



Population declines of a widespread amphibian in agricultural landscapes

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Abstract

Modern agricultural practices are suspected to play a major role in the ongoing erosion of biodiversity. In order to assess whether this biodiversity loss is linked to past habitat modifications (e.g. land consolidation) or to current consequences of modern agriculture (e.g. use of agrochemicals), it remains essential to monitor species that have persisted in agricultural landscapes to date. In this study, we assessed the presence, abundance and recent population trends of one such species, the spined toad (*Bufo spinosus*) along a gradient of habitats from preserved (forests) to highly agricultural sites in rural Western France. Our results showed that both presence and abundance of spined toads were markedly lower in reproductive ponds surrounded by intensive agriculture. The most salient result of our study is the ongoing decline of this species in farmland habitats. Indeed, this result suggests that unknown factors are currently affecting a widespread terrestrial amphibian previously thought to persist in agricultural landscapes. These factors have recently induced strong population declines over the course of a few years. Future investigations are required to identify these factors at a time when anthropogenic activities are currently leading to unprecedented rates of biodiversity loss.

Keywords Abundance · Agroecosystems · *Bufo spinosus* · Biodiversity · Presence

Introduction

Anthropogenic activities are currently leading to unprecedented rates of biodiversity loss (Chapin III et al. 2000; Myers and Knoll 2001; Brooks et al. 2002). Indeed, human activities are now recognized to be responsible of climate change (Vitousek 1994; Steffen et al. 2007), major shifts in land use (Klein Goldewijk and Ramankutty 2004; Young et al. 2005) and environmental contamination (Rudel et al. 2009; Saleh and Aglan 2018), all of which can individually and/or interactively affect wildlife (de Brito Rodrigues et al. 2019; Trudeau et al. 2020; Wagner 2020; Gunstone et al. 2021).

Among the various sources of anthropogenic disturbances to natural ecosystems, modern agricultural practices are suspected to play a major role in the ongoing

erosion of biodiversity for several reasons (Altieri 1999; Dudley and Alexander 2017). First, modern agriculture is responsible for the alteration and the reduction of natural habitats and landscape homogenization (Fahrig 2003) as compared to ancestral agricultural practices. For instance, in Europe, changes in land-use politics that occurred post World War II (WWII) have induced a large-scale land consolidation (Benton et al. 2003; Tschardt et al. 2005). The ancestral rural matrix of small plots and meadows bordered by a dense network of hedges has been homogenized to extended fields hosting monocultures (Benton et al. 2003; Tschardt et al. 2005). Concomitantly, this revolution has provoked a reduction in the spatial connectivity between patches of favourable habitats among the agricultural landscape, limiting therefore the persistence of wildlife (Benton et al. 2003). Second, detrimental effects of modern agriculture are linked to the massive use of chemical substances that are used to increase agricultural yields (Geiger et al. 2010). Many pesticides are used to control weeds, insect and fungi in crops, but they have been suspected or shown to detrimentally impact non-target species (Hasenbein et al. 2017; de Brito Rodrigues et al. 2019), either directly

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through their toxic sublethal or lethal effects (Relyea 2004; Slaninova et al. 2009; Williams et al. 2015) or indirectly through alterations of ecosystem functioning (e.g. reduced food availability, Hart et al. 2006; Wagner 2020).

