Agriculture, Ecosystems and Environment 336 (2022) 108034

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Organic farming positively affects the vitality of passerine birds in agricultural landscapes

Jérôme Moreau [a,b,*], Karine Monceau [b], Gladys Gonnet [b], Marie Pfister [b], Vincent Bretagnolle [b,c]

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

ARTICLE INFO

Keywords:
Agricultural intensification
Behaviour
Conventional farming
Organic farming
Passerine birds
Pesticides

ABSTRACT

Conventional farming has been implicated in global biodiversity loss, with many farmland birds in decline. Organic farming is often considered a more ecological alternative since it generally hosts greater faunal diversity. To date, the impact of conventional agriculture on the decline in avian species has mainly been assessed through the lens of biodiversity loss; few studies have examined the effects of conventional farming on individual life-history trait components. Behaviour represents the final integrated outcome of a range of biochemical and physiological pathways and can be considered a proxy of health as it is more sensitive than other life-history traits, potentially allowing environmental changes to be better tracked. The goal of this study was to understand how exposure to conventional *versus* organic farming affects the behaviour of passerine birds in real conditions. By sampling 6 species of passerine birds in 10 hedgerows in organic landscapes and 10 hedgerows in conventional landscapes during the breeding period, we found evidence that organic farming sharply increased the vitality of individuals, irrespective of species. This was measured through behaviour such as flee attempts, aggressivity, pecking and distress calls when captured, all of which were higher in birds caught in organic hedges than those caught in conventional landscapes. We posit that passerines living in organically farmed landscapes benefit from reduced pesticide exposure rather than a greater abundance of food, as body condition was identical in the two contexts. These findings suggest that the behaviour of passerines can be a useful indicator of the state of the environment and can thus serve as an early warning of specific environmental change in agricultural areas. Further studies assessing the life-history traits of farmland birds may be a valuable aid to understanding the impact of conventional agriculture on biodiversity.

1. Introduction

Over the last half-century, the challenge of feeding a growing human population has led to agricultural intensification that aims to maximize productivity, a process characterized by the improvement of crop varieties, the replacement of habitat heterogeneity by vast monocultures, and the increased use of agrochemical compounds such as non-organic fertilizers and pesticides (Zhang et al., 2013; Robertson et al., 2014). In the same time, unprecedented biodiversity declines were demonstrated in intensive agrosystems, raising concerns about the sustainability of such farming systems (Chamberlain et al., 2000; Stoate et al., 2009). Much literature has been produced on the processes affecting farmland birds (e.g., decreased food availability and suitable habitats, pesticide poisoning, mortality due to harvesting), but only a set of farmland species were investigated (Robinson and Sutherland, 2002; Geiger et al., 2010; Mitra et al., 2011; Mineau and Whiteside, 2013; Chiron et al., 2014; Stanton et al., 2018). Organic agriculture, which combines traditional farming methods with modern technology, has been put forward as an alternative to conventional farming, offering improved sustainability in food production both in terms of biodiversity and human health (Sandhu et al., 2010; Seufert et al., 2012; Gonthier et al., 2014). Indeed, higher bird density and species richness in organic compared to conventional farms were almost invariably found so far (Fluetsch and Sparling, 1991; McKenzie and Whittingham, 2009; Mondelaers et al., 2009; Batary et al., 2010; Chamberlain et al., 2010; Smith et al., 2010; Tuck et al., 2014; Stanton et al., 2018; Gregory et al., 2019; Moreau et al., 2021).

However, this clear difference between conventional and organic

* Corresponding author at: Centre d'Études Biologiques de Chizé, UMR 7372, CNRS & La Rochelle Université, 79360 Villiers-en-Bois, France.
E-mail address: jerome.moreau@u-bourgogne.fr (J. Moreau).

https://doi.org/10.1016/j.agee.2022.108034
Received 6 February 2022; Received in revised form 16 May 2022; Accepted 18 May 2022
Available online 25 May 2022

farming on birds has been assessed almost exclusively using species richness metrics (Robinson and Sutherland, 2002; Geiger et al., 2010; Mitra et al., 2011; Mineau and Whiteside, 2013; Chiron et al., 2014; Stanton et al., 2018), while the impact of these two types of farming on individual life-history traits has been very little studied. The positive effects on bird species of organic compared to conventional agriculture may result from different factors, such as improved food resources and/or higher availability of nesting sites (e.g., grasslands or hedges). Organic farming landscapes tend to have higher crop diversity, higher plant and faunal diversity, larger areas of semi-natural elements and, more generally, higher landscape diversity (Hole et al., 2005; Tuck et al., 2014; Reganold and Watcher, 2016; Gibson et al., 2007). These features allow improved foraging and nesting opportunities for insects (Tuck et al., 2014), hence more resources for birds. In addition, lower pesticide exposure is expected in organic landscapes, either directly (through contact) or indirectly (through consumption of food). While the intake of large quantities of pesticides can be lethal for wild individuals, chronic exposure to smaller amounts could also have sublethal effects on wild populations. Numerous laboratory experiments, as well as some field studies, have detailed the toxic effects of pesticides on birds' life-history traits, which ultimately decrease their survival (Mitra et al., 2011; Lopez-Antia et al., 2015; Millot et al., 2017; Moreau et al., 2021). However, only a handful of studies have investigated the effects of conventional farming on individual life-history traits, and these only concern grassland birds (Hole et al., 2002; Baeta et al., 2012). To improve our knowledge of the effects of the farming environment on birds, our aim was to compare a suite of behavioural traits in birds living in conventional *versus* organic farming landscapes.

An organism's behaviour represents the final integrated outcome of a range of biochemical and physiological processes (Odum, 1971) and may be considered as a proxy of individual health that is more sensitive to stress than survival or other physiological measures (Clotfelter et al., 2004; Hellou, 2011). Numerous chemicals are known to interfere with the endocrine system of animals (Toppari et al., 1996), and individuals are often exposed to multiple chemicals in their environment that can accumulate in body tissues. Subtle alterations in behaviour may be manifested below lethal toxicity levels and can thus be regarded as sensitive toxic response indicators (Hellou, 2011). Yet behavioural alteration has been largely unexploited by ecotoxicologists despite the fact that behaviour is considered to be 10–1000 times more sensitive than the conventional LD50 value (LD stands for "Lethal Dose" corresponding to the amount of a pesticide, given all at once, which causes the death of 50% of a group of test animals) of acute toxicity used in ecotoxicity tests, and thus could be considered an early warning signal to assess environmental quality (Dell'Omo, 2002; Hellou et al., 2008). In addition, behavioral monitoring can be a relatively fast, simple and non-invasive approach to quantify individual responses in the field (Peakall, 1985). For example, behavioural traits in passerine birds have been extensively used as a biomonitoring tool to measure the effects of urbanization (Albayrak and Mor, 2011).

Many farmland birds nest in hedgerows, but forage either in hedgerows or adjacent fields, depending on the species and the crop (Birds of the World, 2022). Common passerine species have small home ranges, therefore, the type of farming system surrounding the hedgerow (i.e., organic or conventional) allows the comparison of their living environment and their core home range. To investigate this, we selected a sample of hedgerows with different farming systems operating in the surrounding fields, organic and conventional, keeping all other parameters (e.g., hedgerow type, crop type) as constant as possible to isolate the effects of 'organic' *versus* 'conventional' landscapes. We then monitored the behaviour of 6 species of passerine birds belonging to different families that breed in these hedgerows, to measure a suite of behaviours in individuals from the same species sampled in organic landscapes or in conventional landscapes. We expect that birds captured in organic farming have a better health condition and consequently more vigorous behavioral responses than birds captured in conventional farming.

