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Elva Fuentes, Jérôme Moreau, Maria Teixeira, Vincent Bretagnolle, Karine Monceau. Effects of conventional vs. organic farming practices on raptor nestling health: Neither black nor white. Agriculture, Ecosystems & Environment, 2023, 358, pp.108719. 10.1016/j.agee.2023.108719. hal-04192120

HAL Id: hal-04192120 https://hal.science/hal-04192120v1

Submitted on 24 Feb 2024

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1	Effects of conventional vs. organic farming practices on raptor nestling health:
2	Neither black nor white
3	
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15 Abstract

16

17 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 18 19 farming (CF) production systems usually involve landscape homogenisation, mechanisation, 20 and the use of synthetic pesticides that may have direct and indirect effects on individuals. By 21 contrast, organic farming (OF) systems typically promote agro-ecosystem health, which 22 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 23 investigated. Still, altered life history traits could impair chick survival and future reproductive 24 25 success, which may in turn impact population dynamics. Here, we investigated the effects of 26 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 27 nervous systems) and body condition of 380 chicks from 137 nests monitored between 2016 28 29 and 2021. At a local scale (<2000 m), only the H/L ratio (indicative of physiological stress) and 30 carotenoid-based ornaments were clearly related to OF percentage. At 600 m around the nest, 31 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 32 33 interactions around OF crop plots. Carotenoid-based ornaments were more strongly coloured 34 with increasing OF around the nest at 1500 m. Considering the role of carotenoids in both 35 detoxification processes and expression of secondary sexual traits, this result may indicate 36 that CF would lead either to a difference in nestlings' diet and/or to a trade-off between 37 organism's maintenance and sexual character. These findings suggest that farming practices at a local scale surrounding nest locations may have subtle effects on chick development, but 38

- 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.

- **Keywords**: Behaviour, carotenoid, *Circus pygargus*, physiology, stress, trade-off

45 Introduction

46

The biodiversity crisis, faced nowadays, spares no species. Among the most affected taxa, bird 47 numbers decreased by 25% in Europe between 1980 and 2016 with farmland birds showing 48 49 the steepest decline (Heldbjerg et al. 2018; Reif & Hanzelka, 2020; Rigal et al. 2023). At the 50 same time, agricultural practices changed to increase yields, leading ecologists to hypothesise 51 a causal link between agricultural intensification and farmland bird decline (Fuller et al. 1995; 52 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. 53 1994; Tews et al. 2013; Santangeli et al. 2015). Landscape homogenisation and the use of 54 55 pesticides also raised concerns because they can have insidious effects on farmland species 56 (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 57 agricultural practices, organic farming (OF) emerged as an alternative in the late 1970s 58 59 (Lockeretz, 2007). OF is defined as a production system excluding synthetic pesticides and 60 fertilisers that uses nature-based solutions (Keesstra et al. 2018) to promote and enhance 61 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

69 effects on birds, by increasing disturbance and decreasing available resources. For instance, 70 manure spreading, manual and mechanical weed and pest control, tillage and multiple 71 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 72 73 farmland birds. Human presence and activity are known to affect bird feeding rates (Exposito-74 Granados et al. 2020), induce physiological stress (Mougeot & Arroyo, 2017; Rabdeau et al. 75 2023), and alter behaviour including parental care (Fernández & Azkona, 1993), sometimes 76 leading to nest failures (Strasser & Heath, 2013). Farming activity has even been shown to 77 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 78 79 agricultural practices that involve clearing of ditches, removal of hedgerows, and 80 intensification of grassland management are associated with lower territory and breeding densities in yellowhammer, Emberiza citrinella (Bradburry et al. 2000) and barn owl, Tyto alba 81 (de Bruijn, 1994). These intensive land-uses commonly found in CF lead to simplified 82 83 landscapes where important habitats for birds are no longer available (Bradbury et al. 2000; 84 Sumasgutner et al. 2019; Tarjuelo et al. 2020) and where their food supplies are reduced 85 through fewer weed seeds and natural insect reservoirs (Matson et al. 1997; Chamberlain & Wilson, 2000; Benton et al. 2002). Insects rely on the availability of non-uniform patches of 86 87 grass, weeds and hedgerows for food and shelter (Benton et al. 2002). These features are thus 88 associated with higher insect diversity (Holland & Fahrig, 2000) and higher bird diversity and 89 abundance (Chamberlain et al. 1999; Chamberlain & Wilson, 2000; Freemark & Kirk, 2001). 90 Hedgerows and landscape complexity also maintain small mammal populations (Butet et al. 91 2006; Gelling et al. 2007) and consequently have a positive effect on populations of birds of 92 prey (Koks et al. 2007; Butet et al. 2010), even if some find such a link only under favourable

93 food conditions (Sumasgutner et al. 2019). OF has been shown to have a positive effect on 94 biodiversity, an effect which is even greater in simplified landscapes (Roschewitz et al. 2005; 95 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 96 97 insects and therefore insectivorous birds (Hole et al. 2005; Lockeretz, 2007). Under OF 98 agricultural systems, natural and semi-natural areas are typically higher than under CF systems 99 (Gibson et al. 2007; Norton et al. 2009), hence OF promotes resources for birds, especially 100 food abundance (Fischer et al. 2011). Different meta-analyses support that view, showing that 101 OF promotes higher overall biodiversity, from flora to insects and bird species richness and 102 abundance (Tuck et al. 2014; Stein-Bachinger et al. 2021). Lastly, farm inputs are the main 103 characteristic contrasting OF from CF. Although organic plant protection products can be used, 104 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 105 fertilisers is the only mandatory practice, other practices such as natural or semi-natural areas 106 107 management being generally recommended but not systematic in OF systems (European 108 regulation (EU) 2018/848). Recent reviews highlighted that synthetic pesticides are the main 109 factor negatively affecting farmland birds (Stanton et al. 2018; Rigal et al. 2023). Pesticides 110 can have indirect effects on birds through the elimination of crop pests and weeds, reducing 111 food and habitat resources (Hole et al. 2005; Gibbons et al. 2014). Furthermore, pesticides lack specificity and can affect non-target species (Sánchez-Bayo & Goka, 2014; Vyas, 2017). 112 113 The use of pesticides can thus have direct effects on birds, either inducing lethal effects 114 (immediate death after exposure) or delayed sublethal effects altering life history traits. In 115 fact, different functions of a bird's organism can be affected by pesticides, from the cellular 116 level to higher physiological functions and behaviours (Mitra et al. 2011; Moreau et al. 2021,

