



**HAL**  
open science

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

Elva Fuentes, Jérôme Moreau, Maria Teixeira, Vincent Bretagnolle, Karine Monceau

### ► To cite this version:

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-04192120>**

Submitted on 24 Feb 2024

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

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



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Effects of conventional vs. organic farming practices on raptor nestling health:**

2 **Neither black nor white**

3  
4 Elva Fuentes<sup>1\*</sup>, Jérôme Moreau<sup>1,2</sup>, Maria Teixeira<sup>2</sup>, Vincent Bretagnolle<sup>1,3</sup>, Karine Monceau<sup>1</sup>

5  
6 <sup>1</sup> UMR 7372, Centre d'Études Biologiques de Chizé, La Rochelle Université & CNRS, 79360

7 Villiers en Bois, France

8 <sup>2</sup> UMR CNRS 6282 Biogéosciences, Équipe Écologie Évolutive, Université de Bourgogne-

9 Franche-Comté, 21000 Dijon, France

10 <sup>3</sup> LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, 79360 Villiers-en-Bois, France

11  
12  
13 \*Corresponding author: [elva.fts@gmail.com](mailto:elva.fts@gmail.com)

14

15 **Abstract**

16

17 Agricultural intensification is one of the main threats to biodiversity. Farmland bird specialists  
18 such as Montagu's harrier, *Circus pygargus*, are particularly at risk and declining. Conventional  
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  
23 agricultural systems on life history traits of Montagu's harrier chicks have not been  
24 investigated. Still, altered life history traits could impair chick survival and future reproductive  
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)  
27 on a set of life history traits covering the behaviour, physiology (haematological, immune and  
28 nervous systems) and body condition of 380 chicks from 137 nests monitored between 2016  
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  
32 stress due to either increased human disturbance or higher intra-/interspecific negative  
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  
38 at a local scale surrounding nest locations may have subtle effects on chick development, but

39 also on trade-offs between important physiological functions. This study highlights the  
40 importance of a multi-trait approach when assessing adverse and beneficial effects of both OF  
41 and CF on individuals.

42

43

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

## 45 **Introduction**

46

47 The biodiversity crisis, faced nowadays, spares no species. Among the most affected taxa, bird  
48 numbers decreased by 25% in Europe between 1980 and 2016 with farmland birds showing  
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,  
53 mechanisation appeared to have a direct negative impact on ground-nesting birds (Crick *et al.*  
54 1994; Tews *et al.* 2013; Santangeli *et al.* 2015). Landscape homogenisation and the use of  
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  
57 *et al.* 2022a). To counter the negative impacts of conventional farming (CF) involving intensive  
58 agricultural practices, organic farming (OF) emerged as an alternative in the late 1970s  
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).

62 Three main interrelated characteristics distinguish OF from CF: agricultural practices,  
63 natural and semi-natural habitat proportion and farm inputs. Agricultural practices can be  
64 harmful to farmland birds either directly or indirectly. A direct impact of agricultural machines  
65 used under intensive practices is the death of ground-nesting birds (Crick *et al.* 1994; Vickery  
66 *et al.* 2001; Tews *et al.* 2013). Incubating adults, broods and chicks are frequently destroyed  
67 during mechanical mowing, tilling and harvesting activities (Schekkerman *et al.* 2009;  
68 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,  
72 2000; Orsini *et al.* 2018), and can be identified as a potential source of disturbance for  
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  
78 lapwing, *Vanellus duvaucelii* (Assandri *et al.* 2017; Mishra *et al.* 2020). Moreover, intensive  
79 agricultural practices that involve clearing of ditches, removal of hedgerows, and  
80 intensification of grassland management are associated with lower territory and breeding  
81 densities in yellowhammer, *Emberiza citrinella* (Bradburry *et al.* 2000) and barn owl, *Tyto alba*  
82 (de Bruijn, 1994). These intensive land-uses commonly found in CF lead to simplified  
83 landscapes where important habitats for birds are no longer available (Bradburry *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 &  
86 Wilson, 2000; Benton *et al.* 2002). Insects rely on the availability of non-uniform patches of  
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  
96 habitat management such as the establishment of hedgerows and field margins benefit  
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,  
105 in Europe for farms to be considered organic the prohibition of use of synthetic pesticides and  
106 fertilisers is the only mandatory practice, other practices such as natural or semi-natural areas  
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  
112 lack specificity and can affect non-target species (Sánchez-Bayo & Goka, 2014; Vyas, 2017).  
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.*  
120 2022a for a recent review). *In natura*, birds are exposed to numerous molecules as multiple  
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  
125 that birds nesting in hedges surrounded by CF were less vigorous than those nesting in hedges  
126 surrounded by OF, and that this might be due to pesticide contamination under CF (Moreau  
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  
133 common voles, *Microtus arvalis*, which display cyclic population dynamics in Western Europe,  
134 hence food availability and diet vary from year to year (Millon & Bretagnolle, 2008). In years  
135 of low vole abundance, Montagu's harriers compensate by feeding on Orthopterans  
136 (grasshoppers and crickets) (Salamolard *et al.* 2000). For this farmland specialist bird, the type  
137 of agricultural system at a local scale might be of great importance during the breeding season.  
138 Indeed, eggs and chicks are located on the ground in crop fields, and the altricial chicks stay  
139 in the nest during the whole rearing period (~35 days). Consequently, at all developmental  
140 stages, Montagu's harrier offspring might be affected by the composition and management



