (Smits et al., 1999). Briefly, 0.5 ± 0.1 mg of PHA (Sigma Chemical, St. Louis, MO, USA) diluted into 0.1 mL of phosphate-buffered saline (PBS) was injected subcutaneously in the wing patagium as described by Sternalski et al. (2012a). The thickness of the patagium was measured three times before injection using a pressure-sensitive dial thickness gauge (spessimeter accuracy ± 0.01 mm) and again 24 h after injection. The response to the PHA skin test corresponds to the change in average thickness (in mm) of the injection site, and thus the magnitude of this change reflects the immune potential of nestlings (Sternalski et al., 2012a; see also Biard et al., 2015).

2.6. Behavioural measures

Behaviour is considered an indicator of individual health that can be altered by multiple chemicals and is often regarded as a more sensitive response to stress or toxicity levels than other physiological measures

(Grue et al., 1997; Clotflelter et al., 2004; Hellou, 2011; Moreau et al., 2022a). When handling chicks (i.e., from capture in the nest to release), the behaviour of bird was scored using four behavioural traits as described by Rabdeau et al. (2019): (i) activity during nest approach (act-nest); (ii) total activity during handling (act-tot); (iii) rate of beak attacks (beak); (iv) rate of claw attacks (claws). Act-nest was assessed when the experimenter approached the nest to catch the chicks and scored as follows: stayed motionless = 0, chicks retreated = 1, chicks ran away = 2. Act-tot was measured throughout handling and scored as follows: chicks stayed motionless = 0, chicks rarely moved = 1, chicks moved regularly = 2, chicks moved continuously = 3. The number of beak and claw attacks were counted during handling and divided by the duration of handling, resulting in a rate (number of attacks per minute).

2.7. Statistical analyses

A principal component analyses (PCA) was performed on the four behavioural scores using singular value decomposition of a standardised (centred and scaled) data matrix (Crawley, 2012). The first axis of the PCA reflecting global activity and vigour during handling (PC1-activity) was retained as its eigenvalue was > 1, and it accounted for 48.69% of the variance. PC1-activity was positively correlated with both rates of beak ($r = 0.56$) and claw ($r = 0.57$) attacks, act-tot ($r = 0.55$) and act-nest ($r = 0.24$) scores.

Normality and homoscedasticity of all response variables were tested using the 'fitdistrplus' package prior to model implementation, and when these assumptions were not met, distribution with the best fit was selected using the same package (Delignette-Muller and Dutang, 2015). Model residuals and spatial autocorrelation (using Moran's I) were also checked using 'DHARMa' package (Hartig, 2022). PC1-activity, body condition, ESR, breath rate score, AChE activity and PHA response were used as response variables in Linear Mixed-effects Models (LMMs). Carotenoid concentration was square-root transformed, haematocrit and H/L ratio were log-transformed prior to LMM execution, since the distributions of these variables did not meet normality. Generalised LMMs fitted with a Poisson distribution (PGLMMs) were implemented for fault bars and colouration scores and a Generalised LMM fitted with a Negative Binomial distribution (NB-GLMM) was used for the total WBC count. For all models (LMMs, PGLMMs and NB-GLMM), the percentage of OF around the nest (log-transformed, hereafter OF effect) and the year as factor were included as fixed effects, and the nest identity as a random effect (to avoid pseudo-replication as chicks can belong to the same nest) (Bolker et al., 2009). The year was considered a fixed effect because we wanted to control for inter-annual variability of environmental conditions (phenology, food availability and weather for instance). Because year could have been considered a random factor, we ran all models changing only the year fixed effect into a random effect. This approach did not change the results obtained with year as a fixed effect, hence we used the results of the first analyses. All models were run with the 'lme4' package (Bates et al., 2015).

As we had no a priori information on the scale of the OF effect on life history traits for each chick, we estimated the percentage OF around the nest for 20 buffer sizes (i.e., radii every 100 m, from 100 m to 2000 m). To this end, the GPS coordinates of nests and a database of the LTSER ZAPVS, which georeferenced the agricultural plots using OF practices, were used with the 'sf' package (Pebesma, 2018). Since OF agricultural plots varied over time, the percentage of OF around nests for a given year was calculated using the georeferenced plots of the corresponding year. We ran 20 models per life history trait (one per buffer size) and extracted an Akaike Information Criterion corrected for small sample size (AICc) using the 'AICcmodavg' package (Mazerolle, 2020). From a set of candidate models, AICc allows selection of the model with the most support, which has the lowest AICc, assuming that models with ΔAICc < 2 (i.e., a difference in AICc between candidate models <2) are similarly supported and cannot be distinguished from each other (Burnham and Anderson, 2004). For every life history trait, a plot was

generated representing the AICc of the 20 models (one for each buffer size), with a red dotted line illustrating the model selection criterion (lowest AICc of the candidate models + 2), with the shape and colour reflecting the significance and direction of the OF effect. To avoid type II errors, we chose to present our results based on effect sizes (estimates of the model) assorted with their 95% confidence intervals (CI) (following Garamszegi, 2006; Nakagawa, 2004; Nakagawa and Cuthill, 2007; Cumming, 2014). The OF effect direction corresponded to the sign of the estimate and was considered significant when 95% CI did not include 0. Calculation of the bootstrapped CI was obtained for 2000 iterations and using the package 'boot' (Canty and Ripley, 2022). We discuss effect sizes assorted with their 95% CI which allow to quantify the biological effect we tested and provide comparable estimates for future research and meta-analyses, still, we provide the results from model comparison using likelihood ratio-based χ^2-statistics in supplementary materials (Fox and Weisberg, 2011).

To assess potential links between variables, Spearman's rank correlation tests were performed. All statistics were conducted with R v4.0.5 software (R Core Team, 2021), implemented using the aforementioned packages.

3. Results

Summary statistics and Spearman's rank correlation coefficients of the 12 life history traits are presented in the Supplementary Material (see Table S1 and Fig. S1). Only ESR and haematocrit (Spearman's rank correlation test, $\rho > -0.42$, $p < 0.0001$, 95% CI = [−0.51; −0.32], n = 343) were correlated (Supplementary Material Fig. S1). The set of candidate models for body condition, fault bars, breath rate score, ESR, haematocrit, carotenoid concentration, AChE activity, WBC count, and PHA skin test did not yield any specific buffer size with substantial support (i.e., AICc <2 with a significant OF effect) for an influence of OF percentage around nests (Fig. S2 in supplementary materials). For cere colouration score and H/L ratio, the best models (i.e., those with ΔAICc <2) identified a positive effect for OF percentage at a range of radii (Fig. 3). The cere colouration score increased with OF percentage around the nest for buffer sizes > 500 m (Fig. 3a). For H/L ratio, a positive relationship was detected between 300 and 900 m (Fig. 3b). Concerning the PC1-activity, a positive relationship with the percentage of OF was detected at 200 m around the nests (Fig. 3c).