117 2022a; Gaffard et al. 2022). Many experimental studies have revealed altered life history traits 118 due to pesticide toxicity, which may compromise bird survival, and consequently populations 119 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 120 121 pesticides are usually applied to fields either at the same time or sequentially, inducing 122 cocktail effects (Gaffard et al. 2022). Moreover, the persistence of some molecules in soil and 123 water can lead to contamination without direct contact with the applied chemicals (Jagannath 124 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 125 surrounded by OF, and that this might be due to pesticide contamination under CF (Moreau 126 127 et al. 2022b).

128 Montagu's harriers, *Circus pygargus*, a migratory raptor species inhabiting agricultural 129 lands in Europe, nest on the ground in cereal crops. In France, populations have declined by 130 10-30% over the past 30 years (Millon & Bretagnolle, 2004; Comolet-Tirman et al. 2015) and 131 the principal cause is believed to be agricultural intensification (Butet & Leroux, 2001; Arroyo 132 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, 133 134 hence food availability and diet vary from year to year (Millon & Bretagnolle, 2008). In years of low vole abundance, Montagu's harriers compensate by feeding on Orthopterans 135 (grasshoppers and crickets) (Salamolard et al. 2000). For this farmland specialist bird, the type 136 137 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 138 in the nest during the whole rearing period (~35 days). Consequently, at all developmental 139 140 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 144 145 along a gradient of OF near their nests. Accordingly, we investigated the relative impacts of 146 OF vs. CF on multiple life history traits of Montagu's harrier chicks at a local scale (up to 2000 147 m) around nests. Compared with OF, CF may decrease food availability (due to both lower 148 quality habitats and intensive management practices) and increase exposure to pesticides 149 (through contact or prey consumption). Therefore, we hypothesised that a higher percentage 150 of CF around the nest may adversely affect fledglings. Since all life history traits involve 151 complex interconnected functions, expectations for a single trait are complicated to raise. A 152 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 153 expect chicks reared in nests surrounded by a lower percentage of OF (i.e., a higher 154 155 percentage of CF) would have a poorer overall health status that might be reflected by inferior 156 body condition, more markers (physical and biochemical) of chronic stress, a depressed 157 immune system, and lower vigour than chicks surrounded by a higher percentage of OF.

158

159 **2. Material and methods**

160

161 **2.1. Ethics statement**

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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).

167

168 **2.2. Study area and model species**

169

170 The study site is located in southwestern France (46°11'N, 0°28'W), in the Long-Term Social-171 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 172 173 France, OF is regulated by the European legislation (European regulation (EU) 2018/848) on 174 organic production, which details all practices to respect for farms to be considered organic, 175 the main one being the complete ban on the use of synthetic pesticides and fertilizers. Other 176 farming practices, including weeding or non-cropped habitat management, being at the 177 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 178 179 diversified crops and a lower nitrogen supply in OF systems. In this intensive agricultural area, 180 cereal crops are the predominant cultures (average coverage of 41.5% between 2009 and 181 2016), followed by corn, sunflowers and oilseed rape (Bretagnolle et al. 2018b). Natural (or 182 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 2009-2016; Bretagnolle et al. 183 184 2018b) thus only organic crop plots were used for analyses (see section 2.7 for further 185 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 186 eggs (Arroyo et al. 1998; Millon et al. 2008). The incubation period lasts 29 days and the 187 188 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 & Arroyo, 2011).

194

195 **2.3. Overall experimental design**

196

197 From 2016 to 2021, the reproduction of Montagu's harrier was monitored from late April until 198 late July. All nests were searched by professional ornithologists, and once located, visited and 199 mapped using a global positioning system (GPS) receiver, they were stored on a geographical 200 information system (GIS; QUANTUMGIS 3.16.5; QGIS Development Team, 2021, see Fig. 1). 201 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 202 203 aluminium ring from the Museum National d'Histoire Naturelle. Sex was determined by the 204 colour of the iris (brown for females and grey for males) (Leroux & Bretagnolle, 1996).

205 For the present study, we focused on data collected during the last visit before 206 fledgling, when nestlings were 26 ± 2 days old. Briefly (see details below), chicks were caught 207 in the nest and carefully handled to take morphometric measurements and breath rate and 208 collect blood samples (Fig. 2). A phytohemagglutinin (PHA) skin injection was performed, and 209 behaviour during handling was also recorded (Fig. 2). Chicks were handled and released at the 210 nest, and the handling time was minimised to reduce potential stress. The following day of 211 the visit, nests were again visited to record chicks' inflammatory response to the PHA skin 212 injection (see details below). A total of 380 chicks were monitored (N₂₀₁₆ = 40, N₂₀₁₇ = 32, N₂₀₁₈ 213 = 81, N₂₀₁₉ = 84, N₂₀₂₀ = 85, N₂₀₂₁ = 58) from 137 nests (N₂₀₁₆ = 15, N₂₀₁₇ = 16, N₂₀₁₈ = 24, N₂₀₁₉
214 = 31, N₂₀₂₀ = 29, N₂₀₂₁ = 22). No sex ratio bias was observed for the entire period (187 females
215 and 193 males; binomial test *p* = 0.80).
216
217 2.4. Morphometric measurements
218

219 2.4.1. Morphometrics for body condition assessment

220

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 & Rodewald 2011;
Duijns *et al.* 2017). Body condition for each nestling was estimated from the scale mass index
following Peig and Green (2009):

225
$$SMI_i = Mass_i \times \left(\frac{Mean \ tarsus \ length \ of \ the \ group}{Mean \ tarsus \ length_i}\right)^{b_{sma}}$$

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).