2. Material and methods

2.1. Experimental design

The study was conducted in the 'Zone Atelier Plaine & Val de Sèvre' (ZA-PVS), a 435 km^2 Long-Term Social-Ecological Research (LTSER) site in central-western France (46°23′N, 0°41′W). The site consists largely of agricultural land, with urban areas making up 9.8% of the area and fragmented woodlands 3.1%. It is bordered in the north by the city of Niort and in the south by Chizé forest (see Bretagnolle et al., 2018). The majority of the area is typical intensive farmland, made up of open landscapes with mainly winter cereals and other arable crops (maize, sunflower, oilseed rape, pea), temporary grasslands (such as alfalfa and clover) and permanent meadows. The site has a rather high diversity of types of farming system, with ~15 farms managed using conservation agriculture practices, ~60 farms using organic methods, and 350 using conventional methods, of which about 50% are mixed dairy/cereal farms. Agricultural land use within the site has been monitored annually at the field scale since 1994 and mapped on vector-based shapefiles (Bretagnolle et al., 2018). Every organically farmed field is identified (see Wintermantel et al., 2019), providing a very detailed description of farming practices regarding pesticide use at field (organic *versus* conventional farming) and landscape scales. On average, conventional farmers use 5–10 different pesticide molecules on their fields (in c. 4–8 applications per year; Bretagnolle and Gaba unpublished data), while organic farmers use none.

We used this detailed knowledge to select 10 hedgerows surrounded by organically farmed landscapes and 10 hedgerows surrounded by conventionally farmed landscapes, each with a 250-m radius buffer zone. The percentage of organic farming was calculated within this 250-m radius buffer. We chose this buffer-zone size to include the breeding home-range size for different passerine species (see below). For hedgerows defined as 'organic hedges', 73–98% of the buffer area was organically farmed, while 'conventional hedges' had almost no organic farming within the buffer area (see Table 1).

Since hedgerows in the two landscape types may differ for other reasons than just the type of agricultural system, we measured several descriptive parameters for each, including total hedgerow length (m), hedgerow height (m), top width at 3 m above ground and bottom width (m), and the approximate length of holes, gaps or clearings within the hedgerow (m). Length and width were estimated using a measuring tape. We estimated hedgerow height and top and bottom width by averaging measurements made at ten different points randomly chosen along the hedgerow (see Arnold, 1983; Green et al., 1994; MacDonald and Johnson, 1995 for exact procedures). We also estimated the length of wooded and shrubby layers in the hedgerow at ground level using a measuring tape. A tree was considered mature (wooded layer) if its diameter at breast height was > 10 cm. To assess the density of the hedgerow, at 10 random points along it we pushed a thin rod through the hedge at 1 m above the ground, then counted the number of contacts between the rod and branches.

In addition, at a larger spatial scale, we recorded the surface area of woods in the vicinity of a hedgerow within a 250-m radius and the dominant type of cultivation. None of the parameters measured for the 20 hedgerows differed significantly between the two types of agricultural systems (see Table 1), except the % of organic farming within the 250-m radius buffers.

2.2. Bird captures

The same net-trapping method was used in each hedgerow to catch birds from sunrise (between 6:00 am and 7:00 am depending on the month) to 11:00 am, during the breeding season, from mid-April to the end of June 2019. Before sunrise, 10 identical 12-m long mist nets were

Table 1
Structural characteristics of 20 hedgerows in two types of agricultural land (organic and conventional). Characteristics assessed are (i) total length, wooded length, shrubby length and length of gaps (m) and (ii) height, top width, bottom width and density (mean ± s.e.m.), measured as the number of contacts between rod and branches with measurements made at ten different locations randomly chosen along the hedgerow. We also estimated (i) the percentage of organic farming, (ii) the percentage of wooded area and (iii) the dominant type of cultivation in a 250-m radius buffer around the hedgerow. None of these parameters measured on the 20 hedges differed significantly between the two types of agricultural systems according to the Kruskall-Wallis test[1] or the linear model taking into account the identity of the hedge as a random factor,[2] except the % of organic farming within the 250-m radius buffer.

Agriculture type	Hedge ID	Total Length (m)	Wooded length (m)	Shrubby length (m)	Length of gaps (m)	Height (m)	Top width (m)	Bottom width (m)	Density	% organic	% wood	Crop
Organic	*3*	411	185	411	0	3.84 ± 0.46	7.48 ± 0.97	3.81 ± 0.14	4.00 ± 0.00	98.41	0	Wheat, Triticale
	4	374 468 557	332	286	3	8.03 ± 0.84	7.04 ± 0.40	2.45 ± 0.14	1.40 ± 0.16	94.46	0	Wheat, Faba bean
	6	468	462	468	0	8.44 ± 0.45	5.83 ± 0.29	2.71 ± 0.20	2.1 ± 0.31	73.59	0	Wheat, Faba bean
	9	557	477	546	2	7.22 ± 0.82	5.60 ± 0.54	2.98 ± 0.21	1.90 ± 0.38	74.65	0	Wheat, Corn
	11	178	116	173	2	9.91 ± 1.06	6.35 ± 0.73	4.03 ± 0.77	1.70 ± 0.26	85.18	0	Wheat, Faba bean
	13	493	493	493	0	11.46 ± 0.69	4.73 ± 0.52	2.55 ± 0.28	2.60 ± 0.16	96.29	6.3	Rapeseed
	14	486	52	467	0	6.67 ± 0.83	6.47 ± 0.55	2.99 ± 0.24	3.10 ± 0.23	93.13	0	Barley
	15	391	251	391	0	10.56 ± 1.62	6.81 ± 0.52	3.44 ± 0.29	3.10 ± 0.18	72.94	0	Sunflower
	31	509	438	312	20	13.13 ± 0.56	7.84 ± 0.80	1.88 ± 0.10	1.60 ± 0.31	73.74	0	Alfalfa
	35	190	158	106	18	12.77 ± 1.26	4.19 ± 0.57	1.37 ± 0.03	1.60 ± 0.22	83.40	0	Wheat
Conven-tional	*16*	215	192	215	0	11.74 ± 1.20	5.96 ± 0.56	2.70 ± 0.32	2.00 ± 0.30	3.51	0	Wheat
	21	527	215	520	1	10.07 ± 1.42	10.69 ± 0.91	2.41 ± 0.09	2.70 ± 0.34	0	0	Wheat
	22	371	352	274	25	19.23 ± 2.25	4.62 ± 0.31	4.69 ± 0.62	1.70 ± 0.47	5.67	0	Faba bean, Wheat
	29	571	325	547	3	7.28 ± 1.25	6.71 ± 0.41	1.58 ± 0.08	2.10 ± 0.31	0	0	Wheat, Corn
	33	188	81	185	1	7.47 ± 1.06	3.64 ± 0.42	2.75 ± 0.38	2.10 ± 0.31	0	0	Wheat, Corn
	34	245	211	242	1	10.52 ± 0.98	5.77 ± 0.65	2.89 ± 0.42	2.30 ± 0.30	0	0	Wheat, prairie
	37	217	161	205	1	11.54 ± 0.82	7.20 ± 0.61	4.17 ± 0.70	2.20 ± 0.30	0	0	Wheat, Faba bean
	38	234	109	231	1	6.83 ± 0.80	7.77 ± 0.54	1.41 ± 0.07	1.70 ± 0.30	3.80	0	Barley, Wheat
	40	535	449	435	9	11.40 ± 0.58	7.57 ± 0.77	3.22 ± 0.89	1.70 ± 0.33	0	0	Rapeseed
	41	590	147	590	1	4.01 ± 0.60	5.26 ± 0.51	2.98 ± 0.23	3.70 ± 0.15	0	0	Wheat
$\chi^2_1 =$		-0.04[1]	-0.94[1]	-0.19[1]	0.58[1]	-0.54[2]	-0.39[2]	-0.14[2]	0.27[2]	-3.82[1]	-0.90[1]	
$P =$		0.97	0.34	0.82	0.56	0.60	0.70	0.89	0.79	0.0001	0.37	

spread alongside the hedges of a given selected site. Nets were monitored every 5–10 min to check if a bird was caught to ensure birds did not remain in the net for more than 10 min. Each hedge was sampled three times (only one hedge per day) to cover the full breeding season, first from 15/04–05/05, then from 07/05–29/05, and finally from 01/06–23/06. Mist nets were set only when the meteorological conditions were favourable (no wind, no rain, and temperature above 8 °C at sunrise). At each capture, the ambient temperature in the shade of the hedge and the time were recorded.