We then selected the model with the lowest AICc to probe the relationships between the trait and the OF percentage around the nest (Fig. 4; Chi-squared test results are given in Table S2 in supplementary materials). Chicks displayed a significantly higher cere colouration score when surrounded by a higher percentage of OF at 1500 m (effect size = 0.14; 95% CI = [0.04; 0.22]), the lowest AICc for this life history trait (Fig. 4a). The lowest AICc for the H/L ratio was at a radius of 600 m around nests; at this distance the H/L ratio significantly increased with increasing OF percentage (effect size = 0.11; 95% CI = [0.04; 0.18]; Fig. 4b). For PC1-activity, the lowest AICc was at 200 m, an increase in OF at this distance from nests significantly increased the global activity of chicks (effect size = 0.20; 95% CI = [0.06; 0.40]; Fig. 4c).

4. Discussion

The aim of the present study was to explore life history traits variation of Montagu's harrier chicks linked to agricultural systems around nests. The results revealed an effect on two of the 12 traits investigated, although moderate. Cere colouration and H/L ratio were positively linked to OF at different radii, suggesting that the effects of the agricultural system operate at different distances, but not necessarily at the same range. The cere colouration score increased with increasing OF percentage at distances > 500 m with the best model selected at 1500 m. The H/L ratio increased significantly with OF at distances from 300 to 900 m, the best model being at 600 m. Global activity of chicks increased with increasing OF percentage at 200 m only. For all other life
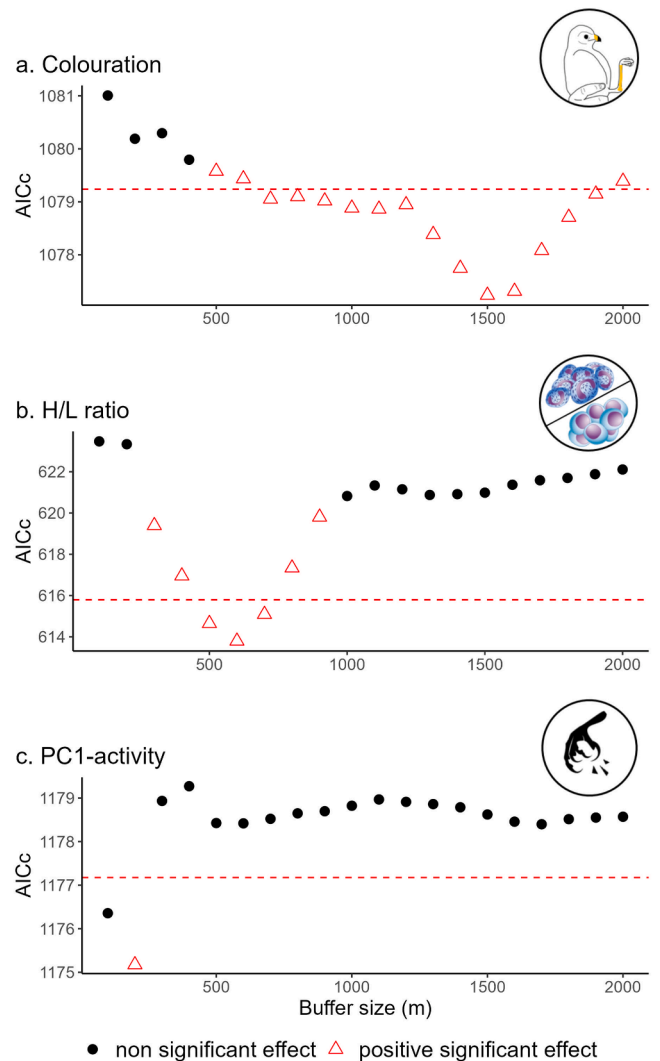

Fig. 3. Model selection using AICc to assess the responses of life history traits (life history traits) of Montagu's harrier, *Circus pygargus*, chicks to the effect of the percentage of organic farming (OF) around the nest at different buffer sizes (from 100 m to 2000 m radius). Measured life history traits are (a) cere colouration score, (b) H/L ratio, and (c) PC1-activity. AICc = Akaike Information Criterion corrected for small sample sizes. Red dotted lines correspond to the lowest AICc of candidate models + 2. Red triangles indicate a positive significant OF effect (i.e., a positive model estimate and assorted 95% confidence interval (CI) not crossing 0). Black dots represent a non-significant OF effect (i.e., the 95% CI of model estimate crosses 0).

history traits, namely body condition, fault bars, breath rate score, ESR, haematocrit, carotenoid concentration, AChE activity, WBC count, and PHA skin test, no effect of OF was detected at any of the buffer sizes.

