



Demography, genetics, and decline of a spatially structured population of lekking bird

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Abstract

Understanding the mechanisms underlying population decline is a critical challenge for conservation biologists. Both deterministic (e.g. habitat loss, fragmentation, and Allee effect) and stochastic (i.e. demographic and environmental stochasticity) demographic processes are involved in population decline. Simultaneously, a decrease of population size has far-reaching consequences for genetics of populations by increasing the risk of inbreeding and the strength of genetic drift, which together inevitably results in a loss of genetic diversity and a reduced effective population size (N_e). These genetic factors may retroactively affect vital rates (a phenomenon coined ‘inbreeding depression’), reduce population growth, and accelerate demographic decline. To date, most studies that have examined the demographic and genetic processes driving the decline of wild populations have neglected their spatial structure. In this study, we examined demographic and genetic factors involved in the decline of a spatially structured population of a lekking bird, the western capercaillie (*Tetrao urogallus*). To address this issue, we collected capture-recapture and genetic data over a 6-years period in the Vosges Mountains (France). Our study showed that the population of *T. urogallus* experienced a severe decline between 2010 and 2015. We did not detect any Allee effect on survival and recruitment. By contrast, individuals of both sexes dispersed to avoid small subpopulations, thus suggesting a potential behavioral response to a mate finding Allee effect. In parallel to this demographic decline, the population showed low levels of genetic diversity, high inbreeding and low effective population sizes at both subpopulation and population levels. Despite this, we did not detect evidence of inbreeding depression: neither adult survival nor recruitment were affected by individual inbreeding level. Our study underlines the benefit from combining demographic and genetic approaches to investigate processes that are involved in population decline.

Keywords Population decline · Inbreeding depression · Dispersal · Gene flow · Effective population size

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Introduction

In a global context of biodiversity decline, understanding the mechanisms underlying population decline is a critical challenge for conservation biologists (Purvis 2000; Naeem et al. 2012; Pimm et al. 2014). Over the last 3 decades, many experimental and field studies investigated the demographic and genetic mechanisms involved in demographic declines

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and extinctions (reviewed in Young et al. 2000; Nunney and Campbell 1993; Frankham 2005). However, their relative contribution remains controversial (Lande 1988; Nunney and Campbell 1993; Spielman et al. 2004; Frankham 2005). On the one hand, theoretical and empirical studies showed that populations are subject to extinction due to genetic factors, even in the absence of any human impact and ecological factor (Lande 1998; Szűcs et al. 2017). On the other hand, studies showed that demographic processes will generally doom small populations to extinction before genetic effects act strongly (Lande 1988; Wootton and Pfister 2013). Investigating the role of both demographic and genetic factors, and their interplay, thus remains an important challenge to better predict population declines and inform conservation strategies.

Both deterministic and stochastic demographic processes are involved in population decline (Lande 1993; Melbourne and Hastings 2008). Deterministic factors such as over-exploitation and habitat loss and degradation decrease population growth, which may ultimately lead to population extinctions (Selwood et al. 2015). Under stochastic processes, demographic declines are caused by a high variance in population growth rate due to environmental stochasticity (e.g. weather fluctuations, catastrophic events) (Lande 1993; Engen et al. 2003) or demographic stochasticity (i.e. random variation of demographic rates)—whose effect increases when population size decreases. Moreover, positive density-dependence of growth rate ('Allee effect'; Stephens et al. 1999; Stephens and Sutherland 1999) may enhance population decline (Courchamp et al. 1999). At low population density, individuals experience a fitness loss due the difficulty to locate mate ('mate finding Allee effect', Gascoigne et al. 2009) and/or to realize cooperative behaviors. This further may translate into a decreased population growth and a higher risk of population extinction (Courchamp et al. 1999; Stephens et al. 1999).

Demographic processes described above have far-reaching consequences on population genetics (Tanaka 1997; Frankham 2005; Jaquière et al. 2009). A severe drop of population size is often associated with increased probability of breeding with relatives (i.e. inbreeding). Population decline also enhances the effects of genetic drift, which inevitably results in a loss of genetic diversity (Crnokrak and Roff 1999; Gibbs 2001; Frankham et al. 2002). Decreasing population size (N_b , often called 'census population size' in genetic studies) also results in a reduction in the effective population size (N_e), a phenomenon that can be enhanced by the characteristics of the mating system (i.e. monogamy or highly skewed mating success) and several demographic features (e.g., overlapping generations or age structure) (Engen et al. 2005; Waples and Yokota 2006; Stubberud et al. 2017).

These genetic factors may retroactively affect fitness components (i.e., survival and recruitment; a phenomenon

coined 'inbreeding depression'), and therefore reduce population growth and accelerate the decline of small populations (Saccheri et al. 1998; O'Grady et al. 2006; Luque et al. 2016). Inbreeding may have a detrimental impact on adult survival (Meagher et al. 2000; Szűcs et al. 2017), fecundity (Westemeier et al. 1998) and offspring survival (Ballou and Ralls 1982; Keller 1998; Briskie and Mackintosh 2004; Spottiswoode and Møller 2004; O'Grady et al. 2006), and may decrease average fitness at the population level (Saccheri et al. 1998; Reed 2005). Simultaneously, a loss of genetic diversity, and therefore of additive genetic variance at quantitative traits, might also lead to a decrease of adaptive potential and possible population declines (Frankham 2005), although a meta-analysis has suggested that the correlation between neutral genetic diversity and adaptive potential is usually low in natural populations (Reed and Frankham 2001).