As a result, agricultural practices are expected to detrimentally affect wildlife at different temporal scales. Indeed, at least in Western Europe, most of the landscape changes linked to land consolidation have occurred after WWII (Antrop 2000) and the subsequent habitat homogenization and fragmentation have been mostly achieved by the mid-1970s or early 1980s (Griffin 1979; Skole and Tucker 1993; Harper et al. 2007; Rudel et al. 2009). As a consequence, it is expected that the effects of such processes on the persistence of wild populations have already been acting for several decades (Debinski and Holt 2000; Fuller et al. 2015). In contrast, the temporal scale of the consequences of agrochemical use on wildlife is much more complex to assess. Indeed, although the reliance on chemical inputs has progressively increased with the development of modern agriculture, the type (fertilizers *versus* pesticides), the quantity and the chemical composition (active compounds) of agrochemicals have constantly changed over time, most notably to circumvent issues linked to the adaptive resistance of pests and, more recently, in response to growing societal concerns (Howden et al. 2007; Bhandari 2014; Prashar and Shah 2016; Hawkins et al. 2019; Sharma et al. 2019). Taken together, these ideas suggest that the consequences of agriculture on wildlife linked to the reduction of natural habitats should have already occurred and that impoverished biodiversity in agricultural areas should be a ghost of past landscape changes (Harding et al. 1998; Cousins 2009; Surasinghe and Baldwin 2014). In contrast, current negative trends of wildlife population should be related to the consequences of other factors such as agrochemicals either directly or due to their interactions with the constraints of habitat structure described above (Potts et al. 2010; Oliver and Morecroft 2014) or current climatic modifications either directly or due to their interactions with habitat structure and/or environmental contamination (De Frenne et al. 2019; De Lombaerde et al. 2022). As a consequence, it remains critical to continue to monitor the populations of species that have persisted in agricultural landscapes.

In this study, we assessed the presence, abundance and recent population trends of one such species, the spined toad (*Bufo spinosus*) in rural Western France. The spined toad is a terrestrial amphibian that has been shown to persist in agricultural habitats (Guillot et al. 2016, but see Meek 2022) when reproductive ponds are still present in the environment. As most terrestrial amphibians, this

species has a biphasic life cycle with an extensive use of terrestrial habitats during most of the year and a short breeding season in ponds where mating occurs and eggs and tadpoles develop (Reading 1998; Semlitsch 2008; Kelleher et al. 2018). In order to describe the effects of agriculture on the persistence of this species, we used three complementary approaches. First, in 2021 and 2022, we assessed the presence of reproductive individuals in ponds located along a gradient of habitats from preserved (forests) to highly agricultural sites. Second, on a representative subsample of the same sites and during the same years, we quantified abundances of reproductive individuals (males and females) during the whole reproductive season. Finally, on a few sites that have been monitored for other purposes since 2015, we used capture data of reproductive males as an index of abundances to describe temporal trends.

Material and methods

Study species

Spined toad (*Bufo spinosus*) is one of the most common terrestrial amphibians in Western Europe. This species can live in a wide variety of habitats and has been shown to persist in agricultural areas (Guillot et al. 2016). Juveniles and adults are terrestrial most of the year, but reproduce in aquatic sites (ponds) where eggs and larvae develop during 2 to 3 months (Reading and Clarke 1983; Reading 1998; Kelleher et al. 2018). At the beginning of the reproductive season, toads migrate to breeding sites where males can remain for several weeks, while females occur shortly for mating and egg-laying (Reading and Clarke 1983; Reading 1991, 1998).

Presence, abundance and recent population trends

First, in 2021 and 2022, we assessed the presence of reproductive toads in 23 ponds that were similar in terms of size and depth (Appendix 1, Appendix 2). All these sites were situated nearby the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS; coordinates 46.1475819, -0.4254604; see site 2 in Appendix 2). These sites were monitored during 2 to 3 nights (separated by 2 to 4 days) during the peak of toad abundance at their aquatic breeding sites. These peaks of toad abundance were based on our abundance surveys (see below) as in our study area, the reproductive phenology of study sites is simultaneous. During these surveys, ponds and their surroundings were monitored at night (between 9 pm and 1

am) with headlamps to locate individuals. All surveys were conducted by the same team in order to avoid observers' effects. We recorded the presence (1 for presence and 0 for absence) of breeding individuals and whether these individuals were males (1 for presence and 0 for absence) or females (1 for presence and 0 for absence) as the sexual dimorphism (females being obviously larger than males) in this species allows straightforward sexing without capture (Hemelaar 1988).