141 of the habitats in the close surroundings. If the agricultural system in the vicinity leads to  
142 altered life history traits, survival may be compromised, reducing future recruitment of  
143 fledglings into the population of this declining species.

144 In the present study, we explored the patterns of life history traits variation in nestlings  
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.  
153 CF) on birds, and eventually to highlight potential trade-offs between life history traits. We  
154 expect chicks reared in nests surrounded by a lower percentage of OF (i.e., a higher  
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**

162

163 All experiments conformed to the French guidelines for the ethical use of animals in research  
164 (APAFIS#18557-2019010822312199v2). Bird handling was allowed and licensed by the Centre

165 de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO; Museum National d'Histoire  
166 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 km<sup>2</sup> area where  
172 annual crop identification is carried out, allowing mapping of organic crop plots in detail. In  
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  
178 CF and OF systems of the study area; the main differences being smaller farm areas, more  
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  
183 (average coverage of 13.5% and 9.8% respectively between 2009-2016; Bretagnolle *et al.*  
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  
186 *et al.* 2018b). This species nests on the ground, mainly in cereal crops, and lays up to eight  
187 eggs (Arroyo *et al.* 1998; Millon *et al.* 2008). The incubation period lasts 29 days and the  
188 rearing period between 30 and 35 days (Arroyo *et al.* 2007). The mean productivity in this site

189 is 2.05 fledglings per breeding attempt (Arroyo *et al.* 2004), breeding success depending  
190 mainly on the availability of common voles, their main prey in this area (Salamolard *et al.*  
191 2000). Foraging range varies with location; in the study area males use home ranges of ~14  
192 km<sup>2</sup> (Salamolard, 1997), but home ranges during the breeding season can stretch to 100 km<sup>2</sup>  
193 (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  
202 between visits  $7 \pm 2$  days). At 15 days old, chicks were sexed and banded with a unique coded  
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  $26 \pm 2$  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 ( $N_{2016} = 40$ ,  $N_{2017} = 32$ ,  $N_{2018}$

213 = 81, N<sub>2019</sub> = 84, N<sub>2020</sub> = 85, N<sub>2021</sub> = 58) from 137 nests (N<sub>2016</sub> = 15, N<sub>2017</sub> = 16, N<sub>2018</sub> = 24, N<sub>2019</sub>  
214 = 31, N<sub>2020</sub> = 29, N<sub>2021</sub> = 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

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

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

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

231

### 232 2.4.2. Fault bars

233

234 Fault bars are malformations in feathers induced by punctual stressors during chick growth,  
235 which may result in feather and even rachis breaks (Jovani & Rohwer, 2016; see Rabdeau *et*