A total of 17 species were caught, of which the six most common became the focus of the study. The six most abundant passerines were the Eurasian black cap (*Sylvia atricapilla*, N = 46), cirl bunting (*Emberiza cirlus*, N = 31), common nightingale (*Luscinia megarhynchos*, N = 26), great tit (*Parus major*, N = 21), common whitethroat (*Sylvia communis*, N = 21) and melodious warbler (*Hippolais polyglotta*, N = 19). All other species were excluded from the analysis due to the low number of individuals (<10) caught, precluding statistical analyses. During breeding, the home range sizes for these different species range from 0.2 ha to 8 ha (Moskat et al., 1993; Naef-Daenzer, 1994; Stoate and Szczur, 2001; Naguib et al., 2001; Halupka et al., 2002; Stevens et al., 2002; Assandri et al., 2017), corresponding to a radius around the edge from 25 to 160 m. These breeding home-range sizes are therefore smaller than the size of our study plots (buffer size of 250-m radius). Given that passerine home range sizes are small (1–2 ha) during the breeding period and certainly smaller than disk sizes (12–15 ha) on which the proportion of organic/conventional farming systems were estimated around hedges, we assume that most time spent by an individual bird was restricted to the targeted area. Small breeding home-range sizes and site fidelity were confirmed by recapture rates (e.g., 45 birds were recaptured in the same hedgerow). To avoid pseudo replication, if a bird was recaptured, it has been immediately released without making measurements. Only its first capture with the data appears in the database.

2.3. Behavioural parameters

For every bird caught, we recorded several types of behaviour (see details and references for procedures below). The behaviour of each bird was always recorded by a unique observer, within 10 min after capture.

Each procedure was performed in the same sequential order to measure: (i) escape vigour, (ii) breath rate, (iii) aggressivity, (iv) handling vigour (during morphological measurement), and (v) tonic immobility. After the full set of measurements and ringing, all birds were released at the site of capture. None of the 164 birds caught was injured or died during the experiments.

2.3.1. Escape vigour (flee attempts from mist net)

To assess the vigour of a bird captured in the net, we developed an original protocol. Once a bird was caught in the mist net, escape vigour was estimated in two steps using a standardized procedure. First, we approached the mist net slowly and, once the bird detected the ringer (i.e., when it tried to flee), we counted the number of flee attempts for 15 s while continuing to walk slowly towards the bird. Second, when near the bird, the experimenter reached one hand out at a distance of 5 cm from the bird's head, opening the hand slowly ten times to record the number of flight attempts. As these two escape metrics were highly correlated for each species (Spearman rho > 0.46, $P < 0.0001$), we summed them to get an overall score of escape vigour. In the rare cases in which two birds were caught at the same time in a net (less than 2% of total individuals caught), these individuals were excluded from the analysis. After these measurements, all captured birds were put singly in a bag for 10 min. We expected that the number of flee would be higher for the birds caught in organic farming because they can afford such energetic cost by living in food-rich environments, and because they would need less energy for pesticide detoxification processes (Lushchak et al., 2018; Wiegand, 2019). Hence these birds would be more vigorous and reactive to escape a possible predator.

2.3.2. Breath rate

After 10 min in the bag, the bird's breath rate was measured to estimate the degree of acute physiological stress experienced during handling (Carere and van Oers, 2004; Markó et al., 2013; Rabdeau et al., 2019). The bird was first taken out of the bag, then the number of breast respiratory movements was counted for 30 s while holding the wings fixed (Markó et al., 2013; Torné-Noguera et al., 2014). We expected the breath rate to be higher for the birds caught in conventional farming due to the chronic stress of living in such environment (less abundant food, presence of pesticides, etc.).

2.3.3. Aggressivity: pecking and distress calls

The aggressive behaviour of individuals was quantified by measuring the pecks and distress calls by handled individuals in standardized trials. These trials consisted of (i) approaching a finger 1–2 cm from the beak of a bird ten times while holding its legs, and (ii) touching the bird's beak ten times with a finger (see Markó et al., 2013 for an example). During this test, we recorded the number of pecks to the hand and the number of distress calls uttered (Fucikova et al., 2009; Laiolo et al., 2009). We expected individuals to be more aggressive in organic farming. More aggressive individuals are expected to have a better protection from a predator and thus a higher survival rate.

2.3.4. Handling vigour (flee attempts/attacks on hand)

We also characterized individual behaviour during handling to measure morphological traits (see below), recording the number of times a bird attempted to flee and/or attack the hand of the experimenter with its bill or claws. Handling vigour was defined as the sum of flee attempts and attacks during morphological measurements. As for escape vigour, we expected the number of flee attempts and attacks on hand to be higher for the birds caught in organic farming; hence these birds are more vigourous and able to escape a possible predator.

2.3.5. Tonic immobility

Tonic immobility is a proxy measure of a bird's boldness toward predators (Réale et al., 2007). Individuals showing higher activity in the presence of a predator have a shorter duration of tonic immobility, an effective behaviour for reducing the probability of being predated because of lower movement stimuli eliciting attack (Thompson et al., 1981; Edelaar et al., 2012). To measure this, we induced tonic immobility by placing the bird on its back in one of the experimenter's hands, fully covering it with the other hand, and exerting light pressure to the breast area (this is intended to mimic immobilization by a predator). After 5 s, the hand was slowly removed, and we measured the time until the bird righted itself and flew away. In the case where an individual did not move after 30 s, it was turned slightly upside down to trigger its escape flight. We expected tonic immobility to last longer for birds caught in organic farming increasing their probability of survivorship during predator attack.

2.4. Morphological traits

The measurements of morphological traits were carried out in standardized order just after the scoring of aggressivity behaviour and before the tonic immobility tests. For each bird, we measured left and right tarsus length twice. All measurements were made by the same person with a digital calliper (precision: ± 0.1 mm) to ensure the same handling time for all individuals. Body mass was recorded to the nearest 0.1 g using an electronic balance (Scout Pro). Body condition was computed for each species separately based on body mass and mean tarsus length (right and left) using the scaled mass index (Peig and Green, 2009) defined as follows for each individual *i*:

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

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

2.5. Statistical analyses

As a preliminary test, a first set of models was used to investigate the potential confounding effects of the time of capture (standardized according to the hour of sunrise), the temperature at the time of behaviour measurement, and the date of capture (transformed in Julian dates) on each measured behaviour. None of these parameters were found to significantly affect any of the recorded behaviours (all statistical test yielded P value > 0.6), and therefore potential confounding factors were ignored in subsequent analyses. Then, we opted for a two-steps approach to test first the occurrence (individuals displaying the behaviour or not) and then the intensity of the different behaviours (including individuals that did not express the behaviour) depending on the agricultural type (organic *versus* conventional farming).