To date, most studies that have simultaneously examined the demographic and genetic mechanisms driving the decline of wild populations (Landguth et al. 2014; Mathieu-Bégné et al. 2018) have neglected their spatial structure. Most natural populations occur in heterogeneous, fragmented landscapes and are therefore spatially structured, i.e., composed of subpopulations occupying more or less discrete habitat patches linked together by dispersal (Thomas and Kunin 1999). Dispersal may play a critical role in population decline by affecting both demographic and genetic processes (Thomas and Kunin 1999; Ronce 2007; Benton and Bowler 2012). At the individual level, dispersal 'decisions' depend on phenotypic traits (e.g. sex, age, social or breeding status), as well as social (i.e. population density, kin competition, inbreeding avoidance) and environmental factors (e.g. patch and landscape characteristics) (Clobert et al. 2009; Matthysen 2012). This results in non-random and generally asymmetric dispersal rates that mitigate the risk of subpopulation decline and extinction (Hill et al. 2002; Gilpin 2012). At the demographic level, dispersal reduces the risk of subpopulation extinction through immigrant inflow (i.e. 'rescue effect', Hanski et al. 1997); immigration increases the size of a subpopulation and thus reduces Allee effect and the influence of demographic stochasticity on population growth rate. At the genetic level, increased dispersal rate or distance enhances gene flow, reduces the strength of genetic drift effects within subpopulations, and homogenises allele frequencies across subpopulations (Slatkin 1987; Hartl and Clark 1989). In addition, gene flow may strongly alter N_e estimates, the direction and the magnitude of the bias depending on the intensity, the continuity, and the randomness of gene flow (Wang and Whitlock 2003; Palstra and Ruzzante 2008). This led to the consideration of hierarchized N_e estimates, i.e. local N_e at the subpopulation level and meta- N_e at the whole population scale (Palstra and Ruzzante 2008). Therefore, considering the spatial structure

of populations is a critical challenge for studies focusing on the contribution of demographic and genetic factors on population declines.

In this study, we examined demographic and genetic factors involved in the decline of a spatially structured population of a lekking bird, the western capercaillie (*Tetrao urogallus*). This species has experienced a severe decline in central and western Europe, mainly due to habitat destruction and alteration (IUCN 2018). Populations of *T. urogallus* are usually composed of a set of leks in which males actively compete for mates and between which dispersal occurs (Wegge and Rolstad 1987; Storch 1997; Cayuela et al. 2019). Leks differ in terms of size (namely the number of competing males) and it has been reported in a related species with the same lekking behaviour that females preferentially reproduce in large leks (Alatalo et al. 1992).

Here, we modeled the populations of *T. urogallus* as a spatially structured population (sensu Thomas and Kunin 1999) made of subpopulations (i.e., discrete groups of breeding adults composed of lekking males and reproductive females) linked together by dispersal movements and gene flow (i.e., effective dispersal; Cayuela et al. 2018a, 2019). We used multievent capture-recapture models to show that the population experienced a dramatic decline over the study period (2010–2015) and to investigate the demographic mechanisms involved in this decrease. We first examined if adult survival and recruitment depended on subpopulation size. Specifically, we expected a lower recruitment and a reduced survival in small subpopulations compared to large subpopulations due to Allee effects and inbreeding risk. We also hypothesized that breeders could avoid a ‘mate finding’ Allee effect by adjusting their dispersal decisions according to subpopulation size. We thus expected that adults (of both sexes) adjusted their dispersal decisions according to subpopulation size: they were more likely to emigrate from small subpopulations and preferentially immigrated into large subpopulations. Second, we examined how demographic–environmental stochasticity may affect survival and recruitment. We hypothesized that recruitment would show higher temporal variance than adult survival, which is a pattern usually observed in iteroparous species (Gaillard and Yoccoz 2003). We also investigated whether survival or recruitment decreased over time.

Next, we examined potential genetic mechanisms contributing to population decline. We hypothesized that the severe population loss was associated with low allelic richness, low expected heterozygosity, and high inbreeding coefficients (at both individual and population levels). We also expected that population decline would be associated with small subpopulation-specific N_e . The reduction in N_e should be amplified by the large variance in male reproductive success; *Tetrao* leks are mainly composed of related males and only a few dominant males reproduce (in *Tetrao tetrix*: Höglund et al.

1999; Rintamäki et al. 2000; Kervinen et al. 2012; in *T. urogallus*: Regnaut et al. 2006; Cayuela et al. 2019). In addition, as dispersal rates and gene flow are non-random and asymmetric in the population (Cayuela et al. 2019), we expected that meta- N_e should be drastically lower than the sum of the local N_e (per subpopulation) in the population. Finally, we tracked evidence of inbreeding depression by examining if individual inbreeding negatively affected adult survival and recruitment.

Material and methods

Study area and bird survey

The study was conducted in the Vosges Mountains, at the northern margin of *T. urogallus* distribution range in France (Fig. 1; for a detailed description of the sampling area, see Cayuela et al. 2019). Large valleys structure the species distribution range into discrete forest patches. The spatially structured population of *T. urogallus* is composed of a set of 11 known subpopulations, i.e., groups of adults composed of males and female individuals detected at lek sites during the display period. Subpopulations may contain several leks close to each other. In the absence of information on

