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Recent changes in the reproductive success of farmland birds: conservation and management implications. The declining grey partridge *Perdix perdix* as a case study

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Several ground-nesting bird species living in European farmlands are experiencing a persistent decline. Poorer reproductive success is suspected to be the main demographic driver. We developed a model to quantify to what extent such recent change may impact the viability of their populations. We took the grey partridge *Perdix perdix*, a typical farmland species, as a well-documented case study, but the model can be adapted to other species. We built a model based on our in-depth demographic knowledge of this species and the large database compiled from our long-term population monitoring programme. We took into account environmental and demographic stochasticity as well as density-dependence processes. We investigated the impact of recent changes in reproductive success on the viability of (unharvested) populations. For this purpose, we considered two periods: 1979–2004 as 'Past' and 2005–2014 as 'Present' (we used data of subsequent years to test the model's goodness of fit). During the 'Past' period, the simulated population was increasing with a mean stochastic growth rate $\lambda_{mean} = 1.01$ (25% of decreasing trajectories), whereas $\lambda_{mean} = 0.89$ during the 'Present' period (74% of decreasing trajectories). We provide detailed results and discuss the possible environmental causes, with a focus on extreme weather events. In a further step, we used our model as a tool to investigate the impact of four hunting bag management strategies on exploited populations. The hunting bag was assumed to be an additive cause of mortality. Hunting leads to a decrease in λ_{mean} but the amplitude (from minor to substantial) depends upon the strategy and the setting-up of parameters. We deliver our model as a tool to support decision-making for sustainable population management and provide the script (ULM software) as Supplementary information.

Keywords: decline, grey partridge, hunting bag management, modelling, population viability analysis, reproductive success

A large number of avian species living in European agroecosystems have experienced a drastic decline in abundance over the past decades (Donald et al. 2006, Wretenberg et al. 2007, Comolet-Tirman et al. 2015, PECBMS 2021a). The numbers of many species, such as the grey partridge *Perdix perdix*, skylark *Alauda arvensis*, yellowhammer *Emberiza citrinella*, lapwing *Vanellus vanellus* or Eurasian curlew *Numenius arquata*, still show a persistent deterioration (BirdLife International 2017, UMS Patrinat 2020), and conservation efforts to address this deterioration are challenging. Indeed, intensively cultivated landscapes are simplified environments associated with diverse environmental pressures for terrestrial wildlife (Newbold et al. 2015), such as poor habitat conditions (Wretenberg et al. 2007, Bowler et al. 2018), pesticide use that decreases food abundance and contaminates food resources, water, soil, air and the bodies of animals (Geiger et al. 2010, Brühl et al. 2013, Hallmann et al. 2014, Bro et al. 2016, Sánchez-Bayo and Wyckhuys 2019), predation (Evans 2004, Panek 2005, Bro et al. 2013, McMahon et al. 2020), and the use of large and fast crop-harvesting machinery responsible for mortality risks and sudden large-scale changes in cover (Humbert et al. 2009). In addition to these historical pressures, extreme weather events, such as heavy rains, heat waves or droughts, are suspected to affect populations, as observed for other bird or wildlife species (Skagen and Adams 2012, Maxwell et al. 2019, Piatt et al. 2020).

In this context of an uncertain environment, the harvesting of declining populations is being questioned, especially when field evidence suggests that poorer reproductive success is the main driver of the decline of fast species, that is, species characterized by short lifespan and high fecundity (Roodbergen et al. 2012, Bro et al. 2015). There are debates about hunting of farmland species in some countries of west-

ern Europe, such as the grey partridge, Eurasian curlew or turtle dove *Streptopelia turtur*.

In this paper, the grey partridge, a typical small galliform inhabiting cereal ecosystems in Europe (Potts 2012, Bro 2016), was chosen as a case study. Grey partridge populations have been monitored for decades in several countries for hunting management purposes (Panek 2006 – Poland, Ewald et al. 2009 – UK, Bro 2016 – France). Long-term monitoring reports an ongoing population decline in Europe (BirdLife International 2015, PECBMS 2021b) and a global downward trend in its reproductive success (Panek 2005, Grubešić et al. 2006, Godin and Reitz 2019).

In this study, we use population matrix modelling to quantify to what extent recent changes in reproductive success (Fig. 1) may impact the viability of an unharvested low-density population (objective 1). We test whether the effect is due to the increased frequency of poor-reproductive success years or to poorer reproductive success in recent years (objective 2). Then, we use the model to investigate the impact of different hunting bag management strategies on a harvested low-density population (objective 3). Population matrix models are indeed suitable, easy-to-use, cost-efficient, rapid and flexible tools to address such questions and are, therefore, useful to support decision-making. We developed the model based on French grey partridge data, but it can easily be adapted to other populations or species, given that field estimates of demographic parameters are available. We provide our scripts as Supporting information (ULM software).

Methods

We present below the stochastic matrix model we developed to investigate grey partridge population dynamics. It is based on demographic parameters calculated from data collected in north-central France. We estimated the reproductive success through a long-term annual covey survey (1979–2014) over an array of hunting estates. We estimated survival rates through two large-scale radiotracking studies in 1995–1997 and 2010–2011 (ca 1300 radio-tagged partridges). We give an overview in Table 1.