231

232 2.4.2. Fault bars

233

Fault bars are malformations in feathers induced by punctual stressors during chick growth, which may result in feather and even rachis breaks (Jovani & 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.

240

241 **2.4.3.** Colouration

242

243 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 244 cere and tarsus (bare parts) were scored by direct comparison with a colorimetric chart from 245 Yolk Colour Fan (Roche, Neuilly-sur-Seine, France). Scores ranged from 0 (almost white / pale 246 247 yellow) to 15 (orange) and were highly correlated with colour parameters obtained using a 248 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 correlation test, $\rho > 0.77$, p < 0.0001, 249 250 95% confidence interval CI = [0.72, 0.81], n = 380), and only cere scores were used for 251 statistical analyses.

252

253 **2.5. Physiological measures**

254

255 2.5.1. Breath rate score

256

Breath rate usually refers to a proxy of physiological stress (Carere & van Oers, 2004; TornéNoguera *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 15s

for three consecutive replicates. The breath rate score was then obtained by averaging thethree replicates.

262

263 2.5.2. Physiological parameters assessed from blood

264

265 2.5.2.1. Blood collection

266

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

275

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 & 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:

281
$$ESR = \frac{volume \text{ not filled by erythrocytes}}{total blood volume in the tube \times time of sedimentation}$$

283 Once ESR was measured, microcapillary tubes were centrifuged at 5000 rpm for 5 min 284 to measure haematocrit. Haematocrit is used as an index of anaemia and corresponds to the 285 proportion of the tube filled with erythrocytes divided by the total volume of blood sample in 286 the tube, given as a percentage (Saino & Møller, 1996; see also Biard *et al.* 2015; Moreau *et* 287 *al.* 2021).

288

289 2.5.2.3. Carotenoid titration

290

Carotenoids are involved in different functions of birds, including as antioxidants, and a high concentration in blood can reflect physiological stress (McGraw & Ardia, 2003). Eppendorf tubes containing ~150 μ L 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 (μ g/mL) using a standardised colorimetric technique (see Biard *et al.* 2010 for additional information).

297

298 2.5.2.4. Acetylcholinesterase activity

299

Acetylcholinesterase (AChE) activity is negatively affected by different 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 μ L of blood diluted in 100 μ L 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

307 Devices, San Jose, CA, USA) as the maximum change in absorbance per minute during kinetics
 308 analysis.

309

310 2.5.2.5. Blood smear

311

312 For each bird, a blood smear was performed with a droplet of blood sample. Slides were air-313 dried and fixed in absolute methanol before being stained with Giemsa solution (Sigma 314 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 315 316 number of leucocytes found among 8000 erythrocytes. A high number of leucocytes reflects 317 stress and inflammatory processes (Ots et al. 1998). Different types of leucocytes were 318 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 319 response to various stressors (Maxwell, 1993; Ots et al. 1998; Moreau et al. 2021; see Biard 320 321 et al. 2015 for details).

322

323 2.5.3. Immune challenge

324

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 pressuresensitive 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).

334

335 **2.6. Behavioural measures**

336

337 Behaviour is considered an indicator of individual health that can be altered by multiple 338 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 339 et al. 2022a). When handling chicks (i.e., from capture in the nest to release), the behaviour 340 341 of bird was scored using four behavioural traits as described by Rabdeau et al. (2019): (i) 342 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 343 experimenter approached the nest to catch the chicks and scored as follows: stayed 344 345 motionless = 0, chicks retreated = 1, chicks ran away = 2. Act-tot was measured throughout 346 handling and scored as follows: chicks stayed motionless = 0, chicks rarely moved = 1, chicks 347 moved regularly = 2, chicks moved continuously = 3. The number of beak and claw attacks 348 were counted during handling and divided by the duration of handling, resulting in a rate 349 (number of attacks per minute).

350

351 **2.7. Statistical analyses**

352

353 A principal component analyses (PCA) was performed on the four behavioural scores using 354 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 (PC1activity) 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.

359 Normality and homoscedasticity of all response variables were tested using the 360 'fitdistrplus' package prior to model implementation, and when these assumptions were not 361 met, distribution with the best fit was selected using the same package (Delignette-Muller & 362 Dutang, 2015). Model residuals and spatial autocorrelation (using Moran's I) were also 363 checked using 'DHARMa' package (Hartig, 2022). PC1-activity, body condition, ESR, breath rate 364 score, AChE activity and PHA response were used as response variables in Linear Mixed-effects 365 Models (LMMs). Carotenoid concentration was square root transformed, haematocrit and H/L 366 ratio were log-transformed prior to LMM execution, since the distributions of these variables 367 did not meet normality. Generalised LMMs fitted with a Poisson distribution (PGLMMs) were 368 implemented for fault bars and colouration scores and a Generalised LMM fitted with a 369 Negative Binomial distribution (NB-GLMM) was used for the total WBC count. For all models 370 (LMMs, PGLMMs and NB-GLMM), the percentage of OF around the nest (log-transformed, 371 hereafter OF effect) and the year as factor were included as fixed effects, and the nest identity 372 as a random effect (to avoid pseudo-replication as chicks can belong to the same nest) (Bolker 373 et al. 2009). The year was considered a fixed effect because we wanted to control for inter-374 annual variability of environmental conditions (phenology, food availability and weather for 375 instance). Because year could have been considered a random factor, we ran all models 376 changing only the year fixed effect into a random effect. This approach did not change the 377 results obtained with year as a fixed effect, hence we used the results of the first analyses. All 378 models were run with the 'lme4' package (Bates et al. 2015).

