

Population dynamics of an endangered forest bird using mark-recapture models based on DNA-tagging

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Abstract

Populations of vertebrates are built of individuals of different sex, age class or stage, which often affect distinctly the population dynamics. Such intrapopulation partitioning of vital rates needs to be identified to develop efficient conservation actions. Using DNA extracted from feces and feathers we combined DNA-tagging and mark-recapture analyses to evaluate sex-specific population dynamics of an endangered population of capercaillie (*Tetrao urogallus*; Phasianidae). We built encounter histories for 120 individuals in the mating seasons of 2009 to 2011, in a study area of about 424 km². Minimum number of individuals per mating season and estimates of population size ranged 56 to 67 and 76 to 115, respectively. Estimates of population size were consistently lower in multiple-season, open-population models than in single-season closed-population models. The super-population in the study area was 149 individuals for the whole study period. Sex-ratio was notably male-biased. Probability of recapture p ranged 0.62 to 0.70, and was similar for males and females. Female apparent survival ϕ was lower than expected, and much lower than male apparent survival. It includes however movements in and out of the sampled population, thus comparison with previously reported values based on conventional tagging should be cautious. Females showed higher turnover, indicated by higher probability β of entering the sampled population, and higher number of entries from the super-population B_{gross} . Realized population growth rate λ was > 1 for both females and males. The combination of non-intrusive DNA-tagging and the analytical framework of mark-recapture models provided inferences on population dynamics that would have been hardly feasible with conventional methods. Male-biased sex ratios, higher female turnover and seemingly low female apparent survival were our key findings. While the whole population needs continuous monitoring, we believe that adult females deserve priority attention in evaluation and design of conservation actions.

Introduction

Small populations are particularly vulnerable to the downside of environmental and demographic stochasticity, which hamper their viability even in the absence of deterministic drivers of decline (Boyce 1992). Extinction risk further increases in peripheral populations (e.g. Carvalho et al. 2019), or when small population size meets insufficient connectivity (Reed 2004), and insufficient density of conspecifics (positive density-dependence; e.g. Stephens and Sutherland 1999). The latter might cause lower viability than expected from mere abundance or habitat quality, especially in social species or those showing complex mating systems (Legendre et al. 1999).

It is precisely in small populations where it is even more important to correctly determine abundance as well as presence (Rout et al. 2010). It is also key understanding the structure of the population: how many males, how many females and how many juveniles compose it, and whether it shows intrapopulation differences in vital rates (Durell 2000). Such information is basic for a conservation strategy of an endangered population. But it is seldom easy obtaining that sort of information in animals, even less if the animals of interest have become rare and elusive. Remnant individuals of threatened populations are those that escaped the causes of decline of their population, or their descendants, and might be more cautious or live in more secluded areas, particularly if their populations were subject to exploitation (McDougall et al. 2006; Biro and Dingemanse 2009). In consequence, evaluating their viability with hard data would probably entail great sampling effort and uncertainty.

Once the question of how many individuals remain in a population is better understood, we should consider that conservation strategies might not be adequate if directed towards an average population trait (Durell 2000; Bolnick et al. 2003). Populations of vertebrates are built of individuals of different sexes, age classes or stages, which often have distinct requirements, play distinct roles in the life cycle, and can be specifically affected by the environment. In other words, they likely affect distinctly the population dynamics (e.g. Lindström and Kokko 1998). It is for instance relevant to know whether the adult sex ratio is demographically balanced (e.g. Bessa-Gomes et al. 2004), or whether a component of the population predominantly determines viability (Caswell 2001).

The advent of methods based on genetic tagging to identify individuals from feces or shed tissues (Palsbøll 1999; Luikart et al. 2010) eases difficulties of surveying rare and threatened populations. Despite the lower quality and quantity of DNA obtained non-invasively, genetic tagging can provide information on a larger number of individuals than physical captures, improving the power of models of population dynamics. In addition, DNA-tagging could help equalize the detectability of individuals at the shy and bold ends of the temperament spectrum (Katzner et al. 2011). However, consistent detectability should still be kept in mind when designing the sampling, and analyzing data (Mulders et al. 2007; Marucco et al. 2011; Mollet et al. 2015).