Second, in 2021 and 2022, we assessed the abundance of reproductive toads in 8 sites from the ones surveyed for toad presence (Appendix 1, Appendix 2). These sites were monitored three times a week (Monday, Wednesday and Friday) from late January (25th in 2021 and 31st in 2022) before the arrival of the first reproductive individuals, until the departure of the last reproductive individuals (April 9 in 2021 and April 11 in 2022). During these surveys, the ponds and their surroundings were monitored at night (between 9 pm and 1 am) with headlamps and the number of males and females sighted was counted. From these nightly count data, we extracted the maximum number of individuals counted during a single night (total, males or females) and the mean number of individuals per night during the whole breeding season for each site (total, males or females). Such monitoring could not be carried out on all the 23 sites for logistical reasons. The 8 sites were selected because they represent the variety of agricultural landscapes that could be found in the area (Appendix 1, Appendix 2).

Finally, we used data collected for other studies to assess recent population trends in 4 sites situated in agricultural settings and 2 sites situated in preserved habitats (Appendix 1, Appendix 2). On these sites, only males were monitored (Guillot et al. 2016; Brischoux et al. 2018, 2021; Brischoux and Cheron 2019; Renoirt et al. 2021a; unpublished data). Since 2015, we aimed at capturing 30 to 40 individuals per study site. Although such sample sizes were readily obtained at agricultural sites during a single night during the reproductive peak at the beginning of our projects, it became increasingly difficult to obtain these numbers during the subsequent years in those given sites (see "Results" section). Importantly, this was the reason why we included forest sites in subsequent years. This also explains why forest sites were monitored posteriorly than initial (agricultural) sites included in these other studies. We used these capture data (number of captured males during a single night situated around the peak of reproduction) in order to monitor a broad proxy of abundances across years. Although we acknowledge that this dataset has not been designed to thoroughly monitor toad abundances, we emphasize that the trends in the number of captured individuals across years should describe, at least in a qualitative way, the recent population trends in specific sites.

Habitat classification

The terrestrial part of the life cycle of toads occurs usually within 1 km from the breeding ponds (Kovar et al. 2009; Janin et al. 2011; Guillot et al. 2016). As a consequence, from aerial pictures of each study site (GoogleEarth), we drew buffers with a radius of 1 km, corresponding to the potential distance travelled by an individual to reach a breeding site (Kovar et al. 2009; Janin et al. 2011; Guillot et al. 2016). We extracted the surface area of the main habitat types surrounding each study site: forests and woods, hedges, agricultural fields, meadows and buildings (small villages) using QGIS (3.22). We used the PC1 value from a principal component analysis (PCA) of these five variables to attribute a habitat score to each site. The PC1 of the sites for which we assessed toad presence accounted for 51.9% of the total variance and was positively correlated with agricultural fields ($r=0.82$) and negatively correlated with forest ($r=-0.91$). The PC1 of the sites for which we assessed toad abundances accounted for 65.0% of the total variance and was positively correlated with agricultural fields ($r=0.90$) and negatively correlated with forest ($r=-0.96$). For the sites used for assessing recent population trends, we used habitat categories (agriculture *versus* forest, see Renoirt et al. 2021a for details).

Statistical analyses

We used Generalized Linear Mixed Models (GLMM) with a binomial distribution to assess the influence of the habitat score on the presence (1) or absence (0) of toads (overall, males or females). Some sites were monitored 2 years of our study ($N=10$), while others were monitored once ($N=13$). Because including the year and site identity as random factors over-parametrized the models, both years were analyzed separately.

We used Generalized Linear Mixed Models (GLMM) to assess the influence of habitat score on toad abundance (total, maximum and mean number) for all individuals and males or females, separately, with the year added as a fixed factor. All count data passed the normality check.

Finally, we used GLMM to analyze our proxy of recent population trends with the number of captured males as a response variable and year and habitat category (agriculture *versus* forest) as predictors; we used site identity as a random factor in our models (the number of sites varied according to year).

Results

Toad presence

Models including overall toad presence were identical as those including the presence of males solely, with only 4

sites (all agricultural with positive PC1 scores) for which males were present but females absent.