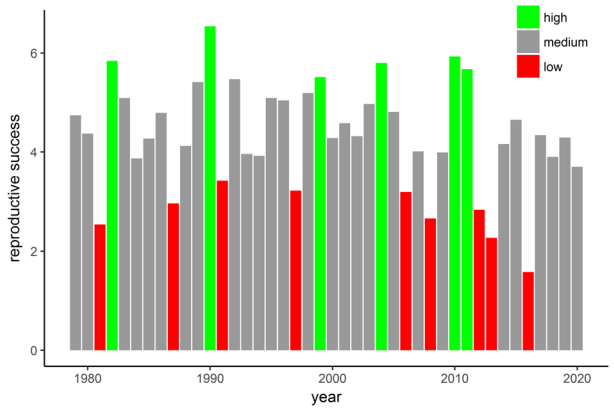

Figure 1. Inter-annual variations in grey partridge mean reproductive success (mRS, offspring/female in summer) in north-central France since 1979. mRS is classified as 'high' when >5.5, 'medium' when ≥3.5 and ≤5.5, and 'low' when <3.5. Source of the data: French national grey partridge population monitoring programme OFB/FNC-FDC (Bro et al. 2003, Bro 2016, Godin 2020).

Field procedures and data

Reproductive success

The French annual grey partridge population monitoring programme includes a survey conducted in late July–August to estimate the mean reproductive success (hereafter 'mRS', mean number of offspring per surviving female in summer). Fields were searched by slowly driving a car along lanes and across fields, at dawn and dusk when birds are feeding. When a covey was detected, we counted the number of males, females and offspring using binoculars. We estimated the age of offspring according to their size and appearance (Bro 2016). We sampled successful pairs as well as pairs without offspring (often groups of adults). More detail on the field procedures can be found in Bro et al. (2003, 2004, 2005).

To investigate the impact of recent changes in reproductive success (Fig. 1) on the viability of partridge populations, we classified the mRS as 'high' (when >5.5), 'low' (when <3.5), 'medium' otherwise. Then we calculated the frequency of years of 'high', 'medium' and 'low' mRS for the recent and the historical periods – named 'Present' (2005–2014) and 'Past' (1979–2004), respectively (Table 1). We defined the recent period when the frequency of years of poor mRS increased (Fig. 1). We devoted data from subsequent years to test model forecasts. To model the demographic stochasticity of the reproductive success, we also calculated from our field data the proportion of females without offspring (FWO) and the mean brood size (mBS, mean number of offspring per female with offspring in summer; Table 1).

Survival rates

We estimated the survival rate of females over spring and summer (S_{ss}) through two large-scale radiotracking studies (Bro et al. 2001, 2013; Table 1). We captured the partridges from late February to late March. We tagged females with a necklace radio transmitter (860 and 437 females monitored on 10 and 13 sites in 1995–1997 and 2010–2011, respectively). Tags were equipped with a motion-sensitive mortality circuit to discern survival. The status (alive, dead or 'missing') of the birds was determined daily. We estimated the survival rate using the Kaplan–Meier method with left-truncated and right-censored data (Millot et al. 2015).

S_{ss} was estimated at 0.47 (Millot et al. 2015). The same estimate was used for both the 'Past' and 'Present' periods because we did not detect any changes, either between the two radiotracking studies (Bro et al. 2013) or from national grey partridge population monitoring (Godin and Reitz 2019).

We set the survival rate over autumn and winter (S_{aw}) to 0.6 as a mean value from an array of field surveys (Table 1).

Model

We built a female life-cycle matrix model (Caswell 2006) using the Unified Life Model (ULM) software (Legendre and Clobert 1995, Ferrière et al. 1996) to write and run our model. We provide the scripts in the Supporting information. We simulated a partridge population occurring on an (closed) area of 30 km² at a density of 5 pairs km^{-2}. This area is the scale of clusters of hunting estates (called 'GIC') that share a common partridge management plan (FDC28 2016), and this density level is considered as low in France.

Table 1. Field estimates of survival rates and reproductive success for the 'Past' and 'Present' periods.

Demographic parameter	Abbreviation	'Past' period (1979–2004)			'Present' period (2005–2014)			Source of data and reference
Reproductive success								
Mean reproductive success (offspring/female in summer)	mRS	'high' >5.5	'medium' [3.5–5.5]	'low' <3.5	'high' >5.5	'medium' [3.5–5.5]	'low' <3.5	
Probability of occurrence of each category of mRS	P	0.23	0.54	0.23	0.20	0.50	0.30	Annual covey survey in Eure-et-Loir (1979–2019), database OFB/FNC-FDC (Bro et al. 2003, 2005, 2015, 2016, Reitz 2011–2017)
Proportion of females observed in summer without offspring	FWO	0.25	0.40	0.50	0.26	0.44	0.58	
Mean brood size (offspring/female with offspring)	mBS	8.8	7.8	6.5	8.4	7.4	5.6	
Survival rates								
Survival rate over spring and summer	S_{ss}	normal distribution (mean = 0.47, SD = 0.134) min = 0.352, max = 0.933						Radiotracking surveys1995–1997 (860 females tagged that survived ≥7 days, 10 study sites; Bro et al. 2001, 2013)2010–2011 (437 females, 13 sites; Bro et al. 2013, 2016#, Millot et al. 2015#)
Survival rate over autumn and winter	S_{aw}	0.6						Population censuses (Reitz and Berger 1995, Bro et al. 2004) Radiotracking surveys - 1995–1997 (151 females tagged that survived ≥7 days, four study sites; Bro 1998 – appendix III)- 2010–2011 (107 females, 10 sites; Bro et al. 2013)Scientific literature (Bro 2016 – appendix XII)