236 *al.* 2023 for an example of recent usage). Chick tails were photographed and the number of  
237 fault bars (all breaks in barbs and barbules) was counted on the most affected rectrix feather  
238 by the same experimenter to avoid observer bias. The number of fault bars on each chick  
239 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  
244 and mediated by different physiological effects (Garcia-Heras *et al.* 2017). The colour of the  
245 cere and tarsus (bare parts) were scored by direct comparison with a colorimetric chart from  
246 Yolk Colour Fan (Roche, Neuilly-sur-Seine, France). Scores ranged from 0 (almost white / pale  
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  
249 0 to 6. Both scores were highly correlated (Spearman's correlation test,  $\rho > 0.77$ ,  $p < 0.0001$ ,  
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

257 Breath rate usually refers to a proxy of physiological stress (Carere & van Oers, 2004; Torné-  
258 Noguera *et al.* 2014; Rabdeau *et al.* 2019). Breath rate was measured using chicks handled in  
259 back position, and corresponded to the number of thoracic movements counted during 15s

260 for three consecutive replicates. The breath rate score was then obtained by averaging the  
261 three replicates.

262

## 263 2.5.2. Physiological parameters assessed from blood

264

### 265 2.5.2.1. Blood collection

266

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

273

### 274 2.5.2.2. Sedimentation rate and haematocrit

275

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

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

282

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

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

297

#### 298 *2.5.2.4. Acetylcholinesterase activity*

299

300 Acetylcholinesterase (AChE) activity is negatively affected by different pesticide molecules  
301 altering neural functions, which in turn has disruptive consequences on diverse behaviours  
302 and complex functions (Grue *et al.* 1997; Eng *et al.* 2017; Moreau *et al.* 2022a). AChE activity  
303 in milliunits per minute (mU/min) was obtained by a method derived from Ellman *et al.* (1961)  
304 using 5 µL of blood diluted in 100 µL of a 1% Triton X-100 solution and measured using a  
305 SpectraMax iD3 microplate reader (Molecular Devices Inc., Sunnyvale, CA, USA) over 40 min  
306 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  
315 under 1000x magnification. Total white blood cells (WBC) count was estimated from the  
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  
319 ratio). The H/L ratio is used as an index of physiological stress, as it is supposed to increase in  
320 response to various stressors (Maxwell, 1993; Ots *et al.* 1998; Moreau *et al.* 2021; see Biard  
321 *et al.* 2015 for details).

322

#### 323 2.5.3. Immune challenge

324

325 Before release into the nest, the immune system of nestlings was challenged using  
326 phytohemagglutinin (PHA) skin tests (Smits *et al.* 1999). Briefly,  $0.5 \pm 0.1$  mg of PHA (Sigma  
327 Chemical, St. Louis, MO, USA) diluted into 0.1 mL of phosphate-buffered saline (PBS) was  
328 injected subcutaneously in the wing patagium as described by Sternalski *et al.* (2012a). The  
329 thickness of the patagium was measured three times before injection using a pressure-  
330 sensitive dial thickness gauge (spessimeter accuracy  $\pm 0.01$  mm) and again 24 h after injection.



331 The response to the PHA skin test corresponds to the change in average thickness (in mm) of  
332 the injection site, and thus the magnitude of this change reflects the immune potential of  
333 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  
339 other physiological measures (Grue *et al.* 1997; Clotflelter *et al.* 2004; Hellou, 2011; Moreau  
340 *et al.* 2022a). When handling chicks (i.e., from capture in the nest to release), the behaviour  
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  
343 beak attacks (beak); (iv) rate of claw attacks (claws). Act-nest was assessed when the  
344 experimenter approached the nest to catch the chicks and scored as follows: stayed  
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,

355 2012). The first axis of the PCA reflecting global activity and vigour during handling (PC1-  
356 activity) was retained as its eigenvalue was  $>1$ , and it accounted for 48.69% of the variance.  
357 PC1-activity was positively correlated with both rates of beak ( $r = 0.56$ ) and claw ( $r = 0.57$ )  
358 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  
387 ‘AICcmodavg’ package (Mazerolle, 2020). From a set of candidate models, AICc allows  
388 selection of the model with the most support, which has the lowest AICc, assuming that  
389 models with  $\Delta\text{AICc} < 2$  (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)  
396 (following Garamszegi, 2006; Nakagawa, 2004; Nakagawa & Cuthill, 2007; Cumming, 2014).  
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  $\chi^2$ -statistics in supplementary materials (Fox &  
403 Weisberg, 2011).