We found a significant negative effect of the habitat score on the presence of both males (2021: $X^2 = 5.557$, $df = 1$, $p = 0.018$; 2022: $X^2 = 4.147$, $df = 1$, $p = 0.041$) and females (2021: $X^2 = 5.256$, $df = 1$, $p = 0.022$; 2022: $X^2 = 6.546$, $df = 1$, $p = 0.01$), with presence decreasing with increasing agriculture (Fig. 1).

Toad abundance

We found a significant negative effect of the habitat score on the maximum number of individuals (estimate = -16.88 , $SE = 3.22$, $Wald = 27.55$, $p < 0.001$), the maximum number of males (estimate = -14.41 , $SE = 3.18$, $Wald = 20.52$, $p < 0.001$, Fig. 1) and the maximum number of females (estimate = -2.50 , $SE = 0.47$, $Wald = 28.15$, $p < 0.001$,

Fig. 1). These numbers varied between years in females (estimate = -2.35 , $SE = 0.93$, $Wald = 6.41$, $p = 0.01$) but not in males ($p = 0.17$).

Finally, we found a significant negative effect of the habitat score on the mean number of individuals (estimate = -4.51 , $SE = 1.34$, $Wald = 11.32$, $p < 0.001$), the mean number of males (estimate = -4.19 , $SE = 1.26$, $Wald = 10.99$, $p < 0.001$) and the mean number of females (estimate = -0.54 , $SE = 0.24$, $Wald = 5.05$, $p = 0.024$). These numbers did not vary between years (all $p > 0.25$).

Indices of population trends

We found a significant interaction between the habitat type and the number of males captured between years (estimate = -0.11 , $SE = 0.04$, $Wald = 7.55$, $p = 0.006$). The