379 As we had no *a priori* information on the scale of the OF effect on life history traits for 380 each chick, we estimated the percentage OF around the nest for 20 buffer sizes (i.e., radii 381 every 100 m, from 100 m to 2000 m). To this end, the GPS coordinates of nests and a database 382 of the LTSER ZAPVS, which georeferenced the agricultural plots using OF practices, were used 383 with the 'sf' package (Pebesma, 2018). Since OF agricultural plots varied over time, the 384 percentage of OF around nests for a given year was calculated using the georeferenced plots 385 of the corresponding year. We ran 20 models per life history trait (one per buffer size) and 386 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 387 selection of the model with the most support, which has the lowest AICc, assuming that 388 389 models with Δ AICc <2 (i.e., a difference in AICc between candidate models <2) are similarly 390 supported and cannot be distinguished from each other (Burnham & Anderson, 2004). For 391 every life history trait, a plot was generated representing the AICc of the 20 models (one for 392 each buffer size), with a red dotted line illustrating the model selection criterion (lowest AICc 393 of the candidate models + 2), with the shape and colour reflecting the significance and 394 direction of the OF effect. To avoid type II errors, we chose to present our results based on 395 effect sizes (estimates of the model) assorted with their 95% confidence intervals (CI) (following Garamszegi, 2006; Nakagawa, 2004; Nakagawa & Cuthill, 2007; Cumming, 2014). 396 397 The OF effect direction corresponded to the sign of the estimate and was considered 398 significant when 95% CI did not include 0. Calculation of the bootstrapped CI was obtained for 399 2000 iterations and using the package 'boot' (Canty & Ripley, 2022). We discuss effect sizes 400 assorted with their 95% CI which allow to quantify the biological effect we tested and provide 401 comparable estimates for future research and meta-analyses, still, we provide the results from

402 model comparison using likelihood ratio-based χ²-statistics in supplementary materials (Fox &
403 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.

407

408 **3. Results**

409

Summary statistics and Spearman's rank correlation coefficients of the 12 life history traits are 410 presented in the Supplementary Material (see Table S1 and Fig. S2). Only ESR and haematocrit 411 412 (Spearman's correlation test, $\rho > -0.42$, p < 0.0001, 95% CI = [-0.51; -0.32], n = 343) were 413 correlated (Supplementary Material Fig. S2). The set of candidate models for body condition, fault bars, breath rate score, ESR, haematocrit, carotenoid concentration, AChE activity, WBC 414 415 count, and PHA skin test did not yield any specific buffer size with substantial support (i.e., 416 AICc <2 with a significant OF effect) for an influence of OF percentage around nests (Fig. S2 in 417 supplementary materials). For cere colouration score and H/L ratio, the best models (i.e., 418 those with Δ AICc <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 >500 419 420 m (Fig. 3a). For H/L ratio, a positive relationship was detected between 300 and 900 m (Fig. 421 3b). Concerning the PC1-activity, a positive relationship with the percentage of OF was 422 detected at 200 m around the nests.

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). Chicks displayed a significantly higher cere colouration score when surrounded by a higher percentage of OF at 1500 m (effect size

426 = 0.14; 95% CI = [0.04; 0.22]), the lowest AICc for this life history trait (Fig. 4a). The lowest AICc
427 for the H/L ratio was at a radius of 600 m around nests; at this distance the H/L ratio
428 significantly increased with increasing OF percentage (effect size = 0.11; 95% CI = [0.04; 0.18];
429 Fig. 4b). For PC1-activity, the lowest AICc was at 200 m, an increase in OF at this distance from
430 nests significantly increased the global activity of chicks (effect size = 0.20; 95% CI = [0.06;
431 0.40]; Fig. 4c).

432

433 **4. Discussion**

434

The aim of the present study was to explore life history traits variation of Montagu's harrier 435 436 chicks linked to agricultural systems around nests. The results revealed an effect on two of the 437 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 438 439 different distances, but not necessarily at the same range. The cere colouration score 440 increased with increasing OF percentage at distances >500 m with the best model selected at 441 1500 m. The H/L ratio increased significantly with OF at distances from 300 to 900 m, the best 442 model being at 600 m. Global activity of chicks increased with increasing OF percentage at 200 443 m only. For all other life history traits, namely body condition, fault bars, breath rate score, 444 ESR, haematocrit, carotenoid concentration, AChE activity, WBC count, and PHA skin test, no 445 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 (<2 000 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