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

407

### 408 **3. Results**

409

410 Summary statistics and Spearman's rank correlation coefficients of the 12 life history traits are  
411 presented in the Supplementary Material (see Table S1 and Fig. S2). Only ESR and haematocrit  
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,  
414 fault bars, breath rate score, ESR, haematocrit, carotenoid concentration, AChE activity, WBC  
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  $\Delta AICc < 2$ ) identified a positive effect for OF percentage at a range of radii (Fig. 3).  
419 The cere colouration score increased with OF percentage around the nest for buffer sizes > 500  
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.

423 We then selected the model with the lowest AICc to probe the relationships between  
424 the trait and the OF percentage around the nest (Fig. 4). Chicks displayed a significantly higher  
425 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

435 The aim of the present study was to explore life history traits variation of Montagu's harrier  
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  
438 linked to OF at different radii, suggesting that the effects of the agricultural system operate at  
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.

446 In the present study, we found evidence for the impacts of farming practices (CF and  
447 OF) on Montagu's harrier chicks at a low spatial scale (<2 000 m) around nests. First, OF was  
448 found to be associated with a higher H/L ratio. This trait is indicative of stress undergone by  
449 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). Anthropoc  
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  
462 higher presence of conspecifics or other raptor species around OF crops is also possible.  
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).  
466 Competition for food resources might increase the time parents spend foraging, leaving chicks  
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  
469 (Arroyo *et al.* 2001). Pairs are often seen mobbing common buzzards, *Buteo buteo*, or black  
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  
476 pathogens. Indeed, H/L ratio is known to increase in response to infectious diseases as well as  
477 psychological disturbances (Ots *et al.* 1998), hence we cannot exclude the potential effect of  
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  
482 thus a higher H/L ratio. Moreover, several studies reported that H/L ratio is species-specific,  
483 and that it may vary between captive and wild individuals, depending on sex, age, nutritional  
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  
486 Montagu's harriers attempted to set reference interval values for haematological parameters  
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  
491 CF may face a trade-off between investment for immune parameters and other life history  
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  
506 diet, which may explain why chick colouration is adversely affected compared with chicks  
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)  
511 for redox processes (Ortiz-Santaliestra *et al.* 2015; Moreau *et al.* 2021, reviewed in Moreau *et*  
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.*  
515 2018). Despite the absence of a significant effect of the agricultural system on plasma  
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



522 alternative prey for Montagu's harriers. Nestling colouration mainly depends on the  
523 proportion of insects and birds in their diet since these are richer in carotenoids (Sternalski *et*  
524 *al.* 2010). Thus, it is likely that chicks surrounded by OF benefit from higher carotenoid levels  
525 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  
530 the authors is a lower exposition of birds to pesticides in OF systems and not an increased  
531 food abundance as birds did not show variation in body condition (Moreau *et al.* 2022b). In  
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**

544

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 quite more complex than just black and white. The  
548 multi-trait approach used here revealed that CF practices can have detrimental effects on  
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  
553 conclusions. In fact, both agricultural systems may impact Montagu's harrier chicks, with  
554 potential consequences for immediate survival during migration and later during adulthood.  
555 Multi-trait approaches are important because population dynamics reflect complex  
556 physiological processes of individuals that shape life history traits (development,  
557 reproduction, and survival), which in turn impact populations.

558         However, the present study is preliminary, as based on a rough cost/benefit analysis  
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  
562 consider that chicks are fed by their father, who may hunt up to several kilometres away,  
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  
565 from a binary point of view (OF vs. CF), and therefore did not capture all parameters such as  
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

569 ground-nesting farmland birds. Finally, OF and CF contrast in their use of pesticides, which  
570 may partly explain some of our results (see Moreau *et al.* 2022a for an overview), especially  
571 knowing that pesticide use is the main driver of birds' decline in Europe (Rigal *et al.*, 2023).  
572 Therefore, in future work, titration of pesticides in blood should be performed to explore their  
573 impact on chick health.