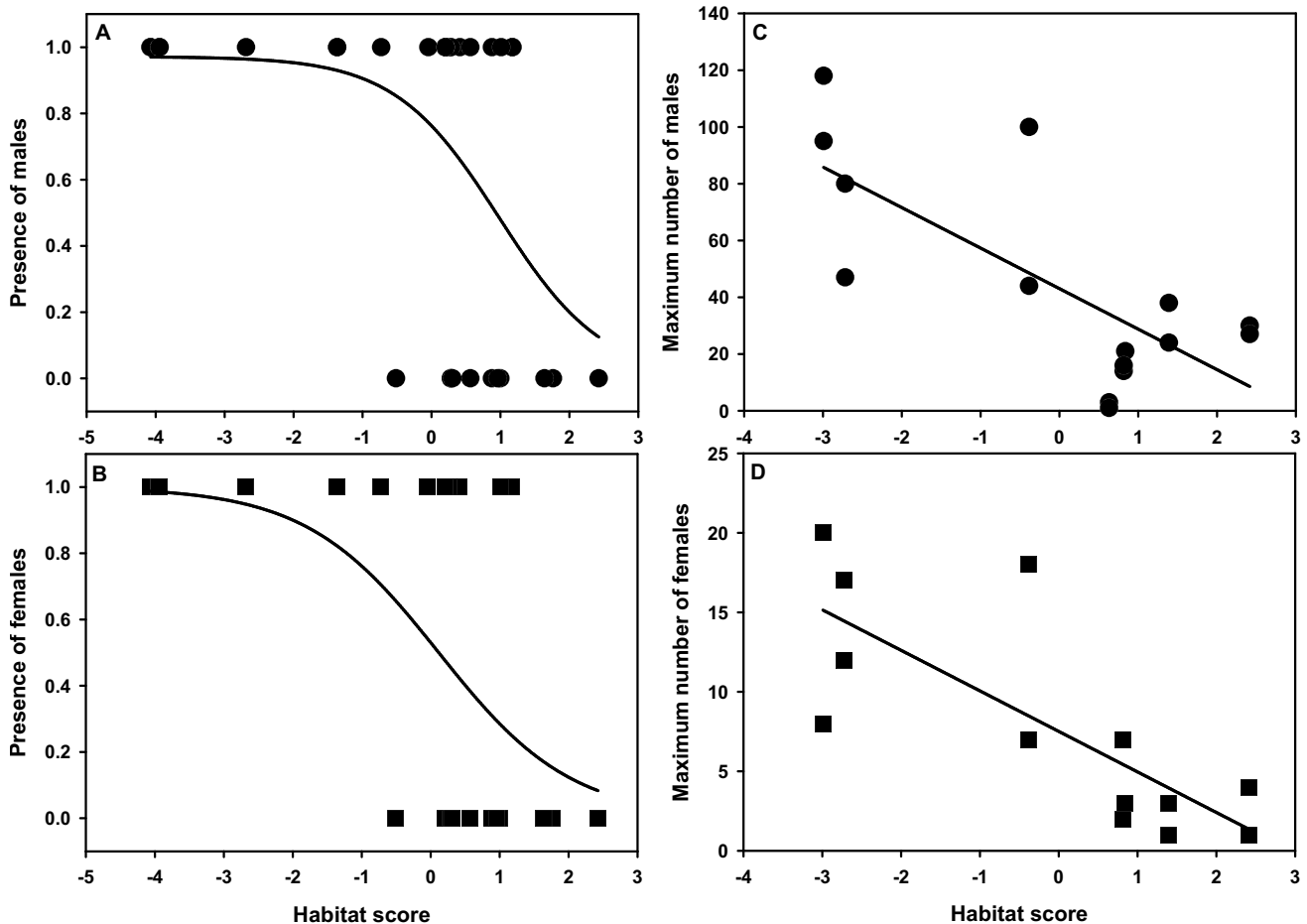


Fig. 1 Left panels: presence (1) and absence (0) of males (A) and females (B) spined toads during two years (2021 and 2022) in 23 breeding sites situated along a gradient of habitats from preserved sites (negative scores) to intensive agriculture (positive scores). Right panels: abundances (maximum number of individuals counted during

a single night during the breeding peak) of male (C) and female (D) spined toads during 2 years (2021 and 2022) in 8 sites situated along a gradient of habitats from preserved sites (negative scores) to intensive agriculture (positive scores). All sites were not monitored during all years and details can be found in Appendix 1

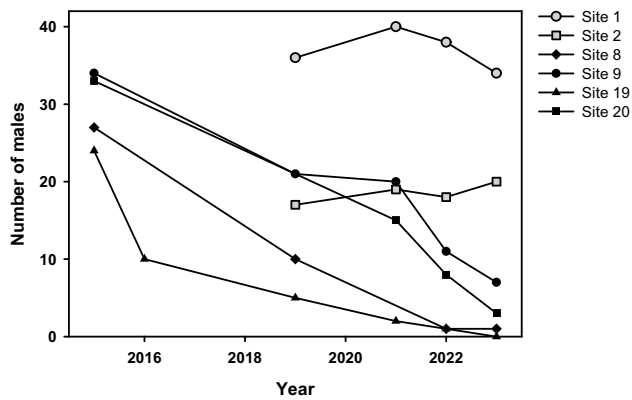


Fig. 2 Number of males captured during the course of other studies on spined toads (see “Material and methods” section for details). We used these capture data (number of captured males during a single night situated around the peak of reproduction) in order to monitor a broad proxy of abundances across years. Grey symbols are used for sites surrounded by forest, while black symbols represent sites surrounded by intensive agriculture. Site numbers refer to those indicated in Appendix 1 and Appendix 2. All sites were not monitored during all years and details can be found in Appendix 1

number of captured males in agricultural sites decreased strongly between years ($F_{1,17} = 32.88$, $p < 0.0001$, Fig. 2), while the number of captured individuals from forest sites remained steady ($F_{1,6} = 0.003$, $p = 0.96$, Fig. 2).

Discussion

Overall, we found that both presence and abundances of a widespread terrestrial amphibian were markedly lower in reproductive ponds surrounded by intensive agriculture. The most salient, yet worrisome, result of our study is the apparent ongoing decline of this species in such farmland habitats. Indeed, this result may suggest that unknown factors are currently affecting amphibian populations and have recently induced strong population decreases over the course of a few years.