Note that sample sizes differ from those reported in this work because one site was not included in these two papers on ecotoxicology.

We thus set the initial population size to 150 females. Immigration and emigration were not taken into account because the grey partridge is highly sedentary (radiotracking studies report that dispersal is mainly <1.5 km, Bro 2016).

Our model operates in discrete time with a time-step of one year. It calculates the number of females in spring $t+1$ (N_{t+1}) knowing N_t. The model assumes that reproduction and breeding are instantaneous events (i.e. the so-called 'birth pulse') to fit available data. The 'birth pulse' matches the time when coveys are surveyed. Our field data (proportion of females without offspring, FWO and the mean brood size, mBS) were collected in summer when the young are a few weeks old, so parameter estimates include demographic events such as nest and egg failures as well as chick mortality. Therefore, we did not model them per se, unlike Bro et al.'s (2000) model based on radiotracking data. We calculated the number of females when the birth pulse occurs as 1.134 times more numerous than the number of females still alive in late August (this ratio is known from radiotracking data).

Environmental stochasticity

We included environmental stochasticity for S_{ss} and mRS because the population growth rate is sensitive to these parameters (Bro et al. 2000, 2015) and field data show fluctuations across areas and years (Bro et al. 2003, 2013). We used a Gaussian distribution to simulate annual variations in S_{ss} (S_{ss} ~ Normal(0.47,0.134) [min: 0.352 – max: 0.933]). For reproductive success, the model randomly selects at each time step t whether the mRS of the year t is 'high', 'medium' or 'low' and sets the corresponding values of FWO and mBS (Table 1).

Demographic stochasticity

We included demographic stochasticity for both survival rates and the number of offspring per female because this process is especially critical when population numbers/densities are low (Tuljapurkar 2013), which is the case of our simulated population. We modelled this stochasticity using a binomial distribution for survival (S_{ss} and S_{aw}) and a Poisson distribution for the brood size (Fig. 2). We used the Poisson distribution because it is the distribution of counted positive data (McCullagh 2019).

Density-dependence

We investigated the density-dependence of mRS in high-density French grey partridge populations in the 1990–2000s (Bro et al. 2003). We analysed the regression between the mRS at summer t against the population density in spring t for 85 areas for which long-term monitoring was available. The relationship was statistically significant for 10% of the areas and meta-analysis indicated that 82% of the regression slopes were negative. We included density-dependence in the model by decreasing the number of offspring in proportion to the spring density when the density was >30 pairs km^{-2}. This threshold was set as an expert judgement based on field observations. Indeed, populations of ca 5 pairs km^{-2} may reach such high densities after a few successive years of good mRS, but they are generally not long-lasting peaks (Bro et al. 2005).

Eure-et-Loir data

We ran the model using the data collected in the Eure-et-Loir 'department' (i.e. a French administrative area), south-west of Paris. It was part of the core area of the species in France in the 1980s (Birkan and Jacob 1988), but grey partridge densities have decreased sharply in recent years (Bro 2016, Godin 2020). The landscape is typical of intensive cereal farming (see photos in Bro et al. 2012a, Bro 2016).

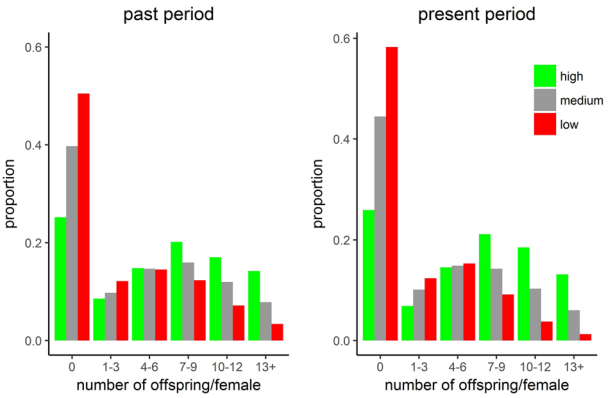

Figure 2. Distribution of the number of offspring per female in summer in Eure-et-Loir during the two periods for each class of mean reproductive success.

In Eure-et-Loir in 2010, spring censuses were conducted on sample plots totalling 1306 km^2 over 70 GIC (236 municipalities). We provide these numbers to give an idea of the scale of the field survey (Bro et al. 2005). In spring 2014, the mean density was ca 5 pairs km^{-2} (Reitz 2015). The reproductive success was estimated on ca 46 GIC with an average of 247 groups of partridges observed each year (detailed data are provided in Table 1). We tested the relationship between mRS against spring density for 24 areas (Bro et al. 2003) and found that 83.3% of the regression slopes were negative (mean: −0.45 ± 0.1 [SE]) and $p < 0.10$ for 4 areas out of 24. Specific S_{ss} was estimated at 0.44.