574

575 **Acknowledgements**

576 We would like to thank everyone who contributed to fieldwork and data collection during the  
577 6 years of this study: Romain Bonnet, Pierre de Bouët du Portal, Landry Boussac, Guillaume  
578 Brouard, Mélissa Desbonnes, Agathe Gaffard, Mazzerine Laboureau, Gildas Lemonnier,  
579 Camille Mangelinck, Mona Moreau, Laure Pellicier, Guillaume Peplinski, Jean- Samuel  
580 Perroteau, Baptiste Perrotin, Juliette Rabdeau, Margaux Ruiz, Anna Terras, Alexis Veldeman  
581 and Alexandre Villers. We are also grateful to all farmers who allowed us to access their fields.  
582 A special thanks to Thomas Schneider-Bruchon for his qualitative help on statistical analyses.

583

584 **Funding**

585 This work was supported by the French National Research Agency (ANR JCJC PestiStress, grant  
586 #19-CE34-0003-01), the French National Centre of Scientific Research (CNRS), the French  
587 National Research Institute for Agriculture, Food and the Environment (INRAE), the University  
588 of La Rochelle, and the region Nouvelle-Aquitaine, with partial funding through the BioBird  
589 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.

594

595 **References**

596

597 Arroyo, B. E., Bretagnolle, V., Leroux, A., 2007. Interactive effects of food and age on breeding  
598 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.

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

603 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.

605 Arroyo, B.E., Leroux, A., Bretagnolle, V., 1998. Patterns of egg and clutch size variation in the  
606 Montagu's Harrier. J. Raptor Res. 32, 136-142.

607 Assandri, G., Giacomazzo, M., Brambilla, M., Griggio, M., Pedrini, P., 2017. Nest density, nest-  
608 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. PLoS  
613 One. 8, e74226.

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

616 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.

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

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

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

626 Biard, C., Saulnier, N., Gaillard, M., Moreau, J., 2010. Carotenoid-based bill colour is an  
627 integrative signal of multiple parasite infection in blackbird. *Naturwissenschaften* 97, 987-  
628 995.

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

632 Bradbury, R. B., Kyrkos, A., Morris, A. J., Clark, S. C., Perkins, A. J., Wilson, J. D., 2000. Habitat  
633 associations and breeding success of yellowhammers on lowland farmland. *J. Appl. Ecol.*  
634 37, 789-805.

635 Bretagnolle, V., Denonfoux, L., Villers, A., 2018a. Are farming and birds irreconcilable? A 21-  
636 year study of bustard nesting ecology in intensive agroecosystems. *Biol. Conserv.* 228, 27-  
637 35.

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

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

644 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.

647 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  
651 conservation of Montagu's harrier in western French wetlands. *Biol. Conserv.* 100, 289-  
652 295.

653 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.

657 Butet, A., Paillat, G., Delettre, Y., 2006. Seasonal changes in small mammal assemblages from  
658 field boundaries in an agricultural landscape of western France. *Agric. Ecosyst. Environ.*  
659 113, 364-369.

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

663 Catitti, B., Gruebler, M. U., Kormann, U. G., Scherler, P., Witczak, S., van Bergen, V. S., Jenni-  
664 Eiermann, S., 2022. Hungry or angry? Experimental evidence for the effects of food

665 availability on two measures of stress in developing wild raptor nestlings. *J. Exp. Biol.* 225,  
666 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., Shrubbs, 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 Clotfelter, 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  
682 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.

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



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

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

694 Edge R, McGarvey DJ, Truscott TG, 1997. The carotenoids as antioxidants - a review. J.  
695 Photochem. Photobiol. 41, 189–200.

696 Ellman, G. L., Courtney, K. D., Andres Jr, V., Featherstone, R. M., 1961. A new and rapid  
697 colorimetric determination of acetylcholinesterase activity. Biochem. Pharmacol. 7, 88-  
698 95.

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

701 Exposito-Granados, M., Parejo, D., Chastel, O., Aviles, J. M., 2020. Physiological stress and  
702 behavioural responses of European Rollers and Eurasian Scops Owls to human  
703 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  
705 morphological characters in an urban population of blackbirds, *Turdus merula*. Anim.  
706 Behav. 61, 969–974.

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

709 Fischer, C., Flohre, A., Clement, L. W., Batáry, P., Weisser, W. W., Tschardtke, T., Thies, C.,  
710 2011. Mixed effects of landscape structure and farming practice on bird diversity. Agric.  
711 Ecosyst. Environ. 141, 119-125.