Although spined toads have been earlier shown to persist in agricultural habitats (Guillot et al. 2016, but see Meek 2022), our results show that, as for many other farmland species, agriculture negatively influenced the presence of reproductive individuals at breeding sites (Keller and Waller 2002; Williams et al. 2015; Tucker et al. 2018). Importantly, although such effect

was found in both males and females, in 4 of the study sites (25% of the sites with a positive habitat score and thus characterized by intensive agriculture), we did not observe any reproductive female. Such result dovetails relatively well with previous observations made on the same species and which have highlighted the lack of reproductive females and subsequent lack of eggs and developing larvae at some sites situated within agricultural landscapes (Renoirt et al. 2021b). Although the putative sex-specific mechanisms presumably affecting females more than males in agricultural habitats remain unknown, the lack of reproductive females at some breeding ponds is likely to jeopardize population persistence in agricultural habitats.

In sites where spined toads were present for reproduction, abundances of both males and females were strongly reduced in agricultural habitats. Several hypotheses can explain this result. First, for growing juveniles and adult individuals, agricultural habitats may be characterized by lower carrying capacity, both in terms of terrestrial microhabitat availability (buffered and concealed retreat sites to evade predation and decrease thermal and hydric constraints, Tuomainen and Candolin 2011; Oliver and Morecroft 2014) during the terrestrial part of the life cycle and/or in terms of trophic resources availability (decreased abundances of prey, Hart et al. 2006; Wagner 2020). Such constraints would inevitably increase intraspecific competition for these limiting resources and thus decrease abundances of toads in agricultural habitats. Second, for developing eggs and larvae, the quality of aquatic breeding sites may be lower in agricultural landscapes. For instance, the presence of environmental contaminants in such sites (Bókony et al. 2018; Leeb et al. 2020) may well negatively influence the survival of embryos and larvae (Bókony et al. 2018; Cheron et al. 2022a; Cheron et al. 2022b, but see Loman and Lardner 2006) and/or the quality of metamorphic individuals (Boone et al. 2005). We emphasize that these hypotheses are not mutually exclusive and it is likely that reduced abundances of spined toads in agricultural landscapes may result from complex interactions between various habitat-specific constraints. Deciphering the relative role of these different constraints will require future investigations.

Importantly, our results on indices of recent population trends may give further insights into these processes. Indeed, although we emphasize that these data were not designed to thoroughly assess population abundances over

time and thus need to be handled with caution (Pechmann et al. 1991, Reid et al. 2013), the trends we highlighted seem to indicate very recent population decreases in agricultural habitats as compared with preserved forest habitats. In line with the ideas developed above (see “Introduction” section), such result may indicate that the structural constraints of agricultural habitats (linked to previous landscape homogenization and fragmentation) may not be the primary driver of the current decreased presence and abundances of spined toads. Indeed, based on examination of aerial photographs (GoogleEarth) and on our knowledge of the study area, no structural changes have occurred since the beginning of our surveys (e.g. land consolidation). In combination with recent population trend, such information suggests that the decline we are currently witnessing may be linked either indirectly to a concomitant decline in prey abundances (Hart et al. 2006; Wagner 2020) and/or to other factors affecting directly spined toads. In this respect, the potential role of environmental contamination seems a likely candidate knowing the detrimental effects of agrochemicals on wildlife (Kendall and Akerman 1992) and more specifically on amphibians (Baker et al. 2013; Trudeau et al. 2020). Alternatively, but not exclusively, it is also plausible that recent changes in climatic conditions, which apply more strongly in open habitats than under forest canopies (De Frenne et al. 2019; De Lombaerde et al. 2022), affected amphibian populations in agricultural areas (e.g. due to increased temperature and reduced precipitation, Lawler et al. 2010). Whatever the underlying mechanisms, the putative sex-specific mechanisms presumably affecting females more than males (see above, Renoirt et al. 2021b) are required to be deciphered.