Methods based on marking and recapturing individuals to infer population dynamics can be adapted to the indirect tracking provided by DNA-tagging (Lukacs and Burnham 2005). Those mark-recapture models use the identifications (*captures*) of individuals to estimate demographic parameters (Sandercock 2003). Several approaches are available within the combined framework of DNA-tagging and mark-recapture models, requiring varied assumptions and offering specific insights. Single-season models assume closed populations to estimate population size, and depend on the probability of recapture and its heterogeneity (Miller et al 2005). Multiple-season estimates use the histories of encounters of identified individuals among mating seasons, and depend both on the total number of individuals contributing to the sampled population (the so called super-population size; Schwarz and Arnason 1996), the annual survival, and the turnover within the sampled population (White and Burnham 1999; Marucco et al 2012). The assumption of population closure in the former seems fair for a sampling event during a single breeding season, particularly if the animals gather in specific areas. On the other hand, monitoring during multiple seasons implies an open population setting because there will be deaths and emigration, and recruitment and immigration. Single-season estimates of population size based on non-invasive sampling are simpler and cheaper, thus appealing for monitoring, although they might overestimate abundance when heterogeneity of encounters is moderate (Puechmaille and Petit 2007). Multiple-season approaches on the other hand would permit evaluating time consistency of the estimates (White and Burnham 1999), thus help identifying exceptionally high or low values, which are particularly relevant in small or declining populations.

Capercaillies (*Tetrao urogallus*; Phasianidae) are large forest birds that need large tracts of primary habitat, and have been identified as indicators of overall forest conservation status (Suter et al. 2002; Laiolo et al. 2011). They are herbivorous, and show marked sexual dimorphism. At about 2kg, females weight half as much as males, and unlike them show cryptic plumage. Birds gather in spring at mating areas, which remain relatively stable throughout the years. The species is polygynous; males contest and display at dawn in front of females in those areas, and dominant males monopolize mating, although it is uncertain to what extent. Males do not participate in the incubation, or the care of precocious young (Johnsgard 1983). We studied a clear example of a rear edge population (Hampe and Petit 2005): the distinct, endangered Cantabrian capercaillie (Storch et al. 2006; Rodríguez-Muñoz et al. 2007), which clings to broad-leaved forests at edge of the vast capercaillie range (Figure 1). About 100 individuals were estimated in 2009 (Morán-Luis et al. 2014) in an area of higher habitat quality than most of the historical range of the population (Quevedo et al. 2006). Indications of population decline were perceived already several decades ago and constrained the population to the western edge of the historical range (Castroviejo et al. 1974; Pollo et al. 2005; Bañuelos and Quevedo 2008), but the ultimate causes of decline remain unclear. Vital rates have never been obtained; there were just hints of low reproductive output compared to other capercaillie populations (Bañuelos et al. 2008), particularly in terms of the fraction of females that reared young through the summer. In the Cantabrian range habitat availability and connectivity has been low for many decades, and previous studies pointed to an indirect link between habitat suitability and decline in occupancy (Quevedo et al. 2006). The population

sustained intense trophy hunting mortality that targeted displaying males until the early 1980s, and poaching proceeded well into the 1990s (Rodríguez-Muñoz et al. 2015).

We sought to improve understanding on which aspects of population dynamics could be driving the worrying decline in occupancy of Cantabrian capercaillie. We used a combination of mark-recapture models and DNA-tagging to estimate sex-specific apparent survival, turnover, and growth rate. While survival is an obvious requirement of demographic analyses, we also looked at sex ratio because if biased it could lower the reproductive output via lowered chances of individuals finding a partner (Robertson et al. 2006; Donald 2007; Weir et al. 2011), and it is an important component of management actions (Lambertucci et al. 2013).