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

715 Fuentes, E., Gaffard, A., Rodrigues, A., Millet, M., Bretagnolle, V., Moreau, J., Monceau, K.,  
716 2023. Neonicotinoids: Still present in farmland birds despite their ban. *Chemosphere* 321,  
717 138091.

718 Fox, J., Weisberg, S., 2011. *Multivariate linear models in R. An R Companion to Applied*  
719 *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,  
721 N., 1995. Population declines and range contractions among lowland farmland birds in  
722 Britain. *Conserv. Biol.* 9, 1425-1441.

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

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

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

730 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:  
732 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  
735 coloration in nestlings of an endangered raptor. *Sci. Total Environ.* 603, 299-307.

736 Gelling, M., Macdonald, D. W., Mathews, F., 2007. Are hedgerows the route to increased  
737 farmland small mammal density? Use of hedgerows in British pastoral habitats.  
738 *Landscape Ecol.* 22, 1019-1032.

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

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

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

746 Goutte, A., Molbert, N., 2022. Benefits of Parasitism in Polluted Environments: A Review and  
747 Perspectives. *Front. Ecol. Evol.* 10, 847869.

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

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

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

757 Hartig F (2022). `_DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)`  
758 `Regression Models_`. R package version 0.4.6, [https://CRAN.R-](https://CRAN.R-project.org/package=DHARMA)  
759 [project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA)

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

763 Hellou, J., 2011. Behavioural ecotoxicology, an “early warning” signal to assess environmental  
764 quality. *Environ. Sci. Pollut. Res.* 18, 1–11.

765 Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed  
766 metacommunity dynamics in farmland landscapes. *Proc. R. Soc. B: Biol. Sci.* 282,  
767 20150002.

768 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.

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

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

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

776 Jovani, R., Rohwer, S., 2016. Fault bars in bird feathers: mechanisms, and ecological and  
777 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  
779 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., Obłozza, P., Mirski, P., 2020. Ranging  
790 behaviour and habitat use in Montagu's Harrier *Circus pygargus* in extensive farmland of  
791 Eastern Poland. *J. Ornithol.* 162, 325-337.

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

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

796 Limiñana, R., López-Olvera, J. R., Gallardo, M., Fordham, M., Urios, V., 2009. Blood chemistry  
797 and hematologic values in free-living nestlings of Montagu's Harriers (*Circus pygargus*) in  
798 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.  
801 Assessing the risk of fipronil-treated seed ingestion and associated adverse effects in the  
802 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  
805 and offspring immunity. *Environ. Res.* 136, 97-107.

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

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

811 Maxwell, M. H., 1993. Avian blood leucocyte responses to stress. *World's Poult. Sci. J.* 49, 34-  
812 43.

813 Mazerolle, M. J., 2020. AICcmodavg: Model selection and multimodel inference based on  
814 (Q)AIC(c). R package version 2.3-1.

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

817 Millon, A., Bretagnolle, V., 2008. Predator population dynamics under a cyclic prey regime:  
818 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  
820 résultats de l'enquête Rapaces 2000. *Rapaces Nicheurs de France*. Delachaux Niestlé,  
821 Paris, 129-140.

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

824 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.

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

828 Moreau, J., Rabdeau, J., Badenhauer, I., Giraudeau, M., Sepp, T., Crépin, M., Gaffard, A.,  
829 Bretagnolle, V. Monceau, K., 2022a. Pesticide impacts on avian species with special  
830 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.

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

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

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

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

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

845 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.

849 O'Dell, D. A., Carlo, M. A., Kimmitt, A., Bikowski, E., Morris, K. R., Dolby, A., 2014. A comparison  
850 of techniques measuring stress in birds. *Virginia journal of science* 65, 133-149.

851 Orsini, S., Padel, S., Lampkin, N., 2018. Labour use on organic farms: a review of research since  
852 2000. *Organic farming* 4, 7-15.

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

856 Ortiz-Santaliestra, M. E., Alcaide, V., Camarero, P. R., Mateo, R., Mougeot, F., 2020. Egg  
857 overspray with herbicides and fungicides reduces survival of red-legged partridge chicks.  
858 *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.