Overall, our study potentially highlights a worrying recent decline in the populations of a widespread terrestrial amphibian previously thought to persist in agricultural landscape. We emphasize that unknown factors are currently affecting these populations very rapidly. Future investigations are required to identify these factors at a time when anthropogenic activities are currently leading to unprecedented rates of biodiversity loss.

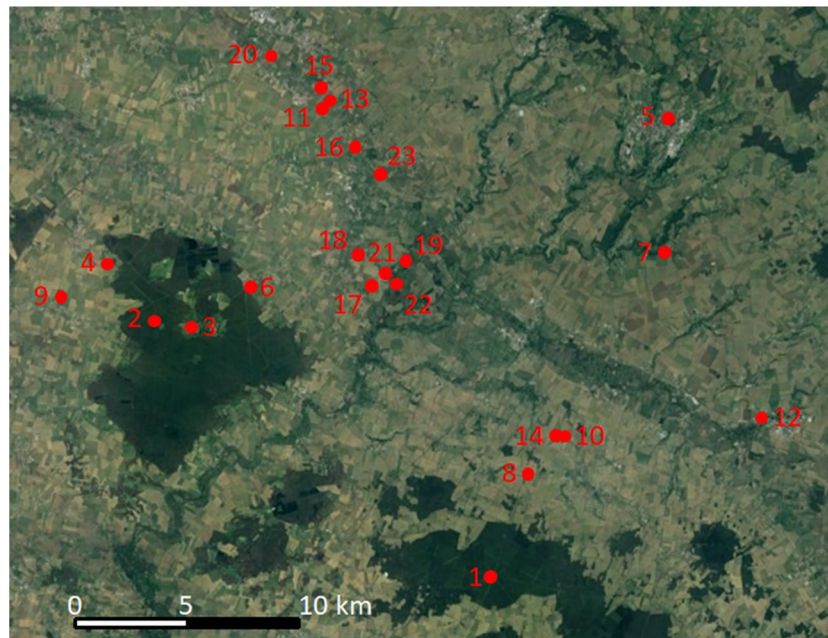
Appendix

Appendix 1. Description of the sampling details for our three complementary approaches (presence, abundance and index of population trends using capture data). Sites are numbered (Site#) according to ascending habitat score (Habitat score) from the PC1 values of a principal component analysis (see “Material and methods” section for details). Years monitored are indicated for each parameter (Presence, Abundance, Captures) used in our analyses

Site#	Habitat score	Presence	Abundance	Captures
1	-4.07	2021–2022	2021–2022	2019, 2021–2023
2	-3.94	2021–2022	2021–2022	2019, 2021–2023
3	-2.69	2022		
4	-1.37	2021–2022	2021–2022	
5	-0.73	2022		
6	-0.51	2022		
7	-0.04	2022		
8	0.20	2021–2022	2021–2022	2015, 2019, 2021–2023
9	0.21	2021–2022	2021–2022	2015, 2019, 2021–2023
10	0.26	2021–2022	2021–2022	
11	0.28	2021–2022		
12	0.28	2022		
13	0.30	2021		
14	0.41	2021	2021	
15	0.56	2021–2022		
16	0.88	2021–2022		
17	0.96	2021		
18	1.00	2022		
19	1.01	2022		2015, 2016, 2019, 2021–2023
20	1.17	2021–2022	2021–2022	2015, 2019, 2021–2023
21	1.64	2022		
22	1.76	2022		
23	2.42	2021		

Appendix 2. Map of the study area showing each study site surveyed. Numbers correspond to the sites detailed in Appendix 1. Site #2 is the Centre d'Etudes Biologiques de Chizé

(CEBC-CNRS; coordinates 46.1475819, – 0.4254604). Background image modified from GoogleEarth



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Author contribution MR, FA and FB conceived the ideas and designed methodology; MR, MC, LJ, ST and FB collected the data; MR, FA, MC and FB analyzed the data; MR, FA and FB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Declarations

Competing interests The authors declare no competing interests.

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