Methods

Sample collection

We collected capercaillie droppings and feathers in the western Cantabrian Range of NW Spain (Morán-Luis et al. 2014). We sampled display areas in spring (mid-March to early June) of 2009, 2010 and 2011, during mating seasons of Cantabrian capercaillie. Each mating season was thus a *sampling event* in the context of mark-recapture models (Lukacs and Burnham 2005). We sought to identify and follow in time capercaillie individuals using DNA-tagging. Our spring sampling of birds attending mating areas likely included both yearlings and adults (Watson and Moss 2008). Hence in our case *the population* refers to potentially breeding birds in the study area, and inferences refer specifically to that group of individuals. Mating season is arguably the period when habitat use by females and males is more similar (Bañuelos et al. 2008), thus heterogeneity of recapture should be less sex-specific. In addition, collecting an adequate number of samples for capture – recapture models would be uncertain in other seasons when habitat use is less understood and birds are more dispersed.

We sampled forest patches that included 62 previously known display areas, of which 83% had capercaillie presence during the mating season at any time since year 2000. Those forest patches were surveyed during 2 to 3 hours by two people. We searched again after 2–3 weeks those places that yielded no samples in the first visit. We used the location of display areas from previous reports as a mere entry point and searched outwards over larger areas seeking to include also birds using mostly the periphery. We recorded the position and aspect of droppings (size, shape and apparent content). Droppings were stored in tubes with silica-gel and frozen at -20 C until DNA extraction. We traced a minimum convex polygon covering display areas, each surrounded by an arbitrary 500 m buffer, as reference to the extent of the study area. We estimated a 56% forest cover in the study area from 1:50.000 maps of forest and land use (Fig. 1).

We extracted DNA from feces using a commercial extraction kit (QIAamp Fast DNA Stool Mini, QUIAGEN), following the manufacturer's specifications with some modifications (Morán-Luis 2017). DNA extraction from feathers was done following Hogan et al. (2008) protocol. We used five microsatellite markers previously developed for *Tetrao urogallus* (TUD2, TUD4, TUD5, TUT1 and TUT3, Segelbacher et al. 2000), and four microsatellite markers developed for the closely related *Tetrao tetrix* (TTD2, TTD6, BG10 and BG15; Caizergues et al. 2001; Piertney & Höglund 2001). Sex assignment was done using primers specifically designed for Cantabrian capercaillie, based on the amplification of a CHD1 gene intron (PU and P8mod; Pérez et al. 2011).

In 2009 we amplified each microsatellite individually, combined afterwards in three post-PCR multiplexes (see reaction conditions in Morán-Luis et al. 2014). In 2010 and 2011 microsatellites were combined for amplification in three PCR multiplexes, based on allele size ranges and fluorescent dyes (see details in the Electronic Supplementary Material). For samples from 2009, PCR products were run in two different genotyping platforms (MegaBace 1000 Automated Sequencer and ABI Prism 3100 Genetic Analyzer) following a thorough protocol for calibration and standardization of allele sizes (Morán-Luis et al. 2014); subsequently only the latter genotyping platform was used (see details in the Electronic Supplementary Material). We followed a modification of the multiple-tube approach (Taberlet and Luikart 1999), so that a consensus genotype for each sample was determined after a minimum of two independent positive PCRs for heterozygotes, and three for homozygotes. Each sample required between 2 and 7 independent amplifications, depending on DNA quality. Profiles were double-blind scored by at least two observers, to ensure a consistent interpretation. We used ALLELEMATCH (Galpern et al. 2012) to assign the genetic profiles to individuals.

We estimated genotyping errors (false alleles and allelic dropout) at each locus across PCRs amplifications using GIMLET (Valière 2002). Observed and expected heterozygosity, and deviations from Hardy-Weinberg equilibrium were estimated with GENEPOP 4.2 (Raymond and Rousset 1995). We used MICROCHECKER (Van Oosterhout et al. 2004) and DROPOUT (McKelvey and Schwartz 2005) to check for potential mismatches in genetic profiles due to allelic dropout, false alleles and null alleles. We also used RELIOTYPE (Miller et al. 2002) to assess the reliability of the genetic profiles. See further details in the Electronic Supplementary Material.