Goodness-of-fit test

We tested the plausibility of our model outputs by comparing the 'Predicted' and 'Observed' densities. 'Observed' densities are densities estimated in spring 2018 on 25 hunting estates of Eure-et-Loir free of any bird release. We did not use the data of the 2019 census because hand-reared birds were extensively released on a large number of hunting estates from summer 2018 to increase partridge densities. 'Predicted' densities are densities of our simulated population after a four-year period ('Present' data). The initial density was set to 4.16 pairs km^{-2} to match the mean density observed on the 25 hunting estates in 2014. The four-year run was replicated 25 times to match the number of hunting estates.

We compared the distribution of both the 'Predicted' and the 'Observed' densities using an ANOVA test (<www.r-project.org>).

Population viability analysis (PVA)

We assessed the viability of our simulated population by examining its evolution over 10 years, replicated 10 000 times. We then calculated the mean stochastic growth rate (Eq. 1, Ferrière et al. 1996), the number of trajectories which had become extinct ($N=1$) and the mean extinction time.

$$\text{mean}\left(\lambda_{\text{stocha}}\right) = \frac{1}{M}\sum_{j=1}^{M}\exp\left(\frac{\ln\left(N_j(T)\right) - \ln\left(N_j(0)\right)}{T}\right) \quad (1)$$

(hereafter 'λ_{mean}')

with T the number of time steps ($T = 10$), M the number of trajectories ($M = 10\,000$) and $N_j(t)$ the population size of the trajectory j at time t. This formula takes into account extinct trajectories. A new random generator seed was selected for each Monte-Carlo simulation.

We first investigated population viability for both the 'Past' and 'Present' periods using the data presented in Table 1. Then we compared the relative impact of the recent changes observed in the characteristics of the RS (i.e. FW0 + mBS, Fig. 2) on the one hand and in the relative frequency of years of high/medium/low mRS (P) on the other hand. For this purpose, we ran our simulated population by reversing the 'Past' and 'Present' data (i.e. 'Past' FW0 + mBS with 'Present' P; then 'Present' FW0 + mBS with 'Past' P). We set the hunting bag to zero during these two first steps. Then, in a third step, we used the model to examine the impact of four different strategies of hunting bag management on the viability of the population.

Hunting rules

The grey partridge is a game bird species that is hunted in autumn in France (generally on a few days from September until November or early December where populations are managed). We analysed the impact of hunting on the viability of the population by removing harvested individuals from the population. We assumed that hunting occurred just after the birth pulse, so we did not add a mortality rate between the two events (the mortality rate is known to be low according to radiotracking data). We also assumed that hunting mortality was additive to other mortality causes in accordance with the principle of parsimony, given the lack of field evidence for any hypothesis of additivity or partial compensation – both have been reported, or suggested, in other galliform species (Rolland et al. 2010, Sedinger et al. 2010, Sandercock et al. 2011). This assumption must be considered as conservative. However, such refinements could be included in the model to compare the outputs of these two hypotheses.

The hunting quota was determined at each time step according to the spring density and the mRS of the population using a 'hunting module' (Supplementary information). Note that the quota was set to zero when we carried out the viability analyses of the unharvested population so that the model structure was the same for all PVAs. Because the quota set by the administration is rarely reached, the completion rate was set to 0.3. We estimated this parameter using data collected in Loir-et-Cher, a neighbouring department, in the late 2000s.

We explored the impact of four strategies of hunting bag management, hereafter referred to as 'scenarios'. Scenario 1 is the one currently applied in Eure-et-Loir. We investigated scenario 2 and 3 to document questions raised by managers when reproductive success is good or poor. Scenario 4 tests an alternative rule by setting a quota per hunter.

- Scenario 1: the total number of grey partridges that may be shot by hunters on the estate during the hunting season is set each year by an administrative hunting quota, the so-called 'hunting plan'. It was implemented in France in the 1980s (Birkan and Jacob 1988). It depends on local field estimates of spring density and mRS (Table 2). The quota is set to zero when the density is low (<5 pairs km^{-2}) or when the mRS is poor (<2.5 offspring/female in summer).
- Scenario 2: this is the same as scenario 1 except that hunting low-density populations (<5 pairs km^{-2}) is allowed in the years of good mRS (>4 offspring/female), the hunting quota is set to 2 birds km^{-2}.
- Scenario 3: this is the same as scenario 1 except that the quota is set to zero when the mRS of the previous year was poor (<3.5 offspring/female), whatever the spring density and the mRS of the current year.
- Scenario 4 (Table 3): we modelled a maximum bag per hunter per hunting season. This rule greatly differs from the hunting plan which defines a maximum bag for the hunting estate whatever the number of hunters that hunt on it. In our model, we explored this rule for a range of 0–5 birds/hunter/hunting season, and 60 hunters hunting on the 30 km^2 estate. These values provide the scale of those reported on questionnaires of inquiries (Bro et al. 2012a, b).