In the present study, we found evidence for the impacts of farming practices (CF and OF) on Montagu's harrier chicks at a low spatial scale (< 2000 m) around nests. First, OF was found to be associated with a higher H/L ratio. This trait is indicative of stress undergone by chicks during their rearing period. Indeed, H/L ratio, is considered a reliable indicator of mild to moderate stress, and to reflect chronic stress levels rather than short-term stress responses (Maxwell, 1993; O'Dell et al., 2014). This result suggests that chicks in areas with a higher OF percentage may suffer more disturbance. Indeed, compared with CF, OF practices involve more repetitive passages (Karlen et al., 1995; Reissig et al., 2016; Orsini et al., 2018), which may equate to more stress experienced by chicks. Furthermore, areas with more OF fields are generally better appreciated than areas with CF fields by urban
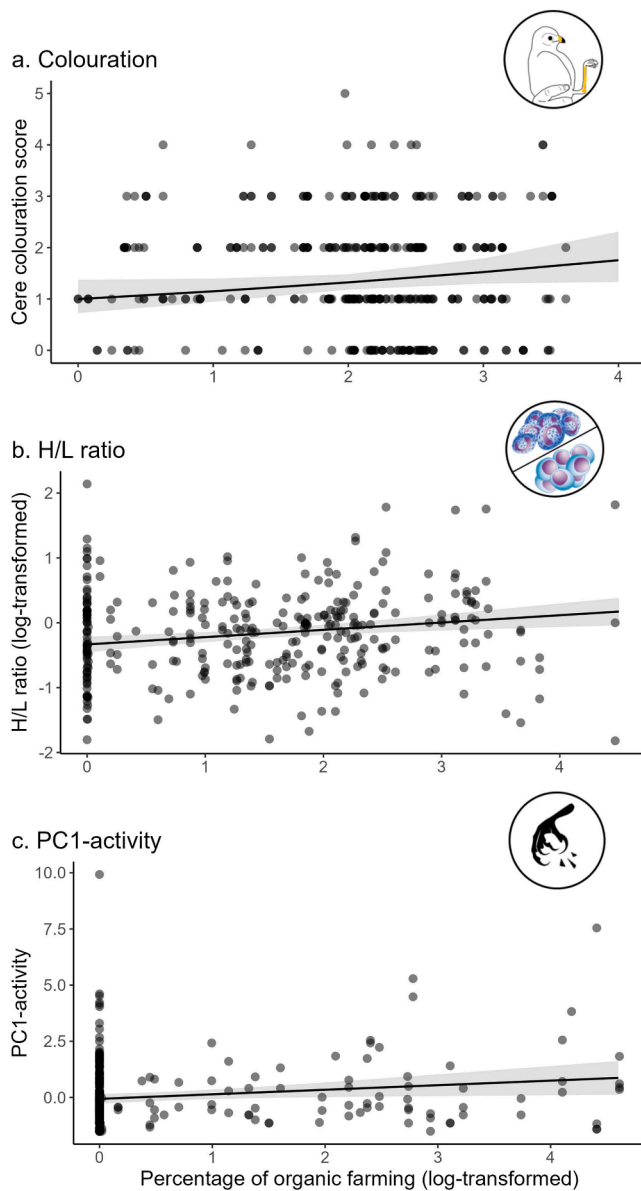
Fig. 4. Organic farming effect on (a) cere colouration score, (b) H/L ratio, and (c) PC1-activity of chicks at 1500 m, 600 m and 200 m around the nest respectively. A dot represents a value measured for a chick (darker = more chicks had this value). Lines predict values of each life history trait depending on the percentage of organic farming. Shading represents the 95% confidence interval.

inhabitants attracted to naturalistic features and elements (Zasada, 2011). Diversified habitats offer more opportunities for recreation and leisure than uniform ones (Hansen et al., 2006). Anthropic disturbances can induce stress in Montagu's harrier chicks, leading to physiological responses to this stress and even to the formation of fault bars (see Rabdeau et al., 2023). Repeated human activities, whether related to OF practices or recreation, could also induce prolonged absence of adults, resulting in reduced parental care, and thus more stress. Additionally, a higher presence of conspecifics or other raptor species around OF crops is also possible. Competition between Montagu's harriers nesting in semi-colonies is presumably low but could increase in years of low vole abundance. The presence of other raptor species foraging in the same area would also increase competition for food (Garcia and Arroyo, 2002). Competition for food resources might increase the time parents spend foraging, leaving chicks alone for longer periods. The presence of

more raptors may increase the risk of predation of Montagu's harrier nests, which are particularly vulnerable and attractive in low vole years (Arroyo et al., 2001). Pairs are often seen mobbing common buzzards, *Buteo buteo*, or black kites, *Milvus migrans,* to protect their nests (authors' personal observations), and this might result in more frequent parental absences. Consequently, an increase in intra- and interspecific negative interactions surrounding OF crop plots would increase the time chicks are unattended.

An alternative explanation for the higher H/L ratio observed for chicks in nests surrounded by a high OF percentage is the presence of a higher number and/or diversity of pathogens. Indeed, H/L ratio is known to increase in response to infectious diseases as well as psychological disturbances (Ots et al., 1998), hence we cannot exclude the potential effect of increased pathogen exposure in OF systems. Pesticides may reduce pathogen diversity in CF systems compared with areas in which OF is more prevalent (Goutte and Molbert, 2022). Therefore, chicks from nests located in these zones might be more prone to parasite exposure, which could, in turn, explain why they exhibit a higher number of heterophil leucocytes, and thus a higher H/L ratio. Moreover, several studies reported that H/L ratio is species-specific, and that it may vary between captive and wild individuals, depending on sex, age, nutritional and infectious status, and even brood size (Ruiz et al., 2002; Limiñana et al., 2009; Ortego et al., 2009; Parejo and Silva, 2009; Banbura et al., 2013; Catitti et al., 2022). Previous studies on Montagu's harriers attempted to set reference interval values for haematological parameters of captive adults and free-living nestlings, but reliable comparisons were difficult to make with the present work, and further investigation is required (Lavin et al., 1993; Limiñana et al., 2009). Additionally, even if chicks in OF and CF areas face similar parasite diversity, their investment in different life history traits might vary. For instance, chicks from nests mainly surrounded by CF may face a trade-off between investment for immune parameters and other life history traits such as growth (Sheldon and Verhulst, 1996; Norris and Evans, 2000). A recent study on grey partridge showed that hatchlings exposed to pesticides were of lower body size compared with those not exposed, but they underwent compensatory growth to compensate for the initial differences (Gaffard et al., 2022). In the present work, we did not observe any difference in body condition, but growth trajectories should be properly investigated to exclude this hypothesis.

At a local scale, a high percentage of CF is presumed to reduce available food resources; carotenoids being provided by the diet, this may explain why the colouration of the cere, a sexual trait indicative of chick quality (Sternalski et al., 2012b), is lower for chicks surrounded by CF compared with chicks surrounded by OF. Still, we did not detect a difference of carotenoid concentrations in chicks' plasma. Nevertheless, even if CF and OF provide an equivalent amount of food resources, it is possible that OF provides a greater diversity of food supply. Indeed, as mentioned above, OF promotes insect and passerine bird diversity, both of which are alternative prey for Montagu's harriers. Nestling colouration mainly depends on the proportion of insects and birds in their diet since these are richer in carotenoids (Sternalski et al., 2010). Thus, it is likely that chicks surrounded by OF benefit from higher carotenoid levels and/or richer carotenoid composition in their diet, resulting in more intense colouration of secondary sexual traits. In fact, carotenoid composition rather than carotenoid level in food items are responsible for colouration differences in some bird species (Eeva et al., 2010), thus studying carotenoids composition in more details using chromatographic methods would help to investigate this. Besides, various studies highlighted the covariation between colouration and immunocompetence in bird nestlings, due to the role of carotenoids in both immune functions and colouration (Saino et al., 2000, 2003; Baeta et al., 2008). Thus, competing demand for carotenoids for colouration and the immune system might occur. However, we did not detect any effect of the agricultural system on the immune responses of nestlings assessed by PHA skin tests at a local scale, while the colouration of the cere was lower in chicks mainly surrounded by CF. Another potential trade-off