863 Ots, I., Murumägi, A., Horak, P., 1998. Haematological health state indices of reproducing  
864 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*  
866 *tinnunculus*. *Naturwissenschaften*, 96, 1193-1202.

867 Peig, J., Green, A. J., 2009. New perspectives for estimating body condition from mass/length  
868 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, <https://doi.org/10.32614/RJ-2018-009>.

871 QGIS Development Team, 2021. QGIS Geographic Information System, Version 3.16.5  
872 Hannover. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.

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



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

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

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

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

887 Reissig, L., Kohler, A., Rossier, R., 2016. Workload on organic and conventional family farms in  
888 Switzerland. *Organic Agriculture* 6, 225-242.

889 Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki,  
890 P., de Carli, E., del Moral, J. C., Domsa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory,  
891 R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., Jiguet, F., Kennedy, J., Klvaňová,  
892 A., Kmecl, P., Kuczyński, L., Kurlavičius, P., Kålås, J. A., Lehikoinen, A., Lindström, Å.,  
893 Lorrillière, R., Moshøj, C., Nellis, R., Noble, D., Eskildsen, D. P., Paquet, J.-Y., Pélissié, M.,  
894 Pladevall, C., Portolou, D., Reif, J., Schmid, H., Seaman, B., Szabo, Z. D., Szép, T.,  
895 Florenzano, G. T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z.,  
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.

901 Ruiz, G., Rosenmann, M., Novoa, F. F., Sabat, P., 2002. Hematological parameters and stress  
902 index in rufous-collared sparrows dwelling in urban environments. *The Condor*. 104, 162-  
903 166.

904 Roschewitz, I., Gabriel, D., Tschardt, T., & Thies, C. (2005). The effects of landscape  
905 complexity on arable weed species diversity in organic and conventional farming. *J. Appl.*  
906 *Ecol.* 42, 873-882.

907 Saino, N., Ambrosini, R., Martinelli, R., Ninni, P., Møller, A. P., 2003. Gape coloration reliably  
908 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.

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

915 Salamolard, M., Butet, A., Leroux, A., Bretagnolle, V., 2000. Responses of an avian predator to  
916 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.

921 Santangeli, A., Arroyo, B., Millon, A., Bretagnolle, V., 2015. Identifying effective actions to  
922 guide volunteer-based and nationwide conservation efforts for a ground-nesting  
923 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.

927 Sheldon, B. C., Verhulst, S., 1996. Ecological immunology: costly parasite defences and trade-  
928 offs 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.

939 Sternalski, A., Mougeot, F., Bretagnolle, V. (2012b). Carotenoid limitation and allocation  
940 priorities in asynchronous raptor nestlings. *Biol. J. Linn. Soc.* 105, 13-24.

941 Sternalski, A., Mougeot, F., Eraud, C., Gangloff, B., Villers, A., Bretagnolle, V., 2010.  
942 Carotenoids in nestling Montagu's harriers: variations according to age, sex, body  
943 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.

947 Sumasgutner, P., Terraube, J., Coulon, A., Villers, A., Chakarov, N., Kruckenhauser, L.,  
948 Korpimäki, E., 2019. Landscape homogenization due to agricultural intensification  
949 disrupts the relationship between reproductive success and main prey abundance in an  
950 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  
953 in the movements and habitat selection of a declining bird. *Biol. Conserv.* 251, 108794.

954 Tews, J., Bert, D., Mineau, P., 2013. Estimated mortality of selected migratory bird species  
955 from mowing and other mechanical operations in Canadian agriculture. *Avian Conserv.*  
956 *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.

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

965 Vitz, A. C., Rodewald, A. D., 2011. Influence of condition and habitat use on survival of post-  
966 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.

972 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**

976

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

983

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

988

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).  
992 Measured life history traits are (a) cere colouration score, (b) H/L ratio, and (c) PC1-activity.  
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).

998

999 **Fig. 4:** Organic farming effect on (a) cere colouration score, (b) H/L ratio, and (c) PC1-activity  
1000 of chicks at 1500 m, 600 m and 200 m around the nest respectively. A dot represents a value  
1001 measured for a chick (darker = more chicks had this value). Lines predict values of each life  
1002 history trait depending on the percentage of organic farming. Shading represents the 95%  
1003 confidence interval.  
1004