We carried out a PVA for each scenario described above and calculated both the proportion of years when the hunting quota was >0 and the mean hunting bag, Bag_{mean}, following Eq. 2:

$$\text{Bag}_{\text{mean}} = \frac{1}{(M^*, T^*)}\sum_{(i,j)=(1,1)}^{(M^*,T^*)}\text{Bag}(i,j) \quad (2)$$

with M^* the trajectories and T^* the years when the hunting bag was > 0.

Table 2. Hunting plan for Eure-et-Loir, that is, maximum number of partridges that can be shot by (the whole group of) hunters on a given hunting estate according to local partridge population characteristics.

	Spring density (pairs km^{-2})				
Mean reproductive success (mRS, offspring/female in summer)	<5	5–10	10–20	20–40	≥40
<2.5	0	0	0	0	0
2.5–3	0	0	0	0.1/pair	0.2/pair
3–3.5	0	2/km^2	0.2/pair	0.3/pair	0.5/pair
3.5–4	0	2/km^2	0.3/pair	0.5/pair	0.75/pair
>4	0	2/km^2	0.4/pair	0.75/pair	1/pair

Table 3. Simulated maximum bag per hunter per hunting season according to local partridge population characteristics.

Mean reproductive success (mRS, offspring/female in summer)	Spring density (pair km^{-2})				
	<5	5–10	10–20	20–40	≥40
<2.5	0	0	0	0	1
2.5–3	0	0	1	1	4
3–3.5	0	1	1	3	5
3.5–4	0	1	2	5	5
>4	1	1	2	5	5

Results

'Predicted' versus 'Observed' densities

Our model predicted a mean density of our simulated population after a four-year period of 2.6 pairs km^{-2} (Fig. 3). No significant difference was detected with the observed densities (2.5 pairs km^{-2}; $F_{1,48} = 0.046$, $p = 0.831$); the model fits the observed density well.

Comparison of PVA during the 'Past' and 'Present' periods (without hunting)

The viability of our simulated partridge population differed depending upon 'Past' versus 'Present' period (Fig. 4). The mean population increased during the 'Past' period (λ_{mean} = 1.01), 0.1% of the trajectories went to extinction and 25% showed a decrease in population size of more than −30% (trajectories with a [−30%: +30%] change in the population size were considered as 'stable'). On the contrary, the mean population decreased during the 'Present' period (λ_{mean} = 0.89). The proportion of trajectories that went to extinction reached 1.9% and 63% led to a decrease in the initial population size > 50%. The decrease exceeded −80% for 31% of the trajectories. The population size increased by more than +30% for 11% of trajectories.

These contrasting trends resulted more from the recent worsening of poor mRS rather than from the recent increase in the frequency of poor mRS. Indeed, λ_{mean} decreased to 0.998 when running our simulated population with 'Past' FWO + mBS and 'Present' P (compared to λ_{mean} = 1.01 for the 'Past' period) but dropped to 0.92 when setting FWO + mBS and P with 'Present' and 'Past' values, respectively. Recent poorer mRS is both attributed to an increase in the proportion of females without offspring and a decrease in the mean brood size (Table 1, Fig. 2).

The French Meteorological Institute recorded an increase in the frequency of extreme rainfall events occurring between April and July, including over the area where grey partridge populations are monitored (MétéoFrance, Fig. 5). Extreme rainfall is defined as rainfall exceeding 60 mm in one day or 80 mm over two consecutive days. An average of 1.2 extreme rainfall events year^{-1} was recorded over the 1979–2004 period, compared to 3.4 year^{-1} over the 2005–2019 period (Fig. 5). The three last years with the highest number of extreme rainfall events (2012, 2013, 2016) match the worst reproductive successes the grey partridge has experienced in France for 35 years.

Impact of the hunting bag on the viability of the 'Present' population

Hunting led to a decrease in λ_{mean} whatever the scenario explored. Note that a scenario should be understood as the strategy together with the setting up of its parameters. The amplitude of the changes in the λ_{mean}, the extinction risk of

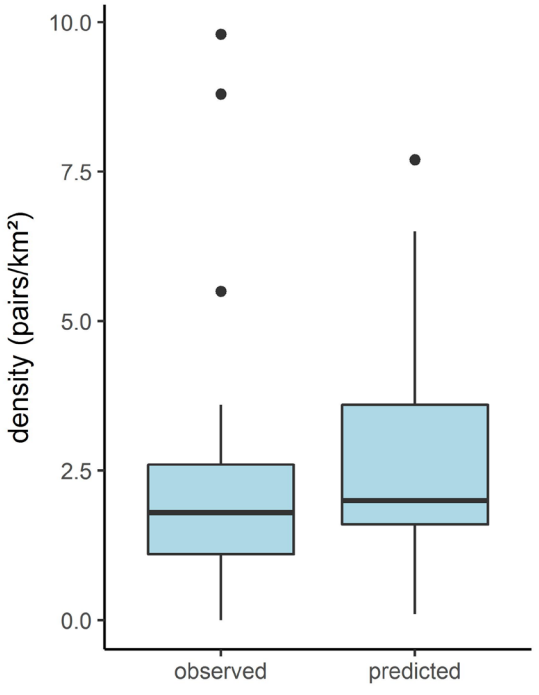

Figure 3. Comparison of the 'predicted' densities of the simulated population after a four-year period (initial density of 4.16 pairs km^{-2}, n = 25 trajectories) and 'observed' densities on 25 estates in Eure-et-Loir in 2018 (mean density in 2014: 4.16).