2.5.1. Occurrence of measured behaviours by captured individuals

The occurrence of each behaviour according to the agricultural type was tested using Binomial Generalized Linear Models (B-GLM). These models computed the likelihood of an individual displaying (i.e., displayed = 1, not displayed = 0) flee attempts/attacks on hand, pecks, distress calls and tonic immobility (flying away before 30 s), with species ID, farming system, their two-way interaction, and body condition as explanatory factors. Hedge ID was added as a nested effect within the farming system (organic *versus* conventional) for all models to control for potential heterogeneity among capture sites. We chose to nest hedge identity inside the farming system since hedge identity is a lower-level factor appearing only within an upper-level factor (here, the farming system) (Schielzeth and Nakagawa, 2013). This step was not performed for flee attempts from mist nets and breath rate as all individuals made at least one of them.

2.5.2. Intensity of measured behaviours by captured individuals

The intensity of each behaviour (including individuals that did not express the behaviour) according to the agricultural type was tested using Negative Binomial Generalized Linear Models (NB-GLM) for the parameters which were count variables (i.e., number of flee attempts/ attacks, pecks, distress calls and breath rate). Negative binomial was preferred to Poisson as it fitted better the data, but tonic immobility and body condition (log-transformed) were tested with Gaussian GLM (G-GLM) as the data was normally distributed. The model structure was the same as for previous models except for body condition which only included the agricultural type and nested hedge effect as explanatory variable because it was computed independently for each species.

In all cases, the statistical significance of each effect was tested using deviance analysis based on likelihood-ratio Chi^2 tests for B- and NB-GLM and *F*-ratio tests for G-GLM. The estimates assorted with their standard deviation for the body condition (the only continuous variable in the models) from each model are provided to allow a better understanding of the results. The sample size could vary from one behaviour to another (see Table 2 and Table 3 for exact sample sizes) because sometimes the measurements could not be taken on some individuals. All statistical tests were performed using R software (v 4.0.4, R Core Team, 2021).

3. Results

The findings showed that the proportion of individuals displaying handling vigour behaviour (flee attempts/attacks on hand), pecking and distress calls during the trials was species dependent for all parameters (Table 2) (Fig. 1). For instance, more *P. major* individuals exhibited pecking and distress call behaviour than *S. communis.* The farming system had a significant influence only on the proportion of individuals displaying pecking behaviour: 46.7% of individuals captured in organically farmed areas exhibited this behaviour, but only 29.7% in conventionally farmed areas (Table 2), with no interaction with species identity. The number of individuals exhibiting lasting tonic immobility (i.e., individuals not flying away from the hand alone) was not affected by any variables included in the model, though the effect of the type of agriculture was close to the significant (72.09% for individuals captured in organic *versus* 56.34% for individuals in conventionally farmed areas) (Table 2). A similar tendency was found for handling vigour behaviour (86.5% in organic farming *versus* 71.6% in conventional farming), but the proportion of individuals uttering distress calls was similar (27.8% in organic farming *versus* 28.4% in conventional farming).

Regarding the intensity of behaviour, every monitored metric varied significantly with the farming system, except breath rate. In the latter, we found only a species effect and a strong influence of the localization of a hedge inside a farming system, indicating strong variation between different hedges inside one farming system (Fig. 2a, Table 3). The number of flee attempts of mist-netted individuals caught in organic hedges was significantly higher than in conventional hedges (Fig. 1a, Table 3). Similarly, the number of flee attempts/attacks on hand (handling vigour) was also significantly higher in organic than conventional hedges, but this was species dependent (e.g., *S. atricapilla* was more vigorous when held than *L. megarhynchos*) (Fig. 1b, Table 3). This handling vigour behaviour also depended on body condition (estimate ± standard error = −0.10 ± 0.03; lower body condition led to higher

Table 2
Occurrence of the behaviours according to the agricultural type, species identity, their interaction, body condition and nested effect of hedges within the agricultural type. Tests were performed using Binomial Generalized Linear Models (B-GLM) to compare the individuals who performed or not the behaviours. Significant effects are in bold. The estimates and standard errors for body condition are also provided for each model. The effects of the categorical variables agricultural type and species are explicated in the text of the results. The sample size for each behaviour appeared below the behavior.

Measured parameters		X_1^2	*df*	*P*
Flee attempts/ attacks on hand[a] N = 163	Agricultural type	2.66	1	0.10
	Species	**14.98**	**5**	**< 0.05**
	Body condition (−0.07 ± 0.09)	0.69	1	0.41
	Agricultural type x species	4.62	5	0.46
	Agricultural type [site]	19.15	18	0.38
Pecks N = 164	**Agricultural type**	**11.48**	**1**	**< 0.001**
	Species	**28.55**	**5**	**< 0.0001**
	Body condition (−0.01 ± 0.08)	0.02	1	0.90
	Agricultural type x species	8.54	5	0.13
	Agricultural type [site]	22.76	18	0.20
Distress calls N = 164	Agricultural type	2.83	1	0.09
	Species	**36.54**	**5**	**< 0.0001**
	Body condition (−0.03 ± 0.09)	0.14	1	0.71
	Agricultural type x species	7.83	5	0.17
	Agricultural type [site]	11.92	18	0.85
Tonic immobility N = 157	Agricultural type	3.18	1	0.07
	Species	3.49	5	0.62
	Body condition (−0.03 ± 0.08)	0.18	1	0.67
	Agricultural type x species	3.04	5	0.69
	Agricultural type [site]	25.97	18	0.10

Table 3
Intensity of the behaviours and body condition differences according to the agricultural type, species identity, their interaction, body condition and nested effect of hedges within the agricultural type. Tests were performed using [a]Negative-Binomial Generalized Linear Models (NB-GLM) or [b]Gaussian Generalized Linear Models (G-GLM) to compare the behavioural response of the individuals (i.e., intensity) and their body condition. Significant effects are in bold. The estimates and standard errors for body condition are also provided for each model (except the one testing for differences in body condition). The effects of the categorical variables agricultural type and species are shown in figures. The sample size for each behaviour appeared below the behavior.

Measured parameters		X_1^2	*df*	*P*
Number of flees from mist net[a] N = 162	**Agricultural type**	**15.67**	**1**	**< 0.0001**
	Species	2.14	5	0.83
	Body condition (−0.01 ± 0.02)	0.26	1	0.61
	Agricultural type x species	5.14	5	0.40
	Agricultural type [site]	12.73	18	0.81
Number of flee attempts/ attacks on hand[a] N = 163	**Agricultural type**	**14.43**	**1**	**< 0.001**
	Species	**20.23**	**5**	**< 0.01**
	Body condition (−0.10 ± 0.03)	**9.31**	**1**	**< 0.01**
	Agricultural type x species	5.35	5	0.37
	Agricultural type [site]	24.45	18	0.14
Number of pecks[a] N = 164	**Agricultural type**	**23.87**	**1**	**< 0.0001**
	Species	**39.28**	**5**	**< 0.0001**
	Body condition (−0.005 ± 0.05)	0.01	1	0.91
	Agricultural type x species	5.38	5	0.37
	Agricultural type [site]	**34.37**	**18**	**< 0.05**
Number of distress calls[a] N = 164	**Agricultural type**	**6.43**	**1**	**< 0.05**
	Species	**65.61**	**5**	**< 0.0001**
	Body condition (−0.07 ± 0.09)	0.48	1	0.49
	Agricultural type x species	6.83	5	0.23
	Agricultural type [site]	15.31	18	0.64
Breath rate[a] N = 164	Agricultural type	0.14	1	0.71
	Species	**29.18**	**5**	**< 0.0001**
	Body condition (0.008 ± 0.005)	2.55	1	0.11
	Agricultural type x species	2.32	5	0.80
	Agricultural type [site]	**51.38**	**18**	**< 0.0001**
Duration of tonic immobility[b] N = 157	**Agricultural type**	**5.37**	**1**	**< 0.05**
	Species	2.38	5	0.79
	Body condition (0.20 ± 0.42)	0.22	1	0.64
	Agricultural type x species	3.07	5	0.69
	Agricultural type [site]	19.75	18	0.35
Body condition (log-transformed)[b] N = 164	Agricultural type	0.69	1	0.40
	Agricultural type [site]	23.31	18	0.18