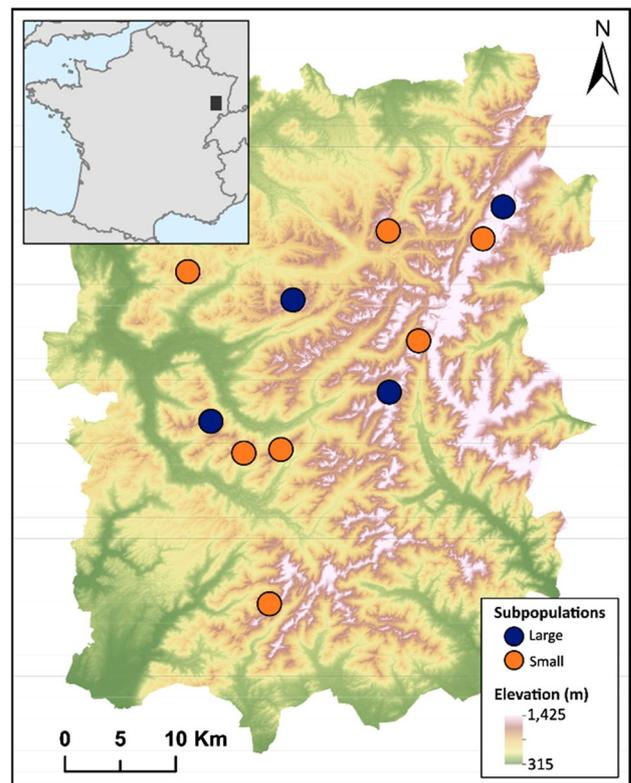


Fig. 1 Map of the study area showing the eleven subpopulations (four large and seven small) studied over the 6-years study period

individual age, we assumed that all individuals attending at lek sites were potential breeders. Euclidean distance between subpopulations ranged from 2.6 to 42 km, with a median of 18 km. Non-invasive samples (95% faeces and 5% feathers) were collected from 2010 to 2015, which allowed us to identify 116 individuals (66 males and 50 females) (Supplementary material S1, Table S1; and Supplementary material S2, Table S2). Four historically large subpopulations (NOI, LLC, VEN, and GdF) and seven small subpopulations (TAN, CrH, FOS, TdR, BAG, GEH, and StA) were identified. During the first year of the study (2010), the maximum number of adults captured in large subpopulations ranged from 6 to 16 individuals, while in small subpopulations it ranged from 1 to 6. A detailed description of the sampling method and the genotyping approach can be found in Supplementary material S2.

We restricted our analyses to samples collected at lek sites during the display season and over a 6-year period using the CR method. Copulations at lek sites in the Vosges Mountains occurred on average 15 days earlier in 2012 than in 1986 (Ménoni et al. 2012), and peaked around mid-April during the study period. Number of annual sampling visits per subpopulations ranged from 5 to 10. We split samples collected during sampling visits into an early sampling session, ranging from mid-March to mid-April, and a late sampling session, ranging from mid-April to mid-May, which allowed us to reduce the number of non-detection events in individual capture-recapture histories. Movements between subpopulations during the period covered by the first sampling session were recorded as early dispersal events and, respectively, movements between subpopulations occurring during the second session as late dispersal events.

Modelling survival and dispersal according to subpopulation size

Using multievent CR models, we examined how population size, survival and recruitment varied over time. We also investigated how subpopulation size affected survival, dispersal and recruitment probability. In multievent CR models, a distinction is made between events and states (Pradel 2005). An event is the field observation coded in the individual's capture history. This observation is related to the latent state (e.g. alive or dead, dispersing or non-dispersing individuals) of the individual that is not directly observable on the field. Multievent CR models are designed to model this uncertainty in the observation process using hidden Markov chains (Pradel 2005).

Specific multievent CR models have been developed to estimate dispersal probabilities from study systems including numerous recapture sites (i.e., habitat patch or subpopulations) (Lagrange et al. 2014; Cayuela et al. 2018a, b). We used a modified version (Tournier et al. 2017) of a multievent

CR model proposed by Cayuela et al. (2017), which allows quantification of survival and dispersal between sites (in our case, subpopulations) that differ in terms of biotic or abiotic characteristics. A detailed description of the model structure is provided in Supplementary material S1. Briefly, the model includes four main parameters: survival (ϕ), departure (ϵ), arrival (α), and recapture (p) probabilities. These demographic parameters may differ according to two different types of subpopulations: small subpopulations and large subpopulations. Survival, departure, and arrival probabilities were modeled both intra-annually (i.e. between the two sessions of the same year) and inter-annually. Our model had robust design structure (Pollock 1982) to quantify departure and arrival probabilities intra-annually and inter-annually. Mortality in adult capercaillie is highest in late winter and early spring, when capercaillie are among the rare available preys for avian and mammalian predators (Saniga 2011), and especially for males aggregated around lekking sites (Wegge et al. 1987). We therefore set the intra-annual survival probability (probability of survival from first to second sampling session) to 1, as is usually done in robust-design models (Kendall et al. 1995, 1997); this assumption was realistic in our study system as intra-annual survival probability was always higher than 0.9.

This parameterization was entered in the program E-SURGE (Choquet et al. 2009). We verified model convergence and the absence of redundant parameters using the advanced diagnostic tools provided by E-SURGE. Competing models were ranked through a model-selection procedure using Akaike information criteria adjusted for a small sample size (AICc) and AICc relative weights (w) (Burnham and Anderson 2004). When the AICc weight of the best supported model was less than 0.9, we performed model averaging. The parameters were model-averaged using the complete set of models. Our hypotheses about recapture and state–state transition probabilities were examined using the general model [$\phi(\text{SIZE} + Y)$, $\epsilon(\text{SIZE} + \text{SEX})$, $\alpha(\text{SEX})$, $p(\text{SIZE} + \text{SEX} + Y)$], which included three effects: (1) subpopulation size (SIZE) coded as states in the model; (2) year-specific variation (Y); (3) group effect for sex-specific variation (SEX). We examined whether recapture probability differed according to subpopulation size (SIZE), between years (Y) and between sexes (SEX). We tested whether survival depended on subpopulation size (SIZE) and varied over years (Y). We did not examine the effect of sex (SEX) on survival as a previous study on this population revealed the absence of sex-specific variation in survival (Cayuela et al. 2019). We tested whether intra- and inter-annual departure rate varied according to subpopulation size (SIZE) and between sexes (SEX). We did not consider time-specific variation in departure rate as dispersal rate displays little variation over time in this