450 to moderate stress, and to reflect chronic stress levels rather than short-term stress responses 451 (Maxwell, 1993; O'Dell et al. 2014). This result suggests that chicks in areas with a higher OF 452 percentage may suffer more disturbance. Indeed, compared with CF, OF practices involve 453 more repetitive passages (Karlen et al. 1995; Reissig et al. 2016; Orsini et al. 2018), which may 454 equate to more stress experienced by chicks. Furthermore, areas with more OF fields are 455 generally better appreciated than areas with CF fields by urban inhabitants attracted to 456 naturalistic features and elements (Zasada, 2011). Diversified habitats offer more 457 opportunities for recreation and leisure than uniform ones (Hansen et al. 2006). Anthropic 458 disturbances can induce stress in Montagu's harrier chicks, leading to physiological responses 459 to this stress and even to the formation of fault bars (see Rabdeau et al. 2023). Repeated 460 human activities, whether related to OF practices or recreation, could also induce prolonged 461 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. 462 463 Competition between Montagu's harriers nesting in semi-colonies is presumably low but 464 could increase in years of low vole abundance. The presence of other raptor species foraging 465 in the same area would also increase competition for food (Garcia & Arroyo, 2002). Competition for food resources might increase the time parents spend foraging, leaving chicks 466 467 alone for longer periods. The presence of more raptors may increase the risk of predation of 468 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 469 470 kites, Milvus migrans, to protect their nests (authors' personal observations), and this might 471 result in more frequent parental absences. Consequently, an increase in intra- and 472 interspecific negative interactions surrounding OF crop plots would increase the time chicks 473 are unattended.

474 An alternative explanation for the higher H/L ratio observed for chicks in nests 475 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 476 psychological disturbances (Ots et al. 1998), hence we cannot exclude the potential effect of 477 478 increased pathogen exposure in OF systems. Pesticides may reduce pathogen diversity in CF 479 systems compared with areas in which OF is more prevalent (Goutte & Molbert, 2022). 480 Therefore, chicks from nests located in these zones might be more prone to parasite exposure, 481 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, 482 and that it may vary between captive and wild individuals, depending on sex, age, nutritional 483 484 and infectious status, and even brood size (Ruiz et al. 2002; Limiñana et al. 2009; Ortego et al. 485 2009; Parejo & 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 486 487 of captive adults and free-living nestlings, but reliable comparisons were difficult to make with 488 the present work, and further investigation is required (Lavin et al. 1993; Limiñana et al. 2009). 489 Additionally, even if chicks in OF and CF areas face similar parasite diversity, their investment 490 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 491 492 traits such as growth (Sheldon & Verhulst, 1996; Norris & Evans, 2000). A recent study on grey 493 partridge showed that hatchlings exposed to pesticides were of lower body size compared 494 with those not exposed, but they underwent compensatory growth to compensate for the 495 initial differences (Gaffard et al. 2022). In the present work, we did not observe any difference 496 in body condition, but growth trajectories should be properly investigated to exclude this 497 hypothesis.

498 Although we did not detect any effect of the agricultural system on the immune 499 responses of nestlings assessed by PHA skin tests at a local scale, colouration of the cere, a 500 sexual trait indicative of chick quality (Sternalski et al. 2012b), was lower in chicks mainly 501 surrounded by CF. Various studies highlighted the covariation between colouration and 502 immunocompetence in bird nestlings, due to the role of carotenoids in both immune functions 503 and colouration (Saino et al. 2000, 2003; Baeta et al. 2008). Thus, competing demand for 504 carotenoids for colouration and the immune system might occur. At a local scale, a large 505 percentage of CF is presumed to reduce available resources; carotenoids are provided by the diet, which may explain why chick colouration is adversely affected compared with chicks 506 507 surrounded by OF. Another potential trade-off leading to lower colouration scores in chicks 508 surrounded by CF is the allocation of carotenoids to detoxification processes (Edge et al. 1997; 509 Krinsky, 1998; see Bustnes et al. 2007). Indeed, exposure of birds to pollutants is known to 510 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 511 512 al. 2022a). Some studies on wild raptors found compensatory responses between different 513 functions, linked to low concentrations of pesticides altering bird health (Bustnes et al. 2004; 514 Rivera-Rodríguez & 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 515 516 carotenoid concentrations in the present work, we can suppose that pesticides used in CF 517 might affect carotenoid allocation in Montagu's harrier nestlings, leading to trade-offs 518 involving other physiological functions such as detoxification and oxidative stress, not 519 measured here. Nevertheless, even if CF and OF provide an equivalent amount of food 520 resources, it is possible that OF provides a greater diversity of food supply. Indeed, as 521 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 in their diet, resulting in more intense colouration of secondary sexual traits.

526 The global activity level of chicks has been found to be higher when the surrounding 527 OF at 200 m increases. This result matches with previous findings on 6 passerine birds (Moreau 528 et al. 2022b), which reported a higher vigour of individuals when they originated from organic 529 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 530 food abundance as birds did not show variation in body condition (Moreau et al. 2022b). In 531 532 our case, the same pattern arises as we did not detect an effect of OF on body condition of 533 Montagu's harrier chicks. Still, as we detected a beneficial effect of OF on chicks' activity only 534 at 200 m around nests, we can question the potential role of pesticides in their behavioural 535 differences. The increased chick activity when there is more OF at 200 m could be alternatively 536 explained by human disturbances. In fact, after crops harvests, nests are exposed to curious 537 walkers who can visit nests untimely, generating aggressive reactions of chicks and eventually 538 sensitization to humans (Rabdeau et al. 2019, 2023). However, even if the effect size seems 539 to indicate a medium effect of OF on the vitality of chicks, the assorted CI is relatively large 540 suggestive of a large variability among chicks (Nakagawa & Cuthill, 2007; Cumming, 2014), 541 interpretation on this result should thus be considered with caution.