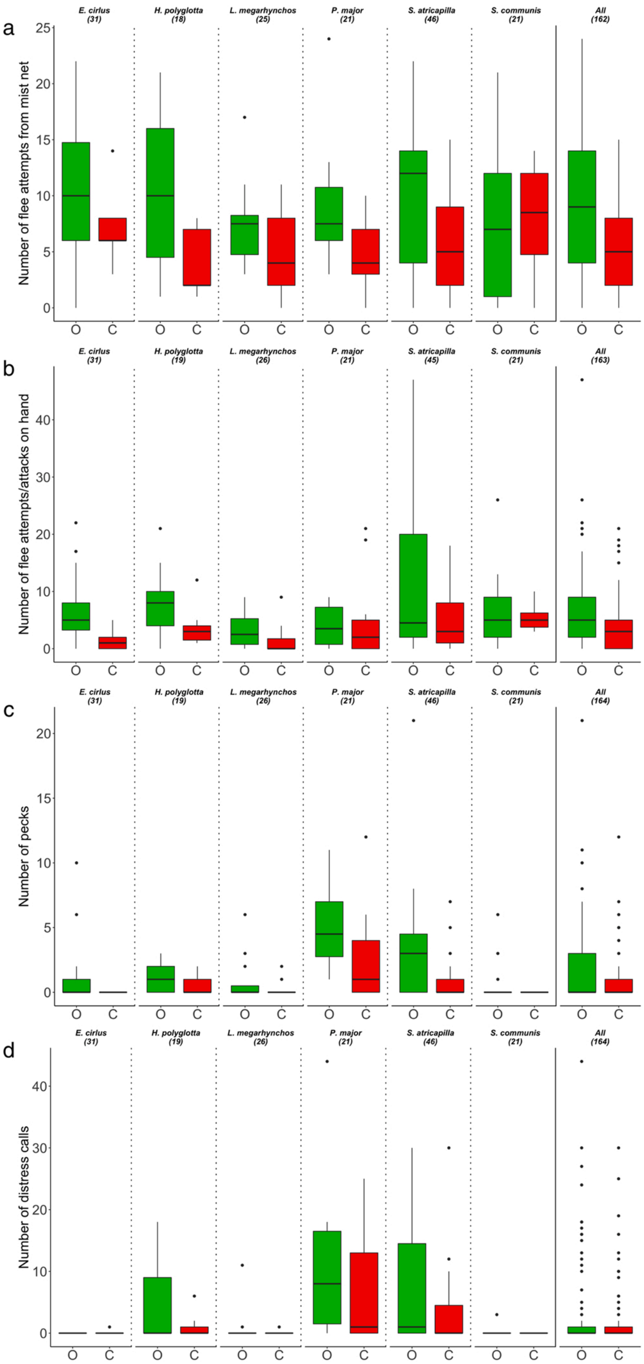

Fig. 1. (a) The number of flee attempts (escape vigour) of caught individual birds while still in the mist net, (b) the number of flee attempts/attacks while in the observer's hand (handling vigour) and (c) the number of pecks and (d) distress calls of handled individuals during standardized trials. Data is presented for each of the 6 species and then for all species together for organic hedges (in green, O) and in conventional hedges (in red, C). Numbers in brackets represent the number of individuals sampled. Bold line is the median; box: middle two quartiles; plain lines: 1.5 x interquartile range; open circle: extreme value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

number of flee attempts/attacks on hand) (Table 3). Aggressive behaviour (pecking and distress calls) was species dependent (e.g., *P. major* exhibited higher pecking and distress calls than *S. communis*) and higher for birds caught in organic compared to conventional hedges (Figs. 1c, 1d, Table 3). In addition, there was strong variation between hedges within a type of farming system influencing the amount of pecking

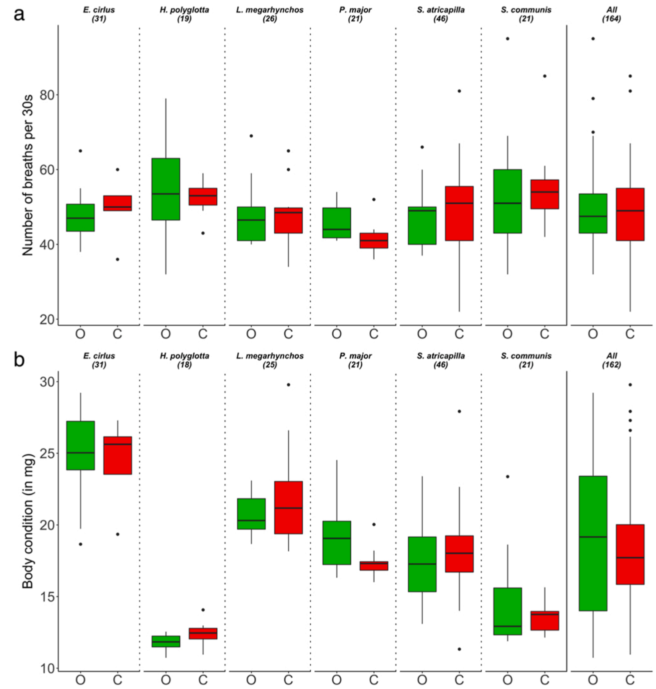

Fig. 2. (a) Breath rate and (b) body condition for each of the 6 species of birds and for all birds together caught in organic hedges (in green, O) and in conventional hedges (in red, C). The numbers in brackets represent the number of adults tested. Bold line is the median; box: middle two quartiles; plain lines: 1.5 x interquartile range; open circle: extreme value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table 3). The farming system also seemed to influence the duration of tonic immobility: in organic hedges, tonic immobility lasted longer (Table 3, Fig. 3). Finally, the body condition of birds was similar between the two agricultural types (Table 3, Fig. 2b).

4. Discussion

The main objective of this study was to analyse whether conventional and organic farming differentially affect a suite of captured bird behaviour and whether this varies with species. Our results showed that

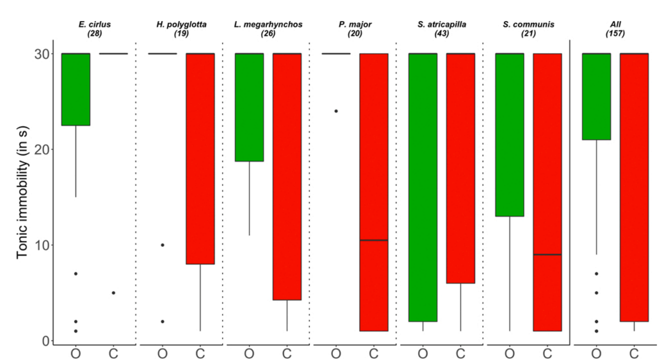

Fig. 3. Tonic immobility for the 6 species of birds and for all birds together caught in organic hedges (in green, O) and in conventional hedges (in red, C). The numbers in brackets represent the number of adults tested. Bold line is the median; box: middle two quartiles; plain lines: 1.5 x interquartile range; open circle: extreme value. The size of the boxes reflects the variability of the behavioral response. An important proportion of birds in conventional agriculture flew away before the 30 s while most of birds stayed in the hand up to 30 s in organic agriculture. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

almost all tested behaviours differed statistically between birds caught in conventional and organic hedgerows in term of the intensity of behavioural displays, but not regarding the occurrence of such behaviours, for which we detected only a difference in the number of flee attempts/attacks on hand. This suggests that the studied behaviours were reduced in intensity, but still present, a pattern suggestive of delayed sublethal effects. Regarding the intensity of the behaviours, the number of flee attempts, handling vigour, pecking and distress calls were higher in organic than in conventional hedges. Moreover, tonic immobility lasted longer for birds caught in organic hedges. In contrast, there was no difference in breath rate or body condition between birds in the two types of farming system. These results were almost independent of the species considered (no significant interaction between agricultural type and species): all six species investigated exhibited decreased vigour when caught in conventional farming environments, indicating a strong effect of conventional farming on their behaviour whatever the ecology of the species.