population (Cayuela et al. 2019). Moreover, we examined whether arrival probability in small subpopulations differed between sexes (SEX). All the combinations of these three effects were tested in the models, leading to the consideration of 64 competing models (Supplementary material S3, Table S1). Moreover, we aimed to examine whether survival showed a negative trend over time. After determining the best-fitting model based on AICc and w , we examined the effect of time (included in the model as a continuous variable) on survival probability using ANODEV as recommended in Grosbois et al. (2008). Moreover, we were also interested in quantifying census population size (N) over the 6-year period. We estimated annual size of whole population and subpopulations using the Horvitz–Thompson estimator (Horvitz & Thompson 1952), an approach commonly used in the capture-recapture framework (e.g., Borchers et al. 1998; McDonald & Amstrup 2001; Brittain & Böhning 2009; Huggins & Hwang 2011).

Modeling recruitment according to subpopulation size

We built a multievent model to estimate recruitment following the structure of Pradel's (1996) model, in which recruitment can be modelled by reversing capture histories and reading them backwards. In our model, the recruitment probability is estimated as the probability that an individual present at time t was not present at $t-1$, i.e. the proportion of “new” individuals in small and large subpopulations at t , while taking into account dispersal between the two kinds of subpopulations. The model has a relatively similar structure to that of the model designed to estimate survival (see Supplementary material S1) and includes four main parameters: recruitment (δ), departure (ϵ), arrival (α), and recapture (p) probabilities.

This parameterization was implemented in the program E-SURGE. Competing models were ranked using AICc and AICc relative weights (w). We performed model averaging when the AICc weight of the best-supported model was less than 0.9. We examined our hypotheses about recapture and state–state transition probabilities from the general model [$\delta(\text{SIZE} + Y)$, $\epsilon(\text{SIZE} + \text{SEX})$, $\alpha(\text{SEX})$, $p(\text{SIZE} + \text{SEX} + Y)$], which includes the same effects that were considered in the survival model. As dispersal is not a biologically meaningful parameter in this models due to capture histories reversion, we kept the combination of effects, $\epsilon(\text{SIZE} + \text{SEX})$ and $\alpha(\text{SEX})$, in all the models. For recruitment and recapture, we tested all the possible combinations of effects, which led to the consideration of 16 competing models (Supplementary material S3, Table S2).

Quantifying allelic richness, inbreeding, gene flow and effective population size

Genetic analyses were conducted using a subset of 92 individuals genotyped at 11 microsatellite markers (ADL184, ADL230, BG15, BG16, BG18, LEI098, TuT1, TuT2, TuT3, TuT4, ADL142; see Supplementary material S2). Evidence for scoring errors, large allele dropout, presence of null alleles, departure from Hardy–Weinberg equilibrium and linkage disequilibrium between all pairs of loci were previously assessed in Cayuela et al. (2019).

Allelic richness (A , the uncorrected allelic richness; A_r , the allelic richness corrected for rarefaction) and expected heterozygosity (H_E) were calculated using FSTAT (Goudet 1995) for the four large subpopulations and at the whole population level. We quantified F_{ST} and asymmetrical migration rates m between the four large subpopulations using GENEPOP v4.1.4 (Rousset 2008) and BayesAss v1.3 (Wilson & Rannala 2003) respectively. BayesAss v1.3 is a bayesian method based on the temporary disequilibrium of genotypes frequencies, a phenomenon resulting from immigration and attenuated by random mating. This method does not assume migration–drift equilibrium, which is an assumption that is frequently violated in natural populations. We computed a total of 2,000,000 MCMC iterations after an initial burn-in of 1,000,000, as suggested by Wilson and Rannala (2003). We estimated effective population size (N_e) using the program COLONY v2.0.6.4 (Jones and Wang 2010; Ackerman et al. 2017). We used default software options but set the mating system to polygamy in males and females (i.e., as females are iteroparous, we considered the possibility that may reproduce with different males over their life) and ‘Optimal Prior for N_e ’ for sibship prior. Effective population sizes N_e were calculated at three hierarchical levels: (i) the subpopulation level, (ii) at the level of four large subpopulations, and (iii) at whole population level (i.e. meta N_e). The ratio N_e/N were calculated by considering N as the population size at the beginning of the study (in 2010). By doing so, we avoided to bias this ratio by the rapid population loss recorded during the 6-year study period.

Examining inbreeding influence on survival and recruitment

We estimated individual inbreeding coefficient using the r package Genhet (Coulon 2010). We considered three inbreeding metrics: (i) the proportion of heterozygous loci (PHt) in an individual, (ii) the internal relatedness (IR), and (iii) the homozygosity by locus (HL).

We examined the effects of the three inbreeding metrics on survival using Cormack–Jolly–Seber capture-recapture models. As we showed that recapture probability differed between sexes (see the result section), the sex was kept in all

the models. We considered four alternative models in which survival varied according to Pht, IR or HL, or was kept constant (using the symbol ‘.’) (Supplementary material S3, Table S3). The models were built in the program E-SURGE and were ranked using AICc and AICc relative weights (w). We used Pradel’s model (described above) to examine the effect of inbreeding on recruitment (Supplementary material S3, Table S4). The effect of the three inbreeding metrics was examined in a similar way as for survival.