542

543 5. Conclusion

545 In the current context of overall biodiversity loss, it is crucial to understand the relative 546 impacts of CF and OF practices which are often opposed one to the other. However, as 547 evidenced by our results, the picture is guite more complex than just black and white. The multi-trait approach used here revealed that CF practices can have detrimental effects on 548 549 chick quality, and that OF can also exert adverse effects on their physiological stress. In fact, 550 studying only the colouration of secondary sexual traits would have led to partial conclusions 551 about the relative effects of CF on chick quality, whereas studying additionally morphometric 552 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 553 potential consequences for immediate survival during migration and later during adulthood. 554 555 Multi-trait approaches are important because population dynamics reflect complex 556 physiological processes of individuals that shape life history traits (development, reproduction, and survival), which in turn impact populations. 557

However, the present study is preliminary, as based on a rough cost/benefit analysis 558 559 of these agricultural systems. One may also consider that we did not expect large effect size 560 for the impact of agricultural systems on chicks since the relationships among the different 561 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, 562 563 potentially masking/compensating for low habitat quality at the local scale (Guixé & Arroyo 564 2011; Krupiński et al. 2020). 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 565 566 the proportion of natural, semi-natural or urban habitats in the landscape potentially 567 influencing chick health. Human activities related to OF and CF should be investigated in more 568 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.

575 Acknowledgements

We would like to thank everyone who contributed to fieldwork and data collection during the 6 years of this study: Romain Bonnet, Pierre de Bouët du Portal, Landry Boussac, Guillaume Brouard, Mélissa Desbonnes, Agathe Gaffard, Mazzerine Laboureau, Gildas Lemonnier, Camille Mangelinck, Mona Moreau, Laure Pellicier, Guillaume Peplinski, Jean- Samuel Perroteau, Baptiste Perrotin, Juliette Rabdeau, Margaux Ruiz, Anna Terras, Alexis Veldeman and Alexandre Villers. We are also grateful to all farmers who allowed us to access their fields. A special thanks to Thomas Schneider-Bruchon for his qualitative help on statistical analyses.

583

584 Funding

This work was supported by the French National Research Agency (ANR JCJC PestiStress, grant #19-CE34-0003-01), the French National Centre of Scientific Research (CNRS), the French National Research Institute for Agriculture, Food and the Environment (INRAE), the University of La Rochelle, and the region Nouvelle-Aquitaine, with partial funding through the BioBird project.

590

591 **Declaration of competing interest**

592 The authors declare that they have no competing financial interests or personal relationships 593 that could have appeared to influence the work reported in the present study.

595 **References**

- 596
- 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.
- 599 Arroyo, B. E., García, J. T., Bretagnolle, V., 2004. Montagu's harrier. BWP update (The Journal
- 600 of the Birds of the Western Palearctic). 6, 41–55.
- 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., Mougeot, F., Bretagnolle, V., 2001. Colonial breeding and nest defence in
- 604 Montagu's harrier (*Circus pygargus*). Behav. Ecol. Sociobiol. 50, 109-115.
- 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.
- 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

609 conservation in a highly intensive farming system. Biol. Conserv. 205, 23-33.

- 610 Banbura, J., Skwarska, J., Banbura, M., Gladalski, M., Holysz, M., Kalinski, A., Markowski, M.,
- 611 Wawrzyniak, J., Zielinski, P., 2013. Spatial and temporal variation in heterophil-to-
- 612 lymphocyte ratios of nestling passerine birds: comparison of blue tits and great tits. PLoS613 One. 8, e74226.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using
 Ime4. J. Stat. Softw. 67, 1-48.
- Baeta, R., Faivre, B., Motreuil, S., Gaillard, M., Moreau, J., 2008. Carotenoid trade-off between
- 617 parasitic resistance and sexual display: an experimental study in the blackbird (*Turdus*
- 618 *merula*). Proc. Biol. Sci. 275, 427e434.

- 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., 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.
- 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, 987995.
- 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.
- 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 21year study of bustard nesting ecology in intensive agroecosystems. Biol. Conserv. 228, 2735.
- 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.

- 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., Kristiansen, K. O., Helberg, M., 2007. Immune status, carotenoid coloration, and
- 645 wing feather growth in relation to organochlorine pollutants in great black-backed gulls.
- 646 Arch. Environ. Con. Tox. 53, 96-102.
- Bustnes, J. O., Hanssen, S. A., Folstad, I., Erikstad, K. E., Hasselquist, D., Skaare, J. U., 2004.
- 648 Immune function and organochlorine pollutants in arctic breeding glaucous gulls. Arch.
 649 Environ. Con. Tox. 47, 530-541.
- 650 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., Michel, N., Rantier, Y., Comor, V., Hubert-Moy, L., Nabucet, J., Delettre, Y., 2010.
- 654 Responses of common buzzard (*Buteo buteo*) and Eurasian kestrel (*Falco tinnunculus*) to
- 655 land use changes in agricultural landscapes of Western France. Agric. Ecosyst. Environ.
- 656 **138**, **152-159**.
- 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.
- 659113, 364-369.
- 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. Scientific
 Reports, 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.
- 667 Carere, C., van Oers, K., 2004. Shy and bold great tits (*Parus major*): body temperature and
 668 breath rate in response to handling stress. Physiol. Behav. 82, 905-912.
- 669 Canty, A., Ripley, B., 2022. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-28.1.
- 670 Chamberlain, D. E., Wilson, J. D., 2000. The contribution of hedgerow structure to the value of
 671 organic farms to birds. *Ecology and Conservation of Lowland Farmland Birds*, 57-68.
- 672 Chamberlain, D. E., Fuller, R. J., Bunce, R. G., Duckworth, J. C., Shrubb, M., 2000. Changes in
- 673 the abundance of farmland birds in relation to the timing of agricultural intensification in
- 674 England and Wales. J. Appl. Ecol. 37, 771-788.
- 675 Chamberlain, D. E., Wilson, J. D., Fuller, R. J., 1999. A comparison of bird populations on
 676 organic and conventional farm systems in southern Britain. Biol. Conserv. 88, 307-320.
- 677 Clotflelter, E.D., Bell, A.M., Levering, K.R., 2004. The role of animal behaviour in the study of
 678 endocrine-disrupting chemicals. Anim. Behav. 68, 665–676.
- 679 Comolet-Tirman, J., Siblet, J. P., Witté, I., Cadiou, B., Czajkowski, M. A., Deceuninck, B., Jiguet,
- 680 F., Landry, P., Quaintenne, G., Roché, J. E., Sarasa, M., Touroult, J., 2015. Statuts et
- 681 tendances des populations d'oiseaux nicheurs de France. Bilan simplifié du premier
- rapportage national au titre de la Directive Oiseaux. Alauda 83, 35-76.
- 683 Crawley MJ., 2012. The R Book. Chichester: Wiley Publishing.
- 684 Crick, H. Q. P., Dudley, C., Evans, A. D., Smith, K. W., 1994. Causes of nest failure among
 685 buntings in the UK. Bird Study. 41, 88-94.
- 686 Cumming, G., 2014. The new statistics: Why and how. Psychol. Sci. 25, 7-29.
- 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.