Such a decrease in vigour may have at least two different origins. In a conventional landscape with high pesticide use, the amount of food available for birds is expected to decrease, while in organic landscapes, insect diversity and density increase (Tuck et al., 2014). However, we found no difference in body condition, nor in breath rate, a measure of acute physiological stress. The absence of difference in breath rate is not surprising since captured birds were certainly under high stress levels during handling, despite we took care to minimise this stress with our protocol. Though breath rate can differ among personality types (Carere and van Oers, 2004), it might be a conservative trait in an acute stressful situation, and therefore, not useful as a trait to monitor the effects of environmental contaminations. Regarding the absence of difference in body condition, one explanation may be that the extensive use of pesticides in conventional agriculture has a direct effect on the physiology and behaviour of birds without altering their body condition. Indeed, several families of pesticides – especially carbamates and organophosphates – inhibit acetylcholinesterase (AChE), which is a key enzyme in the nervous system. Such pesticides have been shown to alter the behaviour of non-target species (Grue et al., 1982; Grue and Shipley, 1984; Foudoulakis et al., 2013; Borges et al., 2014; Santos et al., 2016), resulting in an overall decrease in activity and coordination (review in Grue et al., 1997; Story and Cox, 2001; Walker, 2003; Mitra et al., 2011, but see Farage-Elawar and Francis, 1988). For instance, the activity of male starlings experimentally contaminated with organophosphate was significantly reduced within 2–4 h following exposure (Grue and Shipley, 1981). In cultivated fields, birds can be contaminated by pesticides indirectly through their food or directly through contact.

Pesticide loads may be high, even in hedges, since pesticides can drift from the boom sprayer during application (Kjaer et al., 2014). Moreover, hedgerows can accumulate pesticides, as they intercept spray drift from the cultivated fields (Lazzaro et al., 2008). Studies on the impact of spray drift on biodiversity have been largely restricted to plants and insects (Sinha et al., 1990; Davis et al., 1994; Longley and Sotherton, 1997; Longey et al., 1997): virtually no investigation have been carried out on birds. In one of the few of these, a field experiment demonstrated that adult and nestling great tits were exposed to dimethoate and pirimicarb drift, suggesting a sublethal effect of pesticide drift in hedges (Cordi et al., 1997). In the future, it would be valuable to evaluate the amount of food available between the two types of landscapes, as well as dose pesticides in the captured birds, to measure their actual exposure and define the rate of accumulation of different pesticide molecules.

Whatever the proximate mechanisms behind these behavioural modifications observed in our study, they could lead to negative effects on the population dynamics of passerines, possibly helping to explain their decline in agricultural landscapes. For example, decreased vigour may adversely affect predator avoidance, thus increasing *in natura* mortality. For many birds, predation is the major cause of egg and chick loss and an important component in fledgling and adult mortality (Newton, 1998). Passerine predators, including wild mammals, raptors, but also domestic cats, are known to be involved in bird declines (Gibbons et al., 2007). Our results on tonic immobility may support this hypothesis, as there is increasing evidence that tonic immobility serves a functional purpose in reducing the probability of death during predator attacks and may even reduce a predator's ability to localize prey (Humphreys and Ruxton, 2008; Miyatake et al., 2009). We found that in conventional hedges, tonic immobility was shorter, suggesting that these individuals would have higher activity in the presence of a predator, hence increasing their probability of being predated or of being killed during predation (Edelaar et al., 2012). It is also possible that decreased vigour may be correlated with a decrease in the energy supplied to chicks, which is a good proxy of nestling growth rate and fledgling survival (e.g., Henderson and Hart, 1993).

5. Conclusion

To our knowledge, our study is the first to monitor the behaviour of birds in different agricultural systems in realistic field conditions. Our results indicate that conventional farming alters several major life-history traits, which may impair individual fitness in birds. These findings suggest that passerine birds may be useful indicators of the state of the environment and could be monitored to serve as an early warning signal of specific environmental changes or to assess environmental quality in agroecosystems. However, assessing of the different behaviour we measured here may not always be feasible, as it is necessary to capture individuals (or at least tag them). Our results showed that birds in conventional farming are less vigorous and less active, therefore it is conceivable that other behaviours could show the same pattern while being easier to observe or measure. For instance, the quality of song may be altered in conventional farming systems, with birds singing less often or less intensely. Measuring singing rate does not necessitate captures. Interestingly, there is already some evidence that exposure to some pesticides impede singing ability, mating and breeding (Hart, 1993). Therefore, one future prospect would be to correlate singing behavior to pesticide exposure by comparing organic and conventional landscapes. Birds have long been valued for their capacity to be used as environmental indicators: for example, through mass mortality, modifications in reproductive success and changes in the number or distribution of species communities (Becker, 2003). Thus, it seems urgent to develop studies assessing life-history traits of farmland birds in modern farming systems. In the near future, we need to correlate observed decrease in intensity of the behaviours we measured to molecules applied by farmers in conventional fields. In addition, assessing the pesticide residues in the blood of captured birds and correlating the prevalence and intensity of residues to their health would provide causality cues in explaining farmland bird decline as a result of pesticide exposure by shedding light on the potential physiological pathways leading to weakened behavioural response.

Funding

This work was supported by the University of La Rochelle, the French National Centre of Scientific Research (CNRS), and the French National Research Institute for Agriculture, Food and the Environment (INRAE). This study was partly funded by the projects BIRDPEST funded by RECOTOX 2019, ACI funded by the University of La Rochelle, Agri-BioBird funded by OSU Theta ISITE-BFC, ANR JCJC PestiStress (#19-CE34-0003-01), and the BioBird project funded by the regional government of Nouvelle-Aquitaine.

Declaration of Competing Interest

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

Data Availability

Once the paper has been accepted, the data will be deposited in the Dryad repository.

Acknowledgements

We would like to thank all the farmers who allowed us free access to their fields, as well as all those who contributed to the fieldwork.

Research ethics

All experiments complied with French regulations on animal experimentation. We are grateful to the Nouvelle-Aquitaine Regional Agency of the Environment, Development and Housing for the official capture authorizations (DREAL/2019D/2323).