leading to lower colouration scores in chicks surrounded by CF is the allocation of carotenoids to detoxification processes (Edge et al., 1997; Krinsky, 1998; see Bustnes et al., 2007). Indeed, exposure of birds to pollutants is known to induce oxidative stress, leading to a higher demand for antioxidants (including carotenoids) for redox processes (Ortiz-Santaliestra et al., 2015; Moreau et al., 2021, reviewed in Moreau et al., 2022a). Some studies on wild raptors found compensatory responses between different functions, linked to low concentrations of pesticides altering bird health (Bustnes et al., 2004; Rivera-Rodríguez and Rodríguez-Estrella, 2011; Ortiz-Santaliestra et al., 2015; Garcia-Heras et al., 2018). Despite the absence of a significant effect of the agricultural system on plasma carotenoid concentrations in the present work, we can suppose that pesticides used in CF might affect carotenoid allocation in Montagu's harrier nestlings, leading to trade-offs involving other physiological functions such as detoxification and oxidative stress, not measured here. A proper titration of pesticides in chicks' blood would be needed to rule about this trade-off.

The global activity level of chicks has been found to be higher when the surrounding OF at 200 m increases. This result matches with previous findings on 6 passerine birds (Moreau et al., 2022b), which reported a higher vigour of individuals when they originated from organic hedgerows compared to those captured in conventional ones. The main hypothesis raised by the authors is a lower exposition of birds to pesticides in OF systems and not an increased food abundance as birds did not show variation in body condition (Moreau et al., 2022b). In our case, the same pattern arises as we did not detect an effect of OF on body condition of Montagu's harrier chicks. Still, as we detected a beneficial effect of OF on chicks' activity only at 200 m around nests, the potential role of pesticides in their behavioural differences is questionable. Moreover, we did not detect an effect of agriculture systems on the AChE activity which, until proven otherwise, discard a neurotoxic effect of pesticides on chicks here. The increased chick activity when there is more OF at 200 m could be alternatively explained by human disturbances. In fact, after crops harvests, nests are exposed to curious walkers who can visit nests untimely, generating aggressive reactions of chicks and eventually sensitization to humans (Rabdeau et al., 2019, 2023). Besides, just as for the H/L ratio, increased labour and/or recreation in OF fields compared to CF fields could lead to an even greater exposure of chicks to humans. However, even if the effect size seems to indicate a medium effect of OF on the vitality of chicks, the assorted CI is relatively large suggestive of a large variability among chicks (Nakagawa and Cuthill, 2007; Cumming, 2014), interpretation on this result should thus be considered with caution.

5. Conclusion

In the current context of overall biodiversity loss, it is crucial to understand the relative impacts of CF and OF practices which are often opposed one to the other. However, as evidenced by our results, the picture is quite more complex than just black and white. The multi-trait approach used here revealed that CF practices can have detrimental effects on chick quality, and that OF can also exert adverse effects on their physiological stress. In fact, studying only the colouration of secondary sexual traits would have led to partial conclusions about the relative effects of CF on chick quality, whereas studying additionally morphometric and physiological traits that are indicative of stressors, such as H/L ratio, facilitated complete conclusions. In fact, both agricultural systems may impact Montagu's harrier chicks, with potential consequences for immediate survival during migration and later during adulthood. Multi-trait approaches are important because population dynamics reflect complex physiological processes of individuals that shape life history traits (development, reproduction, and survival), which in turn impact populations.

However, the present study is preliminary, as based on a rough cost/benefit analysis of these agricultural systems. One may also consider that we did not expect large effect size for the impact of agricultural

systems on chicks since the relationships among the different life history traits and how they are shaped are quite complex. For example, this study did not consider that chicks are fed by their father, who may hunt up to several kilometres away, potentially masking/compensating for low habitat quality at the local scale (Guixé and Arroyo, 2011; Krupiński et al., 2020). One way to consider the influence of the diet would be to analyse the composition of pellets through observational and morphological analyses or even using metabarcoding from buccal and/or cloacal swabs (Nota et al., 2019; Brouellette, 2021). Our study only considered the habitats in the vicinity of the nest from a binary point of view (OF vs. CF), and therefore did not capture all parameters such as the proportion of natural, semi-natural or urban habitats in the landscape potentially influencing chick health. Human activities related to OF and CF should be investigated in more detail to further determine the effects of different types and frequencies of disturbances on ground-nesting farmland birds. Finally, OF and CF contrast in their use of pesticides, which may partly explain some of our results (see Moreau et al., 2022a for an overview), especially knowing that pesticide use is the main driver of birds' decline in Europe (Rigal et al., 2023). Therefore, in future work, titration of pesticides in blood should be performed to explore their impact on chick health.

Declaration of Competing Interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in the present study.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108719.

References

Arroyo, B.E., Leroux, A., Bretagnolle, V., 1998. Patterns of egg and clutch size variation in the Montagu's Harrier. J. Raptor Res. 32, 136–142.
Arroyo, B.E., Mougeot, F., Bretagnolle, V., 2001. Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). Behav. Ecol. Sociobiol. 50, 109–115.

Arroyo, B.E., García, J.T., Bretagnolle, V., 2002. Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. Anim. Conserv. 5, 283–290.

Arroyo, B.E., Bretagnolle, V., Leroux, A., 2007. Interactive effects of food and age on breeding in the Montagu's Harrier *Circus pygargus*. Ibis 149, 806–813.

Arroyo, B.E., García, J.T., Bretagnolle, V., 2004. Montagu's harrier. – BWP update (The Journal of the Birds of the Western Palearctic). 6, 41–55.

Assandri, G., Giacomazzo, M., Brambilla, M., Griggio, M., Pedrini, P., 2017. Nest density, nest-site selection, and breeding success of birds in vineyards: management implications for conservation in a highly intensive farming system. Biol. Conserv. 205, 23–33.

Baeta, R., Faivre, B., Motreuil, S., Gaillard, M., Moreau, J., 2008. Carotenoid trade-off between parasitic resistance and sexual display: an experimental study in the blackbird (*Turdus merula*). Proc. Biol. Sci. 275, 427e434.