- 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 DJ, Truscott TG, 1997. The carotenoids as antioxidants a review. J.
 Photochem. Photobiol. 41, 189–200.
- 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-UK 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.
- 704 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. Wildlife Manag. 57, 602-608.
- 709 Fischer, C., Flohre, A., Clement, L. W., Batáry, P., Weisser, W. W., Tscharntke, T., Thies, C.,
- 710 2011. Mixed effects of landscape structure and farming practice on bird diversity. Agric.
- 711 Ecosyst. Environ. 141, 119-125.

- 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.
- 715 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.
- Fox, J., Weisberg, S., 2011. Multivariate linear models in R. An R Companion to Applied
 Regression. Los Angeles: Thousand Oaks.
- 720 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., Mougeot, F., 2018.
- 731 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.
- 733 Garcia-Heras, M. S., Arroyo, B., Simmons, R. E., Camarero, P. R., Mateo, R., García, J. T.,
- 734 Mougeot, F., 2017. Pollutants and diet influence carotenoid levels and integument
- coloration in nestlings of an endangered raptor. Sci. Total Environ. 603, 299-307.

- 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.
 Landscape 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. R. 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.

species: the importance of scale and protecting foraging, not just nesting habitats. Anim.
Conserv. 14, 391-399.

Guixé, D., Arroyo, B., 2011. Appropriateness of Special Protection Areas for wide-ranging

- 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
- 769 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.
- 775 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.
- 778 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.
- 780 Keesstra, S., Nunes, J., Novara, A., Finger, D., Avelar, D., Kalantari, Z., Cerdà, A., 2018. The
- 781 superior effect of nature based solutions in land management for enhancing ecosystem
- 782 services. Sci. Total Environ. 610, 997-1009.

783	Koks, B. J., Trierweiler, C., Visser, E. G., Dijkstra, C., Komdeur, J., 2007. Do voles make
784	agricultural habitat attractive to Montagu's Harrier Circus pygargus? Ibis. 149, 575-586.
785	Krebs, J. R., Wilson, J. D., Bradbury, R. B., Siriwardena, G. M., 1999. The second silent spring?
786	Nature 400, 611-612.
787	Krinsky, N.I., 1998. The antioxidant and biological properties of the carotenoids. Ann. New
788	York Acad. Sci. 854, 443–447.
789	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

791 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 Wildlife Med. 40, 687-695.
- 799 Lockeretz, W., 2007. Organic Farming: An International History. CABI.
- 800 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.
- 803 Lopez-Antia, A., Ortiz-Santaliestra, M. E., Mougeot, F., Mateo, R., 2015b. Imidacloprid-treated
- 804 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, 3443.
- Mazerolle, M. J., 2020. AlCcmodavg: Model selection and multimodel inference based on
 (Q)AlC(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.

819 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.

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.

- Mishra, H., Kumar, V., Kumar, A., 2020. Factors influencing nesting success of the river
- 825 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., 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.
- 831 Moreau, J., Monceau, K., Gonnet, G., Pfister, M., Bretagnolle, V., 2022b. Organic farming
- 832 positively affects the vitality of passerine birds in agricultural landscapes. Agric. Ecosyst.
- 833 Environ. 336, 108034.
- 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.
- 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.,
- 846 Wolfe, M., Hart, B., Mathews, F., Macdonald, D., Fuller, R. J., 2009. Consequences of
- 847 organic and non-organic farming practices for field, farm and landscape complexity. Agric.
- 848 Ecosyst. Environ. 129, 221-227.
- 0'Dell, D. A., Carlo, M. A., Kimmitt, A., Bikowski, E., Morris, K. R., Dolby, A., 2014. A comparison
- of techniques measuring stress in birds. Virginia journal of science 65, 133-149.

- Orsini, S., Padel, S., Lampkin, N., 2018. Labour use on organic farms: a review of research since
 2000. Organic 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., 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.
- 859 Ortiz-Santaliestra, M. E., Resano-Mayor, J., Hernández-Matías, A., Rodríguez-Estival, J.,
- 860 Camarero, P. R., Moleón, M., Real, J., Mateo, R., 2015. Pollutant accumulation patterns in
- 861 nestlings of an avian top predator: biochemical and metabolic effects. Sci. Total Environ.
 862 538, 692-702.
- 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.
- 865 Parejo, D., Silva, N., 2009. Immunity and fitness in a wild population of Eurasian kestrels Falco
- *tinnunculus*. Naturwissenschaften, 96, 1193-1202.
- 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.
- 869 Pebesma, E., 2018. Simple features for R: Standardized support for spatial vector data. The R
- 870 Journal 10, 439-446, <u>https://doi.org/10.32614/RJ-2018-009.</u>
- 871 QGIS Development Team, 2021. QGIS Geographic Information System, Version 3.16.5
- 872 Hannover. Open Source Geospatial Foundation Project. <u>http://qgis.osgeo.org</u>.
- 873 R Core Team, 2021. R: A language and environment for statistical computing. R Foundation
- for Statistical Computing, Vienna, Austria. <u>https://www.R-project.org/</u>.