References

Albayrak, T., Mor, F., 2011. Comparative tissue distribution of heavy metals in house sparrow (*Passer domesticus*, Aves) in polluted and reference sites in Turkey. Bull. Environ. Contam. Toxicol. 87, 457–462.
Arnold, G.W., 1983. The influence of ditch and hedgerow structure, length of hedgerows, and area of woodland and garden on bird numbers on farmland. J. Appl. Ecol. 20 (3), 731–750.
Assandri, G., Morganti, M., Bogliani, G., Pulido, F., 2017. The value of abandoned olive groves for blackcaps (*Sylvia atricapilla*) in a Mediterranean agroecosystem: a year-round telemetry study. Eur. J. Wildl. Res. 63, 26.
Baeta, R., Belisle, M., Garant, D., 2012. Agricultural intensification exacerbates female-biased primary brood sex-ratio in tree swallows. Landsc. Ecol. 27, 1395–1405.
Batary, P., Matthiesen, T., Tscharntke, T., 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. Biol. Conserv. 143, 2020–2027.
Becker, P.H., 2003. Chapter 19 Biomonitoring with birds. Trace Met. Other Contam. Environ. 6, 677–736.
Birds of the World, 2022. In: Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. (Eds.), Cornell Laboratory of Ornithology. Ithaca, NY, USA. ⟨https://birdsoftheworld.org/bow/home⟩.
Borges, S.L., Vyas, N.B., Christman, M.C., 2014. The influence of study species selection on estimates of pesticide exposure in free-ranging birds. Environ. Manag. 53, 416–428.
Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018. Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. Sci. Total Environ. 627, 822–834.
Carere, C., van Oers, K., 2004. Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. Physiol. Behav. 82, 905–912.
Chamberlain, D.E., Joys, A., Johnson, P.J., Norton, L., Feber, R.E., Fuller, R.J., 2010. Does organic farming benefit farmland birds in winter? Biol. Lett. 6, 82–84.
Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771–788. https://doi.org/10.1046/j.1365-2664.2000.00548.x.
Chiron, F., Chargé, R., Julliard, R., Jiguet, F., Muratet, A., 2014. Pesticide doses, landscape structure and their relative effects on farmland birds. Agric. Ecosyst. Environ. 185, 153–160.
Clotfelter, E.D., Bell, A.M., Levering, K.R., 2004. The role of animal behaviour in the study of endocrine-disrupting chemicals. Anim. Behav. 68, 665–676.
Cordi, B., Fossi, C., Depledge, M., 1997. Temporal biomarker responses in wild passerine birds exposed to pesticide spray drift. Environ. Toxicol. Chem. 16 (10), 2118–2124.
Davis, B.N.K., Brown, M.J., Frost, A.J., Yates, T.J., Plant, R.A., 1994. The effects of hedges on spray deposition and on the biological impact of pesticide spray drift. Ecotoxicol. Environ. Saf. 27, 281–293.
Dell'Omo, G., 2002. Behavioral Ecotoxicology. Wiley, New York.
Edelaar, P., Serrano, D., Carrete, M., Blas, J., Potti, J., Tella, J.L., 2012. Tonic immobility is a measure of boldness toward predators: an application of Bayesian structural equation modelling. Behav. Ecol. 23, 619–626.
Farage-Elawar, M., Francis, B.M., 1988. Effects of multiple dosing of fenthion, fenitrothion, and desbromoleptophos in young chicks. J. Toxicol. Environ. Health 23, 217–228.
Fluetsch, K.M., Sparling, D.W., 1991. Avian nesting success and diversity in conventionally and organically managed apple orchards. Environ. Toxicol. Chem. 13 (10), 1651–1659.
Foudoulakis, M., Balaskas, C., Csato, A., Szentes, C., Arapis, G., 2013. Japanese quail acute exposure to methamidophos: experimental design, lethal, sub-lethal effects and cholinesterase biochemical and histochemical expression. Sci. Total Environ. 450–451, 334–347.
Fucikova, E., Drent, P.J., Smits, N., van Oers, K., 2009. Handling stress as a measurement of personality in great tit nestlings (*Parus major*). Ethology 115, 366–374.
Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105.
Gibbons, D.W., Amar, A., Anderson, G.Q.A., Bolton, M., Bradbury, R.B., Eaton, M.A., Evans, A.D., Grant, M.C., Gregory, R.D., Hilton, G.M., Hirons, G.J.M., Hughes, J., Johnstone, I., Newbery, P., Peach, W.J., Ratcliffe, N., Smith, K.W., Summers, R.W., Walton, P., Wilson, J.D., 2007. The predation of wild birds in the UK: a review of its conservation impact and management. RSPB Research Report no 23. RSPB, Sandy.
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 (4), 792–803.
Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.Y., Iverson, A.L., Batary, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. R. Soc. B Biol. Sci. 281, 20141358.
Green, R.E., Osborne, P.E., Sears, E.J., 1994. The distribution of passerine birds in hedgerows during the breeding season in relation to characteristics of the hedgerow and adjacent farmland. J. Appl. Ecol. 31, 677–692.
Gregory, R.D., Skorpilovac, J., Vorisek, P., Butler, S., 2019. An analysis of trends, uncertainty and species selection shows contrasting T trends of widespread forest and farmland birds in Europe. Ecol. Indic. 103, 676–687.
Grue, C.E., Shipley, B.K., 1981. Interpreting population estimates of birds following pesticide applications – behavior of male starlings exposed to an organophosphate pesticide. Stud. Avian Biol. 6, 292–296.
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.
Grue, C.E., Shipley, B.K., 1984. Sensitivity of nestling and adult starlings to dicrotophos, and organophosphate pesticide. Environ. Res. 35, 454–465.
Grue, C.E., Powell, G.V.N., McChesney, M.J., 1982. Care of nestlings by wild female starlings exposed to an organophosphate pesticide. J. Appl. Ecol. 19, 327–335.
Halupka, K., Borowiec, M., Karczewska, A., Kunka, A., Pietrowiak, J., 2002. Habitat requirements of Whitethroats *Sylvia communis* breeding in an alluvial plain. Bird. Stud. 49, 297–299.
Hart, A.D.M., 1993. Relationship between behavior and the inhibition of acetylcholinesterase in birds exposed to organophosporus pesticides. Environ. Toxicol. Chem. 12, 321–336.
Hellou, J., Cheeseman, K., Desnoyers, E., Johnston, D., Jouvenelle, M.L., Leonard, J., Robertson, S., Walker, P., 2008. A non-lethal chemically based approach to investigate the quality of harbour sediments. Sci. Total. Environ. 389, 178–187.
Hellou, J., 2011. Behavioural ecotoxicology, an "early warning" signal to assess environmental quality. Environ. Sci. Pollut. Res. 18, 1–11.
Henderson, I.G., Hart, P.J.B., 1993. Provisioning, parental investment and reproductive success in jackdaws *Corvus monedula*. Ornis Scand. 24, 142–148.
Hole, D.G., Whittingham, M.J., Bradbury, R.B., Anderson, G.Q.A., Lee, P.L.M., Wilson, J. D., Krebs, J.R., 2002. Widespread local house-sparrow extinctions – agricultural intensification is blamed for the plummeting populations of these birds. Nature 418, 931–932.
Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A., 2005. Does organic farming benefit biodiversity? Biol. Cons. 122 (1), 113–130. https://doi.org/10.1016/j.biocon.2004.07.018.
Humphreys, R.K., Ruxton, G.D., 2008. A review of thanatosis (death feigning) as an anti-predator behaviour. Behav. Ecol. Sociobiol. 72 (2), 22.
Kjaer, C., Bruus, M., Bossi, R., Lofstrom, P., Andersen, H.V., Nuyttens, D., Larsen, S.E., 2014. Pesticide drift deposition in hedgerows from multiple spray swaths. J. Pestic. Sci. 39, 14–21.
Laiolo, P., Banda, E., Lemus, J.A., Aguirre, J.I., Blanco, G., 2009. Behaviour and stress response during capture and handling of the red-billed chough *Pyrrhocorax pyrrhocorax* (Aves: Corvidae). Biol. J. Linn. Soc. 96, 846–855.
Lazzaro, L., Otto, S., Zanin, G., 2008. Role of hedgerows in intercepting spray drift: Evaluation and modelling of the effects. Agric. Ecosyst. Environ. 123, 317–327.
Longey, M., Cilgi, T., Jepson, P.C., Sotherton, N.W., 1997. Measurements of pesticide spray drift deposition into field boundaries and hedgerows: 1. Summer applications. Environ. Toxicol. Chem. 16 (2), 165–172.
Longley, M., Sotherton, N.W., 1997. Measurements of pesticide spray drift deposition into field boundaries and hedgerows: 2. Autumn applications. Environ. Toxicol. Chem. 16 (2), 173–178.
Lopez-Antia, A., Ortiz-Santaliestra, M.E., Mougeot, F., Mateo, R., 2015. Imidacloprid-treated seed ingestion has lethal effect on adult partridges and reduces both breeding investment and offspring immunity. Environ. Res. 136, 97–107.
Lushchak, V.I., Matviishyn, T.M., Husak, V.V., Storey, J.M., Storey, K.B., 2018. Pesticide toxicity: a mechanistic approach. EXCLI J. 7, 1101–1136.
MacDonald, D.W., Johnson, P.J., 1995. The relationship between bird distribution and the botanical and structural characteristics of hedges. J. Appl. Ecol. 32, 492–505.
Markó, G., Azcarate, M., Hegyi, G., Herceg, G., Laczi, M., Nagy, G., Senar, J.C., Torok, J., Garamszegi, L.Z., 2013. Behavioural responses to handling stress in the Great Tit: within-individual consistency and the effect of age, sex and body condition. Ornis Hung. 21 (1), 12–25.
McKenzie, A.J., Whittingham, M.J., 2009. Why are birds more abundant on organic farms? J. Food Agric. Environ. 7, 807–814.
Millot, F., Decors, A., Mastain, O., Quintaine, T., Berny, P., Vey, D., Lasseur, R., Bro, E., 2017. Field evidence of bird poisonings by imidacloprid-treated seeds: a review of