Results

Population size, survival, recruitment and dispersal

During the 6-years study period, we identified 116 individuals (50 females and 66 males) and detected 37 dispersal events between subpopulations (14 and 23 for females and males respectively). Our analyses revealed that whole population size in the eleven subpopulations dramatically dropped from 136 to 90 individuals (−33%) between 2010 and 2015 (Fig. 2). Decline was stronger in the four large subpopulations (−31% in GdF, −45% in VEN, −44% in LLC and −51% in NOI) than in the seven small subpopulations (−20% on average) (Fig. 2).

The best-supported survival model was [ϕ (SIZE), τ (SIZE), α (.), p (SEX)] (see the complete model selection procedure in Supplementary material S3, Table S1). However, as its AICc weight was 0.27, we estimated parameters using model-averaging. Recapture probability differed between sexes, males (0.58 , SD: ± 0.03) having a higher recapture probability than females (0.37 ± 0.04). Survival showed little variation over time and was marginally higher in small subpopulations (from 0.70 in 2013 to 0.72 in 2015) than in large subpopulations (from 0.65 in 2013 to 0.68 in 2015) (Fig. 3a). Our study revealed that dispersal was strongly affected by subpopulation size. Departure probability was drastically higher in small subpopulations than in large subpopulations (Fig. 3c). In both males and females, the probability of leaving a small subpopulation was 0.25 ± 0.07 inter-annually and 0.25 ± 0.07 intra-annually, while it was 0.14 ± 0.04 inter-annually and 0.15 ± 0.03 intra-annually in large subpopulations. Simultaneously, individuals had a higher probability to arrive in a large subpopulation than in a small one (Fig. 3d). Intra-annually, the probability of arriving in a large subpopulation was 0.65 ± 0.10 while it was 0.35 ± 0.10 in a small subpopulation. This pattern was less marked inter-annually: the probability of arriving in a large subpopulation was 0.55 ± 0.12 while it was 0.44 ± 0.12 in a small subpopulation.

The best-supported recruitment model was [δ (.), τ (SIZE + SEX), α (SEX), p (SEX)] (see the procedure of model selection in Supplementary material S3, Table S2).

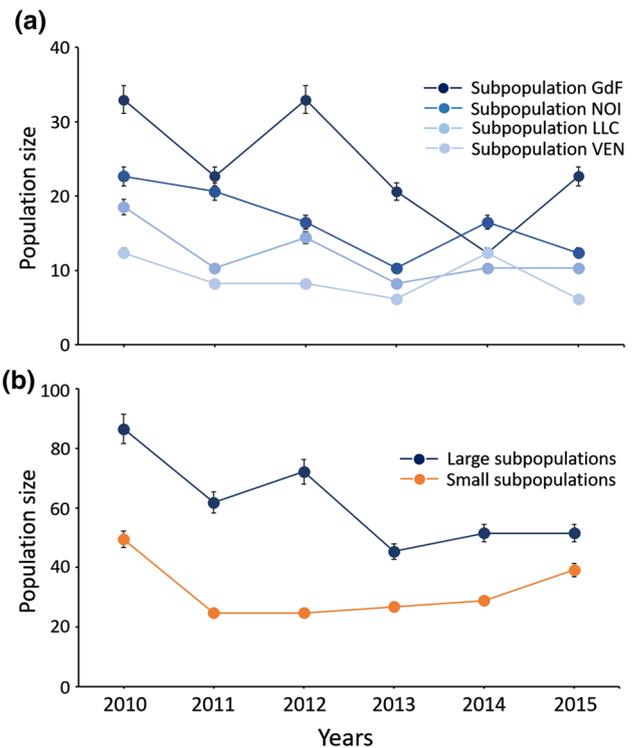


Fig. 2 Decline of the population of western capercaillie (*Tetrao urogallus*) over the 6-years study period (2010–2015). **a** Annual size of the four large subpopulations. **b** Annual size of large and small subpopulations. The subpopulation sizes were estimated using the Horvitz–Thompson estimator (Horvitz and Thompson 1952). Error bars correspond to standard deviation around population size estimates

However, as its AICc weight was 0.19, model-averaging was performed. Recruitment probability did not differ between small and large subpopulations and varied over time (Fig. 3b), ranging from 0.11 ± 0.04 in 2013 and 2015 to 0.19 ± 0.05 in 2012.

Allelic richness, inbreeding, gene flow and effective population size

The allelic richness corrected for rarefaction ranged from 2.23 in GdF and LCC to 2.70 in NOI (Fig. 4). Those values were relatively close to allelic richness calculated for the four main subpopulations (2.61) and the whole population (2.64). The expected heterozygosity (H_e) ranged from 0.39 in GdF to 0.46 in NOI. It was 0.44 at the large subpopulation and the whole population levels. Inbreeding coefficients (F_{IS}) ranged from -0.01 in VEN to 0.11 in NOI and GdF (Fig. 4). Concerning the individual metrics of inbreeding, the proportion of heterozygous loci (Pht) was 0.37 ± 0.17 (min = 0, max = 0.80), the internal relatedness (IR) was 0.17 ± 0.34 (min = -0.53 , max = 1), and the homozygosity by locus (HL) was 0.56 ± 0.20 (min = 0.14, max = 1). In the four large subpopulations, the mean F_{IS} was 0.17 while it