Banbura, J., Skwarska, J., Banbura, M., Gladalski, M., Holysz, M., Kalinski, A., Markowski, M., Wawrzyniak, J., Zielinski, P., 2013. Spatial and temporal variation in heterophil-to-lymphocyte ratios of nestling passerine birds: comparison of blue tits and great tits. PLoS One 8, e74226.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Benton, T.G., Bryant, D.M., Cole, L., Crick, H.Q., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. J. Appl. Ecol. 39, 673–687.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188.

Biard, C., Saulnier, N., Gaillard, M., Moreau, J., 2010. Carotenoid-based bill colour is an integrative signal of multiple parasite infection in blackbird. Naturwissenschaften 97, 987–995.

Biard, C., Monceau, K., Motreuil, S., Moreau, J., 2015. Interpreting immunological indices: the importance of taking parasite community into account. An example in blackbirds *Turdus merula*. Methods Ecol. Evol. 6, 960–972.

Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S., Mednis, A., 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia 143, 365–376.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135.

Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J., Wilson, J.D., 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. J. Appl. Ecol. 37, 789–805.

Bretagnolle, V., Denonfoux, L., Villers, A., 2018a. Are farming and birds irreconcilable? A 21-year study of bustard nesting ecology in intensive agroecosystems. Biol. Conserv. 228, 27–35.

Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Towards sustainable and multifunctional agriculture in farmland landscapes: lessons from the integrative approach of a French LTSER platform. Sci. Total Environ. 627, 822–834.

Brouellette, L., 2021. Cloacal swabbing as a tool to study diet in migrating raptors using DNA metabarcoding. Retrieved from the University of Minnesota Digital Conservancy, ⟨https://hdl.handle.net/11299/223100⟩.

de Bruijn, O., 1994. Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). Ardea 82, 1–109.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Method Res. 33, 261–304.

Bustnes, J.O., Hanssen, S.A., Folstad, I., Erikstad, K.E., Hasselquist, D., Skaare, J.U., 2004. Immune function and organochlorine pollutants in arctic breeding glaucous gulls. Arch. Environ. Contam. Toxicol. 47, 530–541.

Bustnes, J.O., Kristiansen, K.O., Helberg, M., 2007. Immune status, carotenoid coloration, and wing feather growth in relation to organochlorine pollutants in great black-backed gulls. Arch. Environ. Contam. Toxicol. 53, 96–102.

Butet, A., Leroux, A.B., 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. Biol. Conserv. 100, 289–295.

Butet, A., Paillat, G., Delettre, Y., 2006. Seasonal changes in small mammal assemblages from field boundaries in an agricultural landscape of western France. Agric. Ecosyst. Environ. 113, 364–369.

Butet, A., Michel, N., Rantier, Y., Comor, V., Hubert-Moy, L., Nabucet, J., Delettre, Y., 2010. Responses of common buzzard (*Buteo buteo*) and Eurasian kestrel (*Falco tinnunculus*) to land use changes in agricultural landscapes of Western France. Agric. Ecosyst. Environ. 138, 152–159.

Canty, A., Ripley, B., 2022. boot: Bootstrap R (S-Plus) Functions. R package version 1.3–28.1.

Carere, C., van Oers, K., 2004. Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. Physiol. Behav. 82, 905–912.

Catarino, R., Gaba, S., Bretagnolle, V., 2019. Experimental and empirical evidence shows that reducing weed control in winter cereal fields is a viable strategy for farmers. Sci. Rep. 9 (1), 9004.

Catitti, B., Grüebler, M.U., Kormann, U.G., Scherler, P., Witczak, S., van Bergen, V.S., Jenni-Eiermann, S., 2022. Hungry or angry? Experimental evidence for the effects of food availability on two measures of stress in developing wild raptor nestlings. J. Exp. Biol. 225 jeb244102.

Chamberlain, D.E., Wilson, J.D., 2000. The contribution of hedgerow structure to the value of organic farms to birds. Ecol. Conserv. Lowl. Farml. Birds 57–68.

Chamberlain, D.E., Wilson, J.D., Fuller, R.J., 1999. A comparison of bird populations on organic and conventional farm systems in southern Britain. Biol. Conserv. 88, 307–320.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771–788.

Clotflelter, E.D., Bell, A.M., Levering, K.R., 2004. The role of animal behaviour in the study of endocrine-disrupting chemicals. Anim. Behav. 68, 665–676.

Comolet-Tirman, J., Siblet, J.P., Witté, I., Cadiou, B., Czajkowski, M.A., Deceuninck, B., Jiguet, F., Landry, P., Quaintenne, G., Roché, J.E., Sarasa, M., Touroult, J., 2015. Statuts et tendances des populations d'oiseaux nicheurs de France. Bilan simplifié du premier rapportage national au titre de la Directive Oiseaux. Alauda 83, 35–76.

Crawley, M.J., 2012. The R Book. Wiley Publishing, Chichester.

Crick, H.Q.P., Dudley, C., Evans, A.D., Smith, K.W., 1994. Causes of nest failure among buntings in the UK. Bird Study 41, 88–94.

Cumming, G., 2014. The new statistics: why and how. Psychol. Sci. 25, 7–29.

Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: an R package for fitting distributions. J. Stat. Softw. 64, 1–34.

Duijns, S., Niles, L.J., Dey, A., Aubry, Y., Friis, C., Koch, S., Anderson, A.M., Smith, P.A., 2017. Body condition explains migratory performance of a long-distance migrant. Proc. R. Soc. B Biol. Sci. 284, 20171374.

Edge, R., McGarvey, D.J., Truscott, T.G., 1997. The carotenoids as antioxidants - a review. J. Photochem. Photobiol. 41, 189–200.

Eeva, T., Helle, S., Salminen, J.-P., Hakkarainen, H., 2010. Carotenoid composition of invertebrates consumed by two insectivorous bird species. J. Chem. Ecol. 36, 608–613.

Ellman, G.L., Courtney, K.D., Andres Jr, V., Featherstone, R.M., 1961. A new and rapid colorimetric determination of acetylcholinesterase activity. Biochem. Pharmacol. 7, 88–95.

Eng, M.L., Stutchbury, B.J., Morrissey, C.A., 2017. Imidacloprid and chlorpyrifos insecticides impair migratory ability in a seed-eating songbird. Sci. Rep. 7, 1–9.

Exposito-Granados, M., Parejo, D., Chastel, O., Aviles, J.M., 2020. Physiological stress and behavioural responses of European Rollers and Eurasian Scops Owls to human disturbance differ in farming habitats in the south of Spain. Bird. Conserv. Int. 30, 220–235.

Faivre, B., Préault, M., Théry, M., Secondi, J., Patris, B., Cézilly, F., 2001. Breeding strategy and morphological characters in an urban population of blackbirds, *Turdus merula*. Anim. Behav. 61, 969–974.