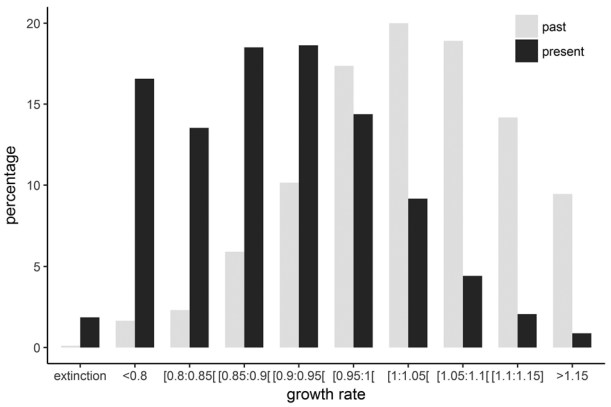

Figure 4. Results of population viability analysis of the simulated population during the 'Past' (1979–2004) and 'Present' (2005–2014) periods.

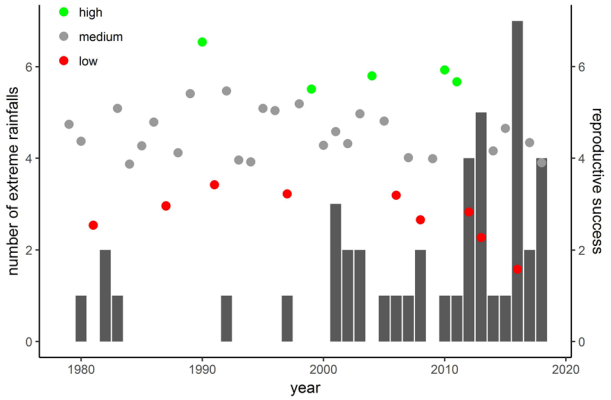

Figure 5. Number of extreme rainfall events (>60 mm in 24 h or >80 mm in 48 h) recorded in north-central France from April to July inclusive (bars) and mean reproductive success of the grey partridge (dots). Source of the data: Météo France and the French national grey partridge population monitoring programme OFB/FNC-FDC.

the population, the percentage of years when the hunting quota was >0 and the size of the hunting bag varied according to the scenario (Table 4). Compared to the no-hunting situation, the quota set by the Eure-et-Loir hunting plan (scenario 1) led to a decrease in λ_{mean} of 0.8% and an increase in the risk of population extinction over ten years of 0.33%. The hunting quota was >0 almost one year out of 4–5, and the hunting bag varied between 18 and 202 birds. Compared to this current hunting plan, allowing hunting of low-density populations in the years when the mRS is good (scenario 2) resulted in a decrease in λ_{mean} of 2.7% and an increase in the risk of extinction of 2.5%. The hunting quota was >0 one year out of 3, and the hunting bag varied between 18 and 293 birds. On the contrary, setting the quota to zero when the mRS was poor the previous year (scenario 3) resulted in population viability similar to unharvested populations. The hunting quota was >0 one year out of 7, and the hunting bag varied between 18 and 247 birds. By contrast with the hunting plan, the maximum quota per hunter per season we examined in scenario 4 tended to favour hunting at the expense of the viability of the game population. Indeed, with the settings used in our example, this scenario was associated with a hunting quota > 0 two years out of 3, and the hunting bag varied between 18 and 90. This maximum value corresponds to 60 hunters × 5 birds/hunter/season × 0.3. The probability of extinction was the highest of all scenarios examined (16.6%) and λ_{mean} decreased by 8%. This result shows that the grid assigning the number of birds that can be shot per hunter per season according to the local partridge spring density and mRS should be carefully adjusted both to the local number of hunters and to the completion rate to best ensure the viability of the game population. The grid proposed in our case study should be scaled down for an actual case. Nevertheless, we present these results to enrich the discussion.