incidents reported by the French SAGIR network from 1995 to 2014. Environ. Sci. Pollut. Res. 24, 5469–5485.
Mineau, P., Whiteside, M., 2013. Pesticide acute toxicity is a better correlate of U.S. grassland bird declines than agricultural intensification. PLoS ONE 8 (2), e57457.
Mitra, A., Chatterjee, C., Mandal, F.B., 2011. Synthetic chemical pesticides and their effects on birds. Res. J. Environ. Toxicol. 5, 81–96.
Miyatake, T., Nakayama, S., Nishi, Y., Nakajima, S., 2009. Tonically immobilized selfish prey can survive by sacrificing others. Proc. R. Soc. B 276, 2763–2767.
Mondelaers, K., Aertsens, J., Van Huylenbroeck, G., 2009. A meta-analysis of the differences in environmental impacts between organic and conventional farming. Br. Food J. 111, 1098–1119.
Moreau, J., Monceau, K., Crépin, M., Derouin-Tochon, F., Mondet, C., Frainkin, M., Teixeira, M., Bretagnolle, V., 2021. Feeding partridges with organic or conventional grain triggers cascading effects in life-history traits. Environ. Poll 278, 116851.
Moskat, C., Baldi, A., Waliczky, Z., 1993. Habitat selection of breeding and migrating icterine warblers *Hippolais icterina*: a multivariate study. Ecography 16, 137–142.
Naef-Daenzer, B., 1994. Radiotracking of great and blue tits: new tools to assess territoriality, home-range use and resource distribution. Ardea 82, 335–347.
Naguib, M., Altenkamp, R., Griessmann, B., 2001. Nightingales in space: song and extra-territorial forays of radio-tagged songbirds. J. Ornithol. 142, 306–312.
Newton, I., 1998. Population Limitation in Birds. Academic Press, London.
Odum, E.P., 1971. Fundamentals of Ecology, Third ed.,. W.B. Saunder, Philadelphia.
Peakall, D.B., 1985. Behavioral responses of birds to pesticides and other contaminants. Residue Rev. 96, 45–77.
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, 1883e1891.
R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
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 (8), e02160.
Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318.
Reganold, J.P., Watcher, J.M., 2016. Organic agriculture in the twenty-first century. Nat. Plants 2, 15221.
Robertson, G.P., Gross, K.L., Hamilton, S.K., Landis, D.A., Schmidt, T.M., Snapp, S.S., Swinton, S.M., 2014. Farming for ecosystem services: an ecological approach to production agriculture. Bioscience 2004, 61–65.
Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 3, 157–176.
Sandhu, H.S., Wratten, S.D., Cullen, R., 2010. Organic agriculture and ecosystem services. Environ. Sci. Policy 13 (1), 1–7. https://doi.org/10.1016/j.envsci.2009.11.002.
Santos, C.S.A., Monteiro, M.S., Soares, A.M.V.M., Loureiro, S., 2016. Brain cholinesterase reactivation as a marker of exposure to anticholinesterase pesticides: a case study in a population of yellow-legged gull *Larus michahellis* (Naumann, 1840) along the northern coast of Portugal. Environ. Sci. Pollut. Res. 23, 266–272.
Schielzeth, H., Nakagawa, S., 2013. Nested by design: model fitting and interpretation in a mixed model era. Method Ecol. Evol. 4, 14–24.
Seufert, V., Ramankutty, N., Foley, J.A., 2012. Comparing the yields of organic and conventional agriculture. Nature 485, 229–232.
Sinha, S.A., Lakhani, K.H., Davis, B.N.K., 1990. Studies on the toxicity of insecticidal drift to the first instar larvae of the large white butterfly *Pieris brassicae* (Lepidoptera: Pieridae). Ann. Appl. Biol. 116, 27–41.
Smith, H.G., Danhardt, J., Lindstrom, A., Rundlof, M., 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. Oecologia 162, 1071–1079.
Stanton, R.L., Morissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agric. Ecosyst. Environ. 254, 244–254.
Stevens, D.K., Donald, P.F., Evans, A.D., Buckingham, D.L., Evans, J., 2002. Territory distribution and foraging patterns of cirl buntings (*Emberiza cirlus*) breeding in the UK. Biol. Cons. 107, 307–313.
Stoate, C., Szczur, J., 2001. Whitethroat *Sylvia communis* and Yellowhammer *Emberiza citrinella* nesting success and breeding distribution in relation to field boundary vegetation. Bird. Stud. 48, 229–235.
Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe - a review. J. Environ. Manag. 91 (1), 22–46. https://doi.org/10.1016/j.jenvman.2009.07.005.
Story, P., Cox, M., 2001. Review of the effects of organophosphorus and carbamate insecticides on vertebrates. Are there implications for locust management in Australia? Wildl. Res. 28, 179–193.
Thompson, R.K.R., Foltin, R.W., Boylan, R.J., Sweet, A., Graves, C.A., Lowitz, C.E., 1981. Tonic immobility in Japanese quail can reduce the probability of sustained attach by cats. Anim. Learn. Behav. 9, 145–149.
Toppari, J., Larsen, J.C., Christiansen, P., Giwercman, A., Grandjean, P., Guillette Jr, L.J., Jegou, B., Jensen, T.K., Jouannet, P., Keiding, N., Leffers, H., McLachlan, J.A., Meyer, O., Muller, J., Rajpert-De Meyts, E., Scheike, T., Sharpe, R., Sumpter, J., Skakkebaek, N.E., 1996. Male reproductive health and environmental xenoestrogens. Environ. Health Perspect. 104, 741e803.
Torné-Noguera, A., Pagani-Núñez, E., Senar, J.C., 2014. Great tit (*Parus major*) breath rate in response to handling stress: urban and forest birds differ. J. Ornithol. 155, 315–318.
Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. J. Appl. Ecol. 51 (3), 746–755. https://doi.org/10.1111/1365-2664.12219.
Walker, C.H., 2003. Neurotoxic pesticides and behavioural effects upon birds. Ecotoxicology 12, 307–316.
Wiegand, C., 2019. Strategies and consequences of indigenous and invasive freshwater mussels living in cyanobacterial and anthropogenic impacted waters. In: Groos, E., Garic, J. (Eds.), Ecotoxicology New Challenges and New Approaches. Elsevier, Oxford, pp. 93–128.
Wintermantel, D., Odoux, J.F., Chadoeuf, J., Bretagnolle, V., 2019. Organic farming positively affects honeybee colonies in a flower-poor period in agricultural landscapes. J. Appl. Ecol. 56 (8), 1960–1969.
Zhang, F., Chen, X., Vitousek, P., 2013. Chinese agriculture: an experiment for the world. Nature 497, 33–35.