Fernández, C., Azkona, P., 1993. Human disturbance affects parental care of marsh harriers and nutritional status of nestlings. J. Wildl. Manag. 57, 602–608.

Fischer, C., Flohre, A., Clement, L.W., Batáry, P., Weisser, W.W., Tscharntke, T., Thies, C., 2011. Mixed effects of landscape structure and farming practice on bird diversity. Agric. Ecosyst. Environ. 141, 119–125.

Fox, J., Weisberg, S., 2011. Multivariate linear models in R. An R Companion to Applied Regression. Los Angeles: Thousand Oaks.

Freemark, K.E., Kirk, D.A., 2001. Birds on organic and conventional farms in Ontario: partitioning effects of habitat and practices on species composition and abundance. Biol. Conserv. 101, 337–350.

Fuentes, E., Gaffard, A., Rodrigues, A., Millet, M., Bretagnolle, V., Moreau, J., Monceau, K., 2023. Neonicotinoids: Still present in farmland birds despite their ban. Chemosphere 321, 138091.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. Conserv. Biol. 9, 1425–1441.

Gaffard, A., Pays, O., Monceau, K., Teixeira, M., Bretagnolle, V., Moreau, J., 2022. Feeding on grains containing pesticide residues is detrimental to offspring development through parental effects in grey partridge. Environ. Pollut. 312, 120005.

Garamszegi, L.Z., 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction. Behav. Ecol. 17, 682–687.

Garcia, J.T., Arroyo, B.E., 2002. Intra-and interspecific agonistic behaviour in sympatric harriers during the breeding season. Anim. Behav. 64, 77–84.

Garcia-Heras, M.S., Arroyo, B., Simmons, R.E., Camarero, P.R., Mateo, R., García, J.T., Mougeot, F., 2017. Pollutants and diet influence carotenoid levels and integument coloration in nestlings of an endangered raptor. Sci. Total Environ. 603, 299–307.

Garcia-Heras, M.S., Arroyo, B., Simmons, R.E., Camarero, P.R., Mateo, R., Mougeot, F., 2018. Blood concentrations of PCBs and DDTs in an avian predator endemic to southern Africa: associations with habitat, electrical transformers and diet. Environ. Pollut. 232, 440–449.

Gelling, M., Macdonald, D.W., Mathews, F., 2007. Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. Landsc. Ecol. 22, 1019–1032.

Gibbons, D., Morrissey, C., Mineau, P., 2014. A review of the direct and indirect effects of neonicotinoids and fipronil on vertebrate wildlife. Environ. Sci. Pollut. Res. 22, 103–118.

Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C., Memmott, J., 2007. Plant diversity and land use under organic and conventional agriculture: a whole-farm approach. J. Appl. Ecol. 44, 792–803.

Goulson, D., 2013. An overview of the environmental risks posed by neonicotinoid insecticides. J. Appl. Ecol. 50, 977–987.

Goutte, A., Molbert, N., 2022. Benefits of parasitism in polluted environments: a review and perspectives. Front. Ecol. Evol. 10, 847869.

Grue, C.E., Gibert, P.L., Seeley, M.E., 1997. Neurophysiological and behavioral changes in non-target wildlife exposed to organophosphate and carbamate pesticides: thermoregulation, food consumption, and reproduction. Am. Zool. 37, 369–388.

Guixé, D., Arroyo, B., 2011. Appropriateness of Special Protection Areas for wide-ranging species: the importance of scale and protecting foraging, not just nesting habitats. Anim. Conserv 14, 391–399.

Hansen, L., Noe, E., Højring, K., 2006. Nature and nature values in organic agriculture. An analysis of contested concepts and values among different actors in organic farming. J. Agr. Environ. Ethic. 19, 147–168.

Hartig F. (2022). _DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models_. R package version 0.4.6, ⟨https://CRAN.R-project.org/package=DHARMa⟩.

Heldbjerg, H., Sunde, P., Fox, A.D., 2018. Continuous population declines for specialist farmland birds 1987-2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. Bird. Conserv. Int. 28, 278–292.

Hellou, J., 2011. Behavioural ecotoxicology, an "early warning" signal to assess environmental quality. Environ. Sci. Pollut. Res. 18, 1–11.

Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed metacommunity dynamics in farmland landscapes. Proc. R. Soc. B: Biol. Sci. 282, 20150002.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? Biol. Conserv. 122, 113–130.

Holland, J., Fahrig, L., 2000. Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agric. Ecosyst. Environ. 78, 115–122.

Jagannath, A., Shore, R.F., Walker, L.A., Ferns, P.N., Gosler, A.G., 2008. Eggshell pigmentation indicates pesticide contamination. J. Appl. Ecol. 45, 133–140.

Jansen, K., 2000. Labour, livelihoods and the quality of life in organic agriculture in Europe. Biol. Agric. Hortic. 17, 247–278.

Jovani, R., Rohwer, S., 2016. Fault bars in bird feathers: mechanisms, and ecological and evolutionary causes and consequences. Biol. Rev. 92, 1113–1127.

Karlen, D.L., Colvin, T.S., Duffy, M.D., 1995. Nutrient, labor, energy and economic evaluations of two farming systems in Iowa. J. Prod. Agric. 8, 540–546.

Keesstra, S., Nunes, J., Novara, A., Finger, D., Avelar, D., Kalantari, Z., Cerdà, A., 2018. The superior effect of nature based solutions in land management for enhancing ecosystem services. Sci. Total Environ. 610, 997–1009.

Koks, B.J., Trierweiler, C., Visser, E.G., Dijkstra, C., Komdeur, J., 2007. Do voles make agricultural habitat attractive to Montagu's Harrier Circus pygargus? Ibis 149, 575–586.

Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second silent spring? Nature 400, 611–612.

Krinsky, N.I., 1998. The antioxidant and biological properties of the carotenoids. Ann. N. Y. Acad. Sci. 854, 443–447.

Krupiński, D., Kotowska, D., Recio, M.R., Żmihorski, M., Obłoza, P., Mirski, P., 2020. Ranging behaviour and habitat use in Montagu's Harrier Circus pygargus in extensive farmland of Eastern Poland. J. Ornithol. 162, 325–337.

Lavin, S., Cuenca, R., Marco, I., Pastor, J., Vinas, L., 1993. Hematological values of Montagu's harrier (Circus pygargus). Comp. Biochem. Phys. A 105, 103–104.