Discussion

Recent decline in grey partridge populations

Grey partridge populations are still declining in Europe (PECBMS 2021b). This pattern is also observed in north-central France, especially in the Beauce region where densities are now generally <5 pairs km^{-2} (Godin 2020). This persistent decline is due more to recent poorer reproductive success than to the higher frequency of years of poor reproductive success. Poorer reproductive success is attributed both to an increase in the proportion of females without offspring (Reitz and Bro 2013) and a decrease in the brood size. Clutch destruction due to crop harvesting and predation, limited food resources due to poor cover and insecticide and herbicide use, and cold and rainy weather conditions during late spring to early summer are factors that are known to impact partridge reproductive success (Potts 2012, Bro 2016). Egg contamination by pesticides (Bro et al. 2016) may also alter reproductive success (Lopez-Antia et al. 2013). We suspect recent extreme weather conditions to have caused poor reproductive success in 2012, 2013 and 2016 (Bro et al. 2017). Indeed, heavy rains can drown the clutches, cold summer temperatures occurring when the chicks hatch can increase their mortality rate, and food resources (invertebrates) may be scarcer (Potts 2012, Bro 2016). Long and/or intense winter cold spells or summer heatwaves, as well as a lack of sunshine in spring, may also influence reproductive success through poor female body condition, a low egg hatching rate or another demographic mechanism impacted by a combination of high temperature and low humidity, or poor gonad development, respectively (Ubuka and Bentley 2011, Bro 2016, Montreuil-Spencer et al. 2019). However, further research is needed to characterize the impact of such extreme weather events on the demographic parameters of this particular species (adult and chick survival, egg hatching rate). Besides, a growing body of literature shows the importance of extreme meteorological events in population conservation for avian (Frederiksen et al. 2008, Glądalski et al. 2020, Piatt et al. 2020), mammal (Chan et al. 2005) or amphibian (Scheele et al. 2012) species. This is a topical concern since such events result from climate change and are hence predicted to continue or even get worse in the future (IPCC 2013). It is, therefore, crucial that species conserva-

Table 4. Results of the population viability analyses for the different hunting bag management strategies examined (parameters set up with 'Present' data).

Hunting bag management strategy	Mean stochastic growth rate (l_{mean})	Probability of extinction (%)	Percentage of years with hunting quota > 0	Hunting bag (Bag_{mean}) mean [min–max]
No hunting	0.888	1.86	0	–
Scenario 1	0.881	2.19	22.4	23 [18–202]
Scenario 2	0.864	4.40	35.6	21 [18–293]
Scenario 3	0.886	1.90	14.3	24 [18–247]
Scenario 4	0.814	16.62	66.6	19 [18–90]

tion and management deal with these major, unpredictable and uncontrolled events (Maxwell et al. 2019).

Hunting bag management

Given the trend and the status of grey partridge populations in Europe (e.g. it features on the Red List of Birds of Conservation Concern and was designated as a Biodiversity Action Plan species in the UK, Sotherton et al. 2014), there is a dormant debate about hunting. We investigated the impact of hunting by modelling the dynamics of a low-density population using well-documented French demographic field estimates. Note that our model considers demographic stochasticity, which is an important process in the dynamics of low-density or small populations (Tuljapurkar 2013) but does not specifically detail dispersal and genetic processes, which are important aspects for the viability of such populations (Frankham et al. 2010). We assessed the impact of hunting by comparing the viability of a hunted population (with the hypothesis of additive mortality) and a non-hunted population. In this work, hunting was only considered through the hunting bag. We did not investigate disturbance or hunting practices such as habitat management, releasing hand-reared birds and predator control. However, such practices could affect population viability and it would be interesting to explore these aspects in future research. We quantified to what extent hunting affects the viability of the population (growth rate and extinction risk of the population) for different hunting bag management scenarios. Our results show that the hunting plan applied in Eure-et-Loir allows hunting one year out of 4–5 and is associated with a decrease in the population growth rate < 1%. In this department, partridge densities have seriously declined over the last 10 years (Bro 2016, Godin 2020) despite the species not having been hunted for > 10 years (Mangin 2009) except in ca 20% of hunting estates in 2010 and 2011, which were two years of good reproductive success (Reitz 2011, 2012). Hunting was not mandatorily banned by means of a decree but the quota was fixed to zero because of poor reproductive success (as defined by the schedule). The hunting bag can then be assumed to have had a limited impact on populations. However, the managers raised the question of whether a hunting bag set to zero in these years of good reproductive success could have allowed the population to recover higher densities. This question was the subject of endless discussions between stakeholders in 2010 and 2011. However, the debate suffered from the lack of any scientific support. The present model came to fill this gap and should be used as a support to decision-making (Maris et al. 2018). We thus examined scenario 2 that allows hunting low-density partridge populations in years when the reproductive success is good. Both social and ecological arguments to allow hunting in these conditions are that it encourages hunters to remain involved in the management of wild populations as well as land management to support partridge populations. Under this scenario, the population growth rate is decreased by ca 2% compared to the current hunting plan. Management practices should, therefore, provide at least similar benefits in terms of the survival of incubating females, clutch success or chick survival to counteract hunting mortality. We attempted to investigate this issue but did not examine it thoroughly because it was rather theoretical (linear relationship) due to a lack of field data. However, practical questions do arise in this situation. Indeed, if hunting low-density populations is allowed, the authorized quota is small and may be smaller than the number of hunters. In such cases, a random draw is usually used to attribute the marks to hunters (birds shot must be marked when collected, as a regulation related to controls of the hunting plan). In this context, another strategy to determine the quota, that is easier to apply, is the quota per hunter per season (scenario 4). Note that in the example used to run the model, hunting was authorized both when densities were low but reproductive success was high, and when reproductive success was poor but densities were high. The setting of parameters (for 60 hunters) allows hunting about two years out of three but leads to adverse effects on partridge population conservation – and, in the end, on hunting itself. Given that this hunting bag management strategy is defined per hunter, it should be carefully set up in function of local situations (demographic status of the game population, number of hunters) to best ensure the viability of the game population.