- 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.
- 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.
- 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. Global Ecol.
 Biogeogr. 29, 1988-2013.
- Reissig, L., Kohler, A., Rossier, R., 2016. Workload on organic and conventional family farms in
 Switzerland. Organic Agriculture 6, 225-242.
- 889 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, 890 891 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., 892 893 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., 894 Florenzano, G. T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z., 895 896 Vikstrøm, T., Voříšek, P., Weiserbs, A., Devictor, V., 2023. Farmland practices are driving 897 bird population decline across Europe. Proc. Natl. Acad. Sci. U.S.A. 120, e2216573120.

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

Ruiz, G., Rosenmann, M., Novoa, F. F., Sabat, P., 2002. Hematological parameters and stress
index in rufous-collared sparrows dwelling in urban environments. The Condor. 104, 162166.

- 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.
- 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,
- 909 16-22.
- 910 Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernard, F., Møller, A. P., 2000. Better red than
- 911 dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings.
- 912 Proc. R. Soc. B: Biol. 267, 57-61.
- Saino, N., Møller, A. P., 1996. Sexual ornamentation and immunocompetence in the barn
 swallow. Behav. Ecol. 7, 227-232.
- 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.
- 917 Salamolard, M., 1997. Utilisation de l'espace par le Busard Cendré Circus pygargus, superficie
- 918 et distribution des zones de chasse. Alauda 65, 307–320.
- 919 Sánchez-Bayo, F., Goka, K., 2014. Pesticide residues and bees—A risk assessment. PLoS One 9,
- 920 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.
- 924 Schekkerman, H., Teunissen, W., Oosterveld, E., 2009. Mortality of black-tailed godwit *Limosa*
- 925 *limosa* and Northern lapwing *Vanellus vanellus* chicks in wet grasslands: influence of
 926 predation and agriculture. J. Ornithol., 150, 133-145.
- Sheldon, B. C., Verhulst, S., 1996. Ecological immunology: costly parasite defences and tradeoffs in evolutionary ecology. Trends Ecol. Evol. 11, 317-321.
- 929 Smits, J. E., Bortolotti, G. R., Tella, J. L., 1999. Simplifying the phytohaemagglutinin skin-testing
- 930 technique in studies of avian immunocompetence. Funct. Ecol. 13, 567-572.
- 931 Stanton, R. L., Morrissey, C. A., Clark, R. G., 2018. Analysis of trends and agricultural drivers of
- 932 farmland bird declines in North America: A review. Agric. Ecosyst. Environ. 254, 244-254.
- 933 Stein-Bachinger, K., Gottwald, F., Haub, A., Schmidt, E., 2021. To what extent does organic
- 934 farming promote species richness and abundance in temperate climates? A review.
- 935 Organic Agriculture 11, 1-12.
- 936 Sternalski, A., Mougeot, F., Pérez-Rodríguez, L., Bretagnolle, V. (2012a). Carotenoid-based
- 937 coloration, condition, and immune responsiveness in the nestlings of a sexually dimorphic
 938 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.
- 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.

944	Strasser, E. H., Heath, J. A., 2013. Reproductive failure of a human-tolerant species, the
945	American kestrel, is associated with stress and human disturbance. J. Appl. Ecol. 50, 912-
946	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.

951 Tarjuelo, R., Benítez-López, A., Casas, F., Martín, C. A., García, J. T., Viñuela, J., Mougeot, F.,

952 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.

957 Torné-Noguera, A., Pagani-Núñez, E., Senar, J. C., 2014. Great Tit (*Parus major*) breath rate in

958 response to handling stress: urban and forest birds differ. J. Ornithol. 155, 315-318.

959 Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A., Bengtsson, J., 2014. Land-use

960 intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis.

961 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. The Condor. 113, 400-411.

- 967 Vyas, N. B., 2017. Rodenticide incidents of exposure and adverse effects on non-raptor birds.
 968 Sci. Total Environ. 609, 68-76.
- 969 Warton, David I., Duursma, Remko A., Falster, Daniel S., Taskinen, S., 2012. smatr 3 an R
- 970 package for estimation and inference about allometric lines. Methods in Ecol. Evol. 3, 257-
- 971 **259**.
- 272 Zasada, I., 2011. Multifunctional peri-urban agriculture—A review of societal demands and
- 973 the provision of goods and services by farming. Land Use Policy 28, 639-648.
- 974

975 Figure legends

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Fig. 1: Spatial distribution of Montagu's harrier 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. Infrastructure corresponds to buildings, sport fields, cemeteries, locks and bridges present in the study area.

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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.

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989 Fig. 3: Model selection using AICc to assess the responses of life history traits (life history 990 traits) of Montagu's harrier, *Circus pygargus*, chicks to the effect of the percentage of organic 991 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. 992 993 AICc = Akaike Information Criterion corrected for small sample sizes. Red dotted lines 994 correspond to the lowest AICc of candidate models + 2. Red triangles indicate a positive 995 significant OF effect (i.e., a positive model estimate and assorted 95% confidence interval (CI) 996 not crossing 0). Black dots represent a non-significant OF effect (i.e., the 95% CI of model 997 estimate crosses 0).

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.