Leroux, A., Bretagnolle, V., 1996. Sex ratio variations in broods of Montagu's Harriers Circus pygargus. J. Avian Biol. 27, 63–69.

Limiñana, R., López-Olvera, J.R., Gallardo, M., Fordham, M., Urios, V., 2009. Blood chemistry and hematologic values in free-living nestlings of Montagu's Harriers (Circus pygargus) in a natural habitat. J. Zoo. Wildl. Med 40, 687–695.

Lockeretz, W., 2007. Organic Farming: An International History. CABI.

Lopez-Antia, A., Ortiz-Santaliestra, M.E., Camarero, P.R., Mougeot, F., Mateo, R., 2015a. Assessing the risk of fipronil-treated seed ingestion and associated adverse effects in the red-legged partridge. Environ. Sci. Technol. 49, 13649–13657.

Lopez-Antia, A., Ortiz-Santaliestra, M.E., Mougeot, F., Mateo, R., 2015b. Imidacloprid-treated seed ingestion has lethal effect on adult partridges and reduces both breeding investment and offspring immunity. Environ. Res. 136, 97–107.

Mason, R., Tennekes, H., Sánchez-Bayo, F., Jepsen, P.U., 2013. Immune suppression by neonicotinoid insecticides at the root of global wildlife declines. J. Environ. Immunol. Toxicol. 1, 3–12.

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277, 504–509.

Maxwell, M.H., 1993. Avian blood leucocyte responses to stress. World'S. Poult. Sci. J. 49, 34–43.

Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R. Package Version 2, 3-1.

McGraw, K.J., Ardia, D.R., 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. Am. Nat. 162, 704–712.

Millon, A., Bretagnolle, V., 2008. Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. Oikos 117, 1500–1510.

Millon, A., Arroyo, B.E., Bretagnolle, V., 2008. Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. J. Zool. 275, 349–358.

Millon, A., Bretagnolle, V., 2004. Les populations nicheuses de rapaces en France: analyse des résultats de l'enquête Rapaces 2000. Rapaces Nicheurs de France. Delachaux Niestlé, Paris, 129–140.

Mishra, H., Kumar, V., Kumar, V., 2020. Factors influencing nesting success of the river lapwing, Vanellus duvaucelii (Lesson, 1826). Avian Biol. Res. 13, 35–43.

Mitra, A., Chatterjee, C., Mandal, F.B., 2011. Synthetic chemical pesticides and their effects on birds. Res. J. Environ. Toxicol. 5, 81–96.

Moreau, J., Monceau, K., Crépin, M., Tochon, F.D., Mondet, C., Fraikin, M., Teixeira, M., Bretagnolle, V., 2021. Feeding partridges with organic or conventional grain triggers cascading effects in life-history traits. Environ. Pollut. 278, 116851.

Moreau, J., Rabdeau, J., Badenhausser, I., Giraudeau, M., Sepp, T., Crépin, M., Gaffard, A., Bretagnolle, V., Monceau, K., 2022a. Pesticide impacts on avian species with special reference to farmland birds: a review. Environ. Monit. Assess. 194, 1–48.

Moreau, J., Monceau, K., Gonnet, G., Pfister, M., Bretagnolle, V., 2022b. Organic farming positively affects the vitality of passerine birds in agricultural landscapes. Agric. Ecosyst. Environ. 336, 108034.

Mougeot, F., Arroyo, B., 2017. Behavioural responses to human activities and implications for conservation. Ecosistemas 26, 5–12.

Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav. Ecol. 15, 1044–1045.

Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol. Rev. 82, 591–605.

Norris, K., Evans, M.R., 2000. Ecological immunology: life history trade-offs and immune defense in birds. Behav. Ecol. 11, 19–26.

Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Hart, B., Mathews, F., Macdonald, D., Fuller, R.J., 2009. Consequences of organic and non-organic farming practices for field, farm and landscape complexity. Agric. Ecosyst. Environ. 129, 221–227.

Nota, K., Downing, S., Iyengar, A., 2019. Metabarcoding-based dietary analysis of hen harrier (Circus cyaneus) in Great Britain using buccal swabs from chicks. Conserv. Genet. 20, 1389–1404.

O'Dell, D.A., Carlo, M.A., Kimmitt, A., Bikowski, E., Morris, K.R., Dolby, A., 2014. A comparison of techniques measuring stress in birds. Va. J. Sci. 65, 133–149.

Orsini, S., Padel, S., Lampkin, N., 2018. Labour use on organic farms: a review of research since 2000. Org. Farming 4, 7–15.

Ortego, J., Zapero, L., Calabuig, G., Cordero, P.J., Aparicio, J.M., 2009. Physiological response to stress in fledgling Lesser Kestrels Falco naumanni: the role of physical condition, sex and individual genetic diversity. Ibis 151, 559–567.

Ortiz-Santaliestra, M.E., Resano-Mayor, J., Hernández-Matías, A., Rodríguez-Estival, J., Camarero, P.R., Moleón, M., Real, J., Mateo, R., 2015. Pollutant accumulation patterns in nestlings of an avian top predator: biochemical and metabolic effects. Sci. Total Environ. 538, 692–702.

Ortiz-Santaliestra, M.E., Alcaide, V., Camarero, P.R., Mateo, R., Mougeot, F., 2020. Egg overspray with herbicides and fungicides reduces survival of red-legged partridge chicks. Environ. Sci. Technol. 54, 12402–12411.

Ots, I., Murumägi, A., Horak, P., 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. Funct. Ecol. 12, 700–707.

Parejo, D., Silva, N., 2009. Immunity and fitness in a wild population of Eurasian kestrels Falco tinnunculus. Naturwissenschaften 96, 1193–1202.

Pebesma, E., 2018. Simple features for R: Standardized support for spatial vector data. R. J. 10, 439–446. https://doi.org/10.32614/RJ-2018-009.

Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118, 1883–1891.

QGIS Development Team, 2021. QGIS Geographic Information System, Version 3.16.5 Hannover. Open Source Geospatial Foundation Project. ⟨http://qgis.osgeo.org⟩.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Rabdeau, J., Badenhausser, I., Moreau, J., Bretagnolle, V., Monceau, K., 2019. To change or not to change experimenters: caveats for repeated behavioural and physiological measures in Montagu's harrier. J. Avian Biol. 50.

Rabdeau, J., Desbonnes, M., Bretagnolle, V., Moreau, J., Monceau, K., 2023. Does anthropization affect the physiology, the behaviour and the life-history traits of Montagu's harrier chicks? Anim. Conserv. 26, 174–188.