The hunting quota must be adapted to the demography of local partridge populations to ensure their long-term conservation, especially where densities are low and/or when reproductive success is poor. To this end, monitoring density and reproductive success is the first key point. The second one is to use a validated tool to recommend a hunting quota adjusted to actual situations. We ran our model to document some issues raised by managers. We quantified the cost of hunting a low-density population when reproductive success is good, and the benefit of banning hunting the year after poor reproductive success (under the hypothesis of additive mortality). We investigated the quota per hunter and per season to show and discuss the potential of adverse impact on the game population, as is the case in our example. Therefore, the quota per hunter should be carefully set up considering both the game population and the number of hunters before it is implemented.

Modelling and management

Modelling is a cost-effective and easy-to-use tool that is now widely used to guide wildlife management and conservation (Fryxell et al. 2014). The model we deliver to managers in this work aims to provide a tool to adjust grey partridges hunting quotas to up-to-date French population data. It can however easily be adapted to populations in other countries or to other exploited species if similar data are available. However, other researchers have developed different models to investigate research (e.g. population dynamics), population management (e.g. recommendations for the hunting bag) or conservation (e.g. habitat management measures) issues.

The Potts model (Potts 1986, Potts and Aebischer 1995) combines a demographic model (the 'k_i-factors model' that details the successive loss rates for breeder, clutch, chick, etc. stages, and processes such as density-dependence and winter dispersal) and the influence of some hunting and farming practices such as habitat management, predator control and pesticide use. The hunting bag was modelled as the proportion of autumn birds that are shot, it increases in a logistic curve with the density of birds. This model helped to

understand the demographic mechanisms of the decline of the species from the late 1960s and the relative impact of some environmental factors. It was also used to recommend management actions to implement to improve partridge densities and breeding success (Sotherton et al. 2014). The simulations of the model were also used to recommend a maximum bag size of ca 25% of the pre-harvested population (Potts 1986). Modelling tools have greatly improved recently with the use of computers – populations can now be modelled as a collection of individuals, spatial factors can be taken into account as well as stochasticity, and the sensitivities of the population growth rate to different parameters can be assessed through viability analyses (Caswell 2006, Tuljapurkar 2013). The agent-based landscape model of Topping et al. (2010) considerably refined the Potts's model by providing comprehensive insight into the ecology and demography of the grey partridge with regard to farming practices, predation and weather.

Other models have been developed with the specific aim to provide guidelines to ensure a sustainable hunting bag. Letty et al. (1998) compared two methods to calculate the hunting bag and used a stochastic population matrix model to assess the impact of the hunting bag on the viability of a grey partridge population. They found that a quota corresponding to a proportion of the autumn population of partridges best ensures the viability of the population. More recently, Wann et al. (2020) proposed a different approach to provide hunting recommendations for a northern bobwhite *Colinus virginianus* population in the US. They investigated the correlation between the harvest rate (using a large-scale monitoring program) and proxies of hunting pressure (numbers of hunters and dogs during hunts, and hunter hours). Finally, they provided a graphical tool to limit the hunting pressure to a given level according to both the number of hunters permitted to hunt in the area and the autumn bobwhite numbers.

Various models have been developed because their structure is adapted to the issue addressed and to available field data. All of them have their advantages and limits, but they share the absolute necessity to be fitted to the local situation where it is applied and to be updated periodically to check the goodness-of-fit.

Conservation perspectives and recommendations

The current decline in grey partridge populations is driven by repeated years of worse reproductive success than known in the past. Extreme weather events that now occur almost every year, at least at a regional scale, are believed to be good candidate explanations of this phenomenon. However, further research is needed to build up comprehensive knowledge of how heatwaves, extreme rain events or late cold spells impact reproductive success (i.e. through female body condition or survival, clutch size, egg hatching rate, the development of chicks or their survival rate, the abundance of invertebrates, etc.) and to evaluate to what extent the species is vulnerable to these events and can adapt to them. The objective is to guide the design of 'new' conservation measures if necessary to improve reproductive success, such as cover intended as thermal refuges or water sources to withstand prolonged heat waves or droughts. Such research is all the more important in that these recent additive threats are predicted to increase in the future (IPCC 2013) and may impact a number of species (Maxwell et al. 2019). Of course, other factors such as the impact of endocrine disruptors or other reprotoxic substances used as pesticides should also be investigated (Lopez-Antia et al. 2013). In the current context of weather uncertainty, it is especially crucial to apply the already-known recommendations to manage populations and improve their habitat, as described in detail in Potts (2012) and Bro (2016), in order to help populations to recover after years of poor reproductive success.

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Author contributions

SG developed and ran the model, FR has managed the long-term database since the 1980s and provided the data, EB conceived and supervised the work. All the authors wrote the paper and gave approval for publication.

Data availability statement

Data are available as Supplementary information at <www.wildlifebiology.org/appendix/wlb-00806>.

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Supplementary information (available online as Appendix wlb-00806 at <www.wildlifebiology.org/appendix/wlb-00806>).