To assess the ability of the selected microsatellite loci to discriminate individuals, we calculated the probability of identity PI and probability of identity of siblings PI_{SIB} (Mills et al. 2000; Waits et al. 2001). These estimate the probability that any two individuals from the population share the same genetic profile, even if they are full siblings. PI and PI_{SIB} for each marker as well as cumulative PI and PI_{SIB} for each sample were estimated using GIMLET (Valière 2002). We considered that the risk of two individuals sharing the same genotype was negligible at cumulative $PI_{SIB} < 0.01$ (Mills et al. 2000; Waits et al. 2001).

The number of individuals identified each spring indicated the minimum population size (Table 2; N_{min}) in the study area during the mating season. DNA-based mark-recapture models consider first encounters of each of those unique genotypes as a *mark*, or initial identification of an individual, tallying *recapture* whenever the same individual is encountered again in another sample. We estimated single-season population size N_{cap} in the springs of 2009, 2010 and 2011 using CAPWIRE, an algorithm designed for non-invasive genetic sampling (Miller et al. 2005; Pennell et al. 2013). To prevent the excessive influence in the estimates of individuals that were disproportionately encountered, we used just one of any two samples from the same location (up to a distance of 25 m) and sampling event that yielded identical genotypes. Still, individuals can show differential capturability in the dataset, so we used an estimator that accounts for that possibility (Two Innate Rates Model, TIRM), and also calculated population size separately for males and females. Even so, some individuals were captured much more frequently than assumed by TIRM estimations; in those cases we used a partitioning method (PART) implemented for CAPWIRE in the namesake R package to account for this type of overdispersion in the data (Pennell et al. 2013; R Core Team 2018). The partitioning method divides data into three groups based on the number of recaptures in the same sampling event. Individuals detected many times are excluded, since they provide little information about population size and are inconsistent with the modeling assumption of just two capture rates. The other two groups (individuals captured between few and a moderate number of times) are then analyzed using the TIRM model, and the number of individuals in the upper group is subsequently added to the N_{cap} estimate.

We estimated contemporary effective population size N_e for the period of study using *NeEstimator* 2.1 (Do et al. 2014). The method assumes that only genetic drift (and not mutation, selection or migration) is responsible for the signal in the data. We assumed random mating and followed indications to exclude rare alleles with low frequencies P_{crit} assuming they were rare enough to be the result of recent mutations (Waples and Do 2010). We set P_{crit} to 0.02 ($n=120$ samples) and chose a *jackknife* procedure to get the 95% confidence interval. We repeated the analyses using only those genotypes without missing data.

Multiple-season models and demographic parameters

Multiple-season open-population models are based on live encounters, i.e. captures or re-sightings of distinguishable individuals, or like in our case on DNA identification of individual birds. We built encounter histories for individuals identified by DNA tagging during the three consecutive mating seasons of 2009, 2010, and 2011. We used three types of models developed for open populations to estimate several demographic parameters (Table 1; Fig. 2). We built additive models, so that we could evaluate the variation in demographic parameters as a function of several factors, specifically sampling occasion (the mating seasons of 2009 to 2011), and sex, the latter based on expected differential survival of capercaillie males and females (e.g. Grimm and Storch 2000). We used MARK 8.0 (White and Burnham 1999).

First, we used Cormack-Jolly-Seber models (CJS) that focus mostly on estimating survival of identified ('marked') animals. CJS models estimate apparent survival (ϕ), and probability of recapture p at occasion $t+1$ of individuals identified at occasion t (Cormack 1964; Jolly 1965; Seber 1965). Unless dispersal to and from the studied population could be considered negligible, apparent survival normally underestimates true survival because individuals that leave the study area are tallied as dead (e.g. Cilimburg et al. 2002; Marucco et al. 2012).

Second, we used the POPAN formulation of Jolly-Seber models (Jolly 1965; Seber 1965), which track the fate of both identified and unidentified (unmarked) individuals. The POPAN formulation assumes that the animals encountered during the study period are part of a larger *super-population*, defined as the total number of birds that entered the sampled population at some time between the first and last sampling events. This formulation provides estimates of additional demographic parameters like the probability of entry (β) of individuals into the population (Schwarz and Arnason 1996), abundance each spring (N_{popan}), gross and net new entries in the population (B_{gross} and B_{net}), and the size N_s of the super-population (Williams et al. 2011; Table 1). POPAN models estimate also apparent survival from occasion t to $t+1$ (ϕ) and probability of capture (p).