Regulation (EU) 2018/848 of the European parliament and of the Council of 30 May 2018 on organic production and labelling of organic products and repealing Council Regulation (EC) No 834/2007.

Reif, J., Hanzelka, J., 2020. Continent-wide gradients in open-habitat insectivorous bird declines track spatial patterns in agricultural intensity across Europe. Glob. Ecol. Biogeogr. 29, 1988–2013.

Reissig, L., Kohler, A., Rossier, R., 2016. Workload on organic and conventional family farms in Switzerland. Org. Agric. 6, 225–242.

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J.C., Domsa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., Jiguet, F., Kennedy, J., Klvaňová, A., Kmecl, P., Kuczyński, L., Kurlavičius, P., Kålås, J.A., Lehikoinen, A., Lindström, Å., Lorrillière, R., Moshøj, C., Nellis, R., Noble, D., Eskildsen, D.P., Paquet, J.-Y., Pélissié, M., Pladevall, C., Portolou, D., Reif, J., Schmid, H., Seaman, B., Szabo, Z.D., Szép, T., Florenzano, G.T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z., Vikstrøm, T., Voříšek, P., Weiserbs, A., Devictor, V., 2023. Farmland practices are driving bird population decline across Europe. Proc. Natl. Acad. Sci. U. S. A 120, e2216573120.

Rivera-Rodríguez, L.B., Rodríguez-Estrella, R., 2011. Incidence of organochlorine pesticides and the health condition of nestling ospreys (Pandion haliaetus) at Laguna San Ignacio, a pristine area of Baja California Sur, Mexico. Ecotoxicology 20, 29–38.

Roschewitz, I., Gabriel, D., Tscharntke, T., Thies, C., 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. J. Appl. Ecol. 42, 873–882.

Ruiz, G., Rosenmann, M., Novoa, F.F., Sabat, P., 2002. Hematological parameters and stress index in rufous-collared sparrows dwelling in urban environments. Condor 104, 162–166.

Saino, N., Møller, A.P., 1996. Sexual ornamentation and immunocompetence in the barn swallow. Behav. Ecol. 7, 227–232.

Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernard, F., Møller, A.P., 2000. Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. Proc. R. Soc. B: Biol. 267, 57–61.

Saino, N., Ambrosini, R., Martinelli, R., Ninni, P., Møller, A.P., 2003. Gape coloration reliably reflects immunocompetence of barn swallow (*Hirundo rustica*) nestlings. Behav. Ecol. 14, 16–22.

Salamolard, M., 1997. Utilisation de l'espace par le Busard Cendré *Circus pygargus*, superficie et distribution des zones de chasse. Alauda 65, 307–320.

Salamolard, M., Butet, A., Leroux, A., Bretagnolle, V., 2000. Responses of an avian predator to variations in prey density at a temperate latitude. Ecology 81, 2428–2441.

Sánchez-Bayo, F., Goka, K., 2014. Pesticide residues and bees—A risk assessment. PLoS One 9, 94482.

Santangeli, A., Arroyo, B., Millon, A., Bretagnolle, V., 2015. Identifying effective actions to guide volunteer-based and nationwide conservation efforts for a ground-nesting farmland bird. J. Appl. Ecol. 52, 1082–1091.

Schekkerman, H., Teunissen, W., Oosterveld, E., 2009. Mortality of black-tailed godwit *Limosa limosa* and Northern lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. J. Ornithol. 150, 133–145.

Sheldon, B.C., Verhulst, S., 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends Ecol. Evol. 11, 317–321.

Smits, J.E., Bortolotti, G.R., Tella, J.L., 1999. Simplifying the phytohaemagglutinin skin-testing technique in studies of avian immunocompetence. Funct. Ecol. 13, 567–572.

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agric. Ecosyst. Environ. 254, 244–254.

Stein-Bachinger, K., Gottwald, F., Haub, A., Schmidt, E., 2021. To what extent does organic farming promote species richness and abundance in temperate climates? A review. Org. Agric. 11, 1–12.

Sternalski, A., Mougeot, F., Eraud, C., Gangloff, B., Villers, A., Bretagnolle, V., 2010. Carotenoids in nestling Montagu's harriers: variations according to age, sex, body condition and evidence for diet-related limitations. J. Comp. Physiol. B 180, 33–43.

Sternalski, A., Mougeot, F., Pérez-Rodríguez, L., Bretagnolle, V., 2012a. Carotenoid-based coloration, condition, and immune responsiveness in the nestlings of a sexually dimorphic bird of prey. Physiol. Biochem. Zool. 85, 364–375.

Sternalski, A., Mougeot, F., Bretagnolle, V., 2012b. Carotenoid limitation and allocation priorities in asynchronous raptor nestlings. Biol. J. Linn. Soc. 105, 13–24.

Strasser, E.H., Heath, J.A., 2013. Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. J. Appl. Ecol. 50, 912–919.

Sumasgutner, P., Terraube, J., Coulon, A., Villers, A., Chakarov, N., Kruckenhauser, L., Korpimäki, E., 2019. Landscape homogenization due to agricultural intensification disrupts the relationship between reproductive success and main prey abundance in an avian predator. Front. Zool. 16, 1–14.

Tarjuelo, R., Benítez-López, A., Casas, F., Martín, C.A., García, J.T., Viñuela, J., Mougeot, F., 2020. Living in seasonally dynamic farmland: The role of natural and semi-natural habitats in the movements and habitat selection of a declining bird. Biol. Conserv. 251, 108794.

Tews, J., Bert, D., Mineau, P., 2013. Estimated mortality of selected migratory bird species from mowing and other mechanical operations in Canadian agriculture. Avian Conserv. Ecol. 8, 8.

Torné-Noguera, A., Pagani-Núñez, E., Senar, J.C., 2014. Great Tit (*Parus major*) breath rate in response to handling stress: urban and forest birds differ. J. Ornithol. 155, 315–318.

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. J. Appl. Ecol. 51, 746–755.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647–664.

Vitz, A.C., Rodewald, A.D., 2011. Influence of condition and habitat use on survival of post-fledging songbirds. Condor 113, 400–411.

Vyas, N.B., 2017. Rodenticide incidents of exposure and adverse effects on non-raptor birds. Sci. Total Environ. 609, 68–76.

Warton, David I., Duursma, Remko, A., Falster, Daniel, S., Taskinen, S., 2012. smatr 3 - an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259.

Zasada, I., 2011. Multifunctional peri-urban agriculture—A review of societal demands and the provision of goods and services by farming. Land Use Policy 28, 639–648.