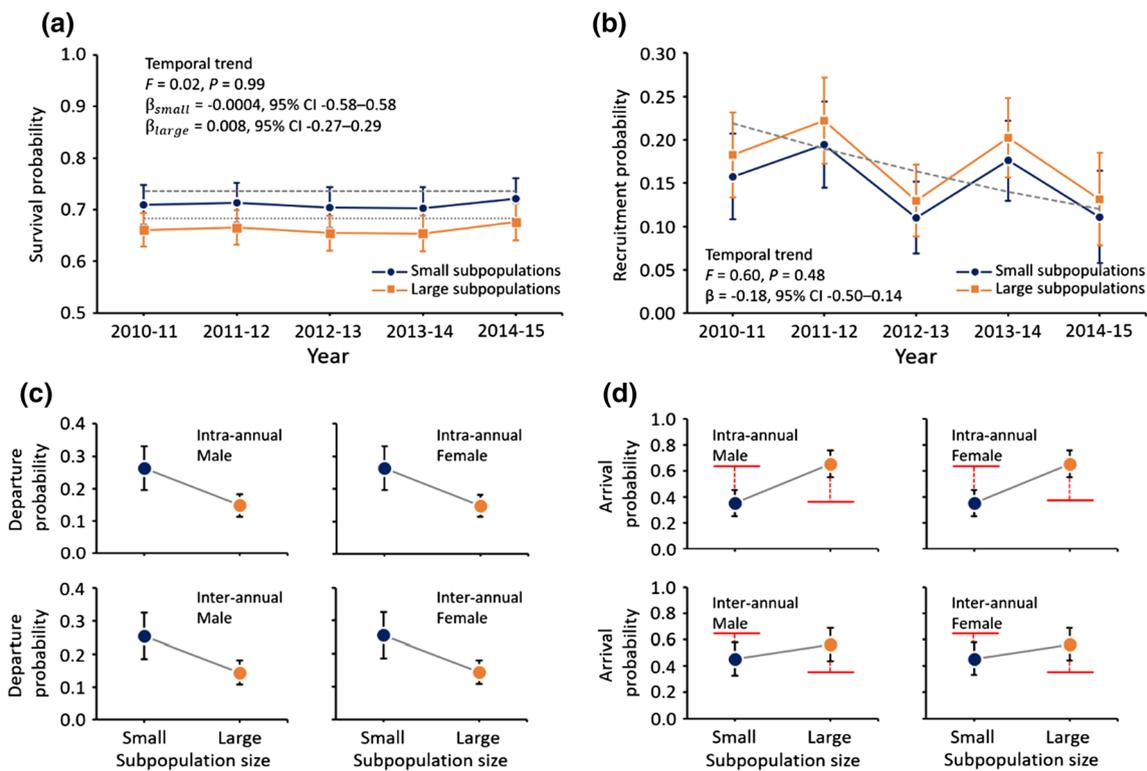
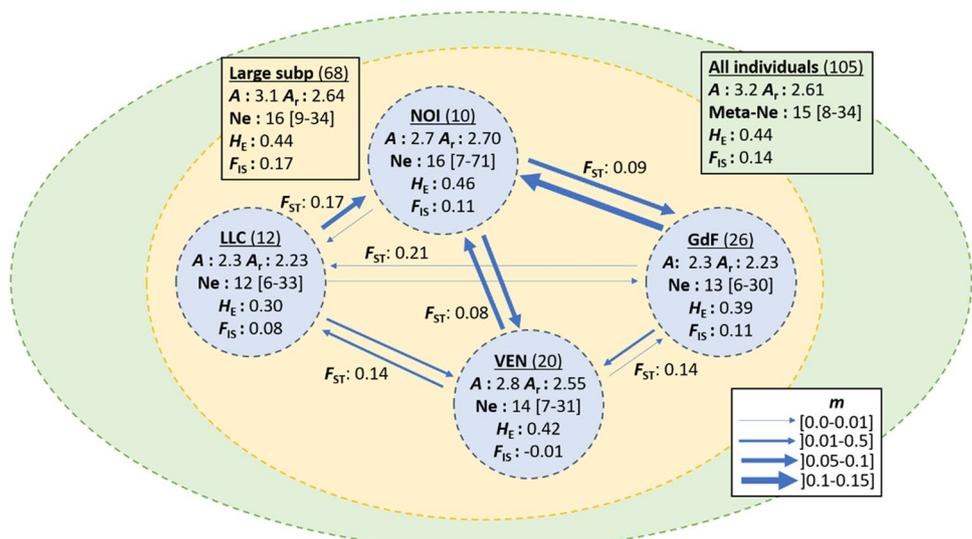


Fig. 3 Survival, recruitment and dispersal in a declining population of western capercaillie (*Tetrao urogallus*) over a 6-year study period (2010–2015). Model-averaged estimates and their standard errors are extracted from multievent capture-recapture models. Survival (a) marginally differs between large and small subpopulations and shows little temporal variation. Survival does not show any significant temporal trend (small subpopulations = grey dashed line, large subpopulations = grey dotted line) according to the ANODEV performed from multievent models. Recruitment (b) does not vary between

large and small subpopulations. It shows substantial variation over time but no significant temporal trend (grey dashed line). Dispersal (c–d) strongly depends on subpopulation size. Departure probability (c) is lower in large subpopulations than in small subpopulations. By contrast, arrival probability is higher in large subpopulations than in small subpopulations. The red bar shows the probability of arriving in a subpopulation (small or large) under random expectation. Error bars correspond to standard deviation around modeled-averaged parameter estimates

Fig. 4 Effective population size (N_e for the four large subpopulations, and meta- N_e for the whole population), asymmetrical migration rate (m), allelic richness, and inbreeding coefficient (F_{IS}) in a declining population of western capercaillie (*Tetrao urogallus*). For the four large subpopulations, we show estimates of N_e , m , F_{IS} , allelic richness (A , uncorrected richness; A_r richness corrected for rarefaction), and expected heterozygosity (H_E). We also give F_{ST} values for each pair of large subpopulations



was 0.14 in the whole population. Moreover, F_{ST} values between the four large subpopulations ranged from 0.08 to

0.21 (Fig. 4). Asymmetrical migration rates m between the four large subpopulations ranged from less than 0.01 to 0.12 (Fig. 4).