Third, we used the reverse-time Pradel models (Pradel 1996) implemented in MARK to estimate the realized growth rate (λ), i.e. the observed change in population size from t to $t+1$, based on survival and seniority. The latter is the probability that an individual identified at time t was present in the population at $t-1$. Pradel models estimate also apparent survival (ϕ) and probability of capture (p).

We estimated apparent life-span (understood as permanence in the population) as $-1 / \ln \phi$, from apparent survival estimates obtained in CJS, POPAN and Pradel models.

Model fitting and selection

We used the parametric bootstrap procedure (1000 replicates) provided in MARK to evaluate that model's assumptions were met in most parameterized models of sex-specific apparent survival (see caveats in White 2002; Cooch and White 2017). Such goodness of fit procedure simulates encounter histories that meet the assumptions of the models, based on the actual number of animals found. We derived all possible partial models from the most parameterized sex-specific and time-variant model, checked all outputs dropping those with poorly estimated parameters given the data, and adjusted those with not estimable parameters due to the intrinsic structure of the model (Cooch and White 2017).

We used model-averaging based on normalized AIC weights (w_i) to obtain parameter estimates. We considered all models from the candidate set at once, thus including model selection uncertainty in the estimate of each parameter and its associated variance (Anderson et al. 2000; Burnham and Anderson 2002).

Results

We obtained 74% extraction and 79% amplification success from an initial batch of 752 samples. After genotype profile validation with ALLELEMATCH, and removal of samples from one lek located at the edge of the study area that could only be sampled in 2011, we got valid individual identification from 408 samples, using at least 7 microsatellites in 390 of them. For another 18 samples, which corresponded to 14 unique genotypes and 4 recaptures, consensus identification was based on 6 microsatellites after incorporating additional information on sex, display area, and distance (see the Electronic Supplementary Material). Cumulative PI_{SIB} was lower than 0.01 with the seven least informative microsatellite loci (Electronic Supplementary Material). The number of alleles per microsatellite locus was 4.6 ± 1.1 (mean $\pm$ SD). Estimated and observed heterozygosity were 0.62 ± 0.08 and 0.52 ± 0.12 , respectively (mean $\pm$ SD).

We identified 120 capercaillies throughout the study period (46 females, 67 males and 7 individuals that could not be sexed). That figure represents the minimum number of capercaillies present in the 424 km² study area between 2009 and 2011. In successive field seasons we encountered 69 of those 120 identified birds; we encountered 11 of them in the three field seasons. Median number of recaptures per individual each spring, which influences single-season estimates of population size, was 2.0 (Table 2).

We identified 56 to 67 capercaillies each spring (Table 2; N_{min}). Single-season estimates of population size (N_{cap}) ranged from 101 to 115 individuals (Table 2). Estimates of population size from open population models (Table 2; N_{popan}) were consistently lower, ranging from 76 individuals in 2009 to 95 in 2011. The gross super-population N_{Sgross} for the period 2009-2011 was 79 males and 70 females (95% CI: 69 - 88 and 53 - 88, respectively). The net super-population N_{Snet} , or individuals present in the study area at least one spring, was 76 males and 59 females (95% CI: 67 - 86 and 44 - 73, respectively). Sex ratio was notably and consistently skewed towards males, both in directly identified individuals N_{min} and in estimates N_{cap} , N_{popan} and N_{Snet} (Table 2). It was less biased in the gross super-population N_{Sgross} .

The effective population size N_e based on genetic data for the 2009-2011 period was 22.4 (16.6 – 30.3 95% CI). We got almost the same result after excluding individuals with missing data: $N_e = 21.3$ (16.0 – 28.7 95% CI; n=73 individuals with 9 microsatellites).