As dispersal probabilities (see capture-recapture analyses) and migration rates are asymmetrical, the meta- N_e was therefore lower than the sum of the local N_e (per subpopulation) in the population. The estimates of N_e were relatively similar in the four large subpopulations (Fig. 4), ranging from 12 (95% CI 3–33) in LLC to 16 (95% CI 7–71) in NOI. Furthermore, the mean N_e in the four subpopulations was 16 (95% CI 9–34). The meta- N_e estimated for the whole population was 15 (95% CI 8–34). The ratios N_e/N was always lower than 1 in the large subpopulations (VEN=0.93, LCC=0.67, GdF=0.52; not estimated for NOI) and at whole population level (0.15).

Examining inbreeding influence on survival and recruitment

The model with constant survival [$\phi(\cdot)$, $p(\text{SEX})$] was better supported than the models including one of three inbreeding metrics (Supplementary material S3, Table S3). In addition, the slope coefficient of inbreeding metrics did not significantly differ from 0 (PHt: -0.06 ± 0.16 ; IR: 0.06 ± 0.16 ; HL: 0.01 ± 0.16), suggesting that adult survival was not driven by individual inbreeding regardless of the inbreeding metric considered.

Similarly, the model with constant recruitment [$\delta(\cdot)$, $p(\text{SEX})$] was better supported than the models incorporating the three inbreeding metrics (Supplementary material S3, Table S4). Furthermore, the coefficient slope of each metric was not significantly different from 0 (PHt: 0.21; IR: -0.39 ; HL: -0.25) and had large confidence intervals (PHt: -0.40 to 0.81; IR: -1.09 to 0.30; HL: -0.91 to 0.41). This suggests that adult recruitment was not affected by individual level of inbreeding.

Discussion

Our study showed that the population of *T. urogallus* experienced a severe decline between 2010 and 2015. We did not detect any Allee effect on survival or recruitment. By contrast, individuals of both sexes dispersed to avoid small subpopulations, suggesting a potential behavioral response to a mate finding Allee effect. Survival was relatively constant over time, while recruitment was more variable. In parallel to this demographic decline, the population displayed a low genetic diversity and a high inbreeding (compared to that reported in this species, Segelbacher et al. 2002, 2003; Rodríguez-Muñoz et al. 2007, Klinga et al. 2015). The effective population size at both subpopulation and population levels was low. Furthermore, we did not find evidence of

inbreeding depression as inbreeding affected neither survival nor recruitment probability.

Demographic processes

Our study revealed a dramatic demographic decline (-52%), which was likely caused by a decline in recruitment rate rather than a decrease in adult survival; recruitment did compensate adult mortality which led to population decline over the 6-year period. Indeed, adult survival estimates were similar to that reported in other population of *T. urogallus* (Storch 2007 and references therein). The low temporal variation of survival probability indicated limited demographic and environmental stochasticity for this vital rate and suggested demographic buffering (i.e., reduction of the temporal variance of the demographic parameter having the highest contribution to population growth rate; Hilde et al. 2020). Moreover, our analyses did not reveal any temporal trend in survival that could explain the population decline. By contrast, recruitment rate was more variable between years, with substantial drops in 2013 and 2015. The trend analysis did not reveal any statistically significant gradual changes of recruitment over time. However, the negative coefficient slope of time effect in the model suggests that we failed to detect a negative trend, probably due to a lack of statistical power; the small population size and the shortness of study period likely decreases model estimate accuracy for this parameter.

Our findings revealed that the population loss was stronger in the large subpopulations (-40%) than in the small ones (-20%), which argued against positive density-dependence on population growth ('demographic Allee effect', Stephens et al. 1999). They also indicated that survival and recruitment were not affected by subpopulation size, suggesting the absence of Allee effect on fitness components. By contrast, dispersal probabilities (both departure and arrival) were asymmetrical and indicated a behavioral response to 'mate finding Allee effect' (i.e. difficulty to locate mate due to low conspecific density). Both males and females had a lower probability of emigrating from large subpopulations; in parallel, dispersers of both sexes more often immigrated into large subpopulations. In tetraonids, a previous study showed that females preferentially reproduce in large leks, which results in a higher reproductive success for the males attending these leks (Bradbury and Gibson 1983; Beehler and Foster 1988). Aggregation of individuals reduces the demographic Allee effect and limit the effects of demographic stochasticity in the largest subpopulations. By contrast, it reduces the chance of new lek formation (Warren et al. 2017) and enhances the risk of small lek disappearance (low 'rescue effect', Hanski et al. 1997).

The high variation of recruitment over time (and possibly over space) suggests that intrinsic and/or extrinsic factors

affecting the recruitment process were the main drivers of population decline. Our study shows that recruitment variation was likely independent of subpopulation size. However, habitat loss and alteration could have a detrimental effect on female fecundity and chick survival, and therefore on adult recruitment few years later. As well, weather variation may have a strong recruitment in Galliformes (*Callipepla californica*: Botsford et al. 1988; *T. tetrix*: Moss 1986; *T. urogallus*: Moss and Oswald 1985; Moss et al. 2001), which may affect population dynamics and synchrony (Lindström et al. 1996). For instance, Moss et al. (2001) showed that gradual shift from early to mid-April of spring warming reduced synchrony between the start of vegetation growth and peak of juvenile energetic demands, and potentially decreased female reproductive success. Rapid change in vegetation phenology in the Vosges Mountains also correlated with delayed peak of activity at capercaillie lek and suggests a negative impact of climatic factors on recruitment rate in this population (Ménoni et al. 2012). The detrimental effects of environmental variation could amplify inbreeding depression in the populations of *T. urogallus* (Armbruster and Reed 2005; Fox and Reed 2011). Improving our knowledge about the effects of environmental variation on demographic rates is a critical challenge to better predict the long-term viability of *T. urogallus* populations.

Genetic processes

Our study highlighted low genetic diversity and high inbreeding in this declining population. The mean allelic richness (2.64 at the whole population level), and the expected heterozygosity (0.44) were low compared to those reported in *T. urogallus* populations from central and northern Europe and relatively similar to those measured in small, fragmented populations (Segelbacher et al. 2002, 2003; Rodríguez-Muñoz et al. 2007). The inbreeding coefficient F_{IS} (0.14) was among the highest reported in the range of *T. urogallus* (Segelbacher et al. 2002, 2003; Rodríguez-Muñoz et al. 2007; Klinga et al. 2015), close to the F_{IS} of 0.15 reported in a population from western Carpathians (Klinga et al. 2015). Fragmentation of the distribution range of the species during the twentieth century (Storch 2007) led to the loss of genetic connectivity between the Alpine core population and peripheral, small populations, as described by Segelbacher et al. (2003). At that time, i.e. approximately 5–6 generations ago, the authors already reported high levels of genetic differentiation between the population in the Vosges Mountains and the Alpine population ($F_{ST} > 0.10$). It is thus very likely that the level of genetic differentiation between these two populations further increased, exacerbated by the decline of the population and the low subpopulation-specific N_e .

At the subpopulation level, the ratio N_e/N_b was less than 1, which results from the mating system of *T. urogallus* where few dominant males monopolize most of the mates, leading to a skewed reproductive success. This pattern is congruent with results from a previous study focusing on bird species with a lekking behaviour (Stiver et al. 2008; Verkuil et al. 2014). At the whole population level, the meta- N_e is far less than the sum of the subpopulation-specific N_e . This likely results from a non-random dispersal (depending on subpopulation size) that should result in asymmetric gene flow between small and large subpopulations. Migration rates m between large subpopulations are also asymmetric, which suggests that other social factors than subpopulation size affects dispersal. A previous study on this population found that females disperse in response to inbreeding risk whereas males preferentially join subpopulations composed of relatives (Cayuela et al. 2019). Furthermore, landscape resistance (especially landform) also results in asymmetric gene flow in the population (Cayuela et al. 2019). These results emphasize the importance of considering dispersal patterns and population genetic structuring for the estimation and the interpretation of N_e (Wang and Whitlock 2003; Palstra and Ruzzante 2008).

Although we highlighted a high inbreeding level at both subpopulation and population scales, we did not find evidence of inbreeding depression at adult stage in our study system. Both survival and recruitment of adults were not affected by individual inbreeding. Given the small size of the population, one cannot rule out the possibility that the absence of significant effect was due to a low statistical power. That being said, for survival, the slope of coefficients associated with the inbreeding metrics were not significantly different from 0, which suggests small effect size rather than low accuracy of the estimates. For recruitment, the accuracy of model estimates was low, likely to due to small sample size. To our knowledge, no evidence for detrimental effect of inbreeding on adult survival has been reported in capercaillie. By contrast, inbreeding has been reported to negatively affect egg hatchability rate in the Greater prairie chicken (Westemeier et al. 1998), susceptibility to parasite and juvenile mortality in capercaillie (Isomursu et al. 2012), and male lifetime mating success in Black grouse (Höglund et al. 2002), which all have to potential to negatively impact recruitment in the population. To conclude, we did not find direct evidence that high inbreeding level had a detrimental impact of survival-related or recruitment-related performances in adults of *T. urogallus*. However, as the effects of inbreeding depression can be stronger at early stages than later in stage (Crnokrak and Roff 1999) and may accumulate across life history stages (Grueber et al. 2010), further studies should investigate the effect of inbreeding on hatching rate, survival rates of nestlings, and survival during the first year of life in *T. urogallus* populations. The effect of

inbreeding depression at early stages should be examined using genome-wide markers generated from new generation sequencing technologies to quantify genetic load and identify potentially deleterious mutations in the genomic background.

Relative effects of demographic and genetic processes

The rapid decline of the population (50% of loss in six years, i.e. in less than two generations) suggests a higher contribution of the demographic factors than the genetic ones in the decline of the population. This interpretation is congruent with the statements of Lande (1988; and others later, Elgar and Clode 2001; Wootton and Pfister 2013) who postulated that demographic factors usually act faster than genetic ones in population declines and biological extinction processes. Although we did not detect inbreeding effect on adult survival and recruitment, it remains nevertheless possible that inbreeding speeds up the population decrease, by affecting female fecundity, egg hatchability, and chick survival—three parameters not considered in this study and which also contribute to adult recruitment. However, in lek-breeding species, mechanisms related to sexual selection (i.e. disassortative mating or heterozygosity-based mate choice; Tregenza and Wedell 2000; Ryder et al. 2009) and dispersal (i.e. context-dependent dispersal based on inbreeding avoidance, Lebigre et al. 2010; Cayuela et al. 2019) may limit the risk of inbreeding. Future studies should be undertaken to better understand if and how these behavioural mechanisms allow mitigating inbreeding depression and the contribution of genetic factors in population declines.

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Author contribution statement HC and GJ conceived and designed the study. FG and AL collected the data. HC, JGP, ML, JG, FF, and BL managed and analyzed the genetic and demographic data. HC wrote the manuscript; other authors provided editorial advice.

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