Probability of recapture (p) was not affected by sex or time (Table 3), i.e. it was similar for males and females and remained relatively constant through the three field seasons (Fig. 3). It ranged 0.65 to 0.70 in POPAN and Pradel models. In CJS models, which take into account only identified individuals and thus yielded probabilities for the number of sampling events – 1, probability of recapture was slightly lower (Fig. 3).

Apparent survival ϕ was sex-specific in CJS, POPAN and Pradel models and did not differ appreciably between springs 2009 to 2011 (Table 3). Female apparent survival ranged 0.49 to 0.59, whereas males

ranged 0.85 to 0.90 (Fig. 3). Those estimates of apparent survival translate into a much shorter apparent life-span or long-term permanence in the study area for females (range 1.4 – 1.9 yr and 6.2 – 9.5 yr for females and males, respectively).

Probability that individuals from the net super-population entered the sampled population (β) was higher for females (Fig. 3 and Table 3). The average net entry of individuals between t and $t+1$ B_{net} was 15 for both males and females (95% CI: 8 - 22), whereas gross entry B_{gross} was 16 for males and 21 for females (95% CI: 8 – 24 and 10 – 31, respectively).

Realized population growth rate λ estimated in Pradel models was > 1 for both females and males, albeit showing wide confidence intervals (Fig. 3). In addition, Pradel model selection did not identify a particularly parsimonious model, but several ones of similar weight.

Bootstrap tests of goodness-of-fit showed no indication of lack of fit or overdispersion for full CJS ($P = 0.55$; $\hat{c} = 0.62$) or Pradel models ($P = 0.65$; $\hat{c} = 0.55$). Bootstrap goodness-of-fit is not available for POPAN models in MARK, although we did not expect distinct behavior because we used the same dataset.

Discussion

We used a combination of fieldwork, non-invasive DNA-tagging and mark-recapture models to study population dynamics of Cantabrian capercaillie, a forest bird that has attracted conservation concern for decades (Castroviejo et al. 1974; Storch et al. 2006). We confirmed that the population appears critically small in terms of viability (Westemeier et al. 1998; Moss 2001; Frankham et al. 2014): our estimates of population size in the mating season ranged 76-115 individuals, depending on whether we used models based on single or multiple field seasons; estimates based on the latter were consistently lower (Table 2). Those capercaillies were part of the 135 individuals that were in the study area at least during one of the three mating seasons (the super-population N_{Snet}). Comparing the number of capercaillies that we identified and sexed ($n = 113$) with the estimates of net and gross super-population size suggests that sampling missed respectively 16% of the birds present during the mating season, and 24% of the birds present any time during the study period. The notion of a super-population is useful to illustrate the inherent difficulties of counting mobile animals, especially when their behavioral patterns can lead to asynchronous or generally uneven presence in the sampled population (Williams et al. 2011).

Estimating it appears particularly appropriate in non-intrusive studies like ours, where the actual animals are seldom seen. At any rate, it seems a safe assumption that there were other capercaillies outside the study area, although the latter has been considered the core of the remnant capercaillie population in the Cantabrian Mountains (Quevedo et al. 2006; Morán-Luis et al. 2014).

Particularly relevant from a population viability viewpoint is the effective population size, N_e . It captures better than census population size the genetic diversity and status of a population (Charlesworth 2009). Estimating it alongside vital rates is an advantage of models based on DNA-tagging. We found a N_e of

22 individuals for the whole studied period. At 16% of the super-population size N_{net} of 135 birds, the ratio of effective to census population size was close to expected values for structured vertebrate populations (Frankham 1995; Charlesworth 2009), albeit low considering that we sampled the sector of the population that visited the mating areas, but likely not the whole population.

A strongly biased sex-ratio is one possible determinant of low N_e to census population size ratio (Frankham 1995). In principle our results of male-biased sex-ratios (Table 2) would not be surprising because those are common in adult birds, possibly as consequence of higher mortality of females after balanced offspring sex ratios (Donald 2007). However, polygynous species do not necessarily conform to the overall pattern (Bessa-Gomes et al. 2004; Székely et al. 2014). We expected a balanced or even female-biased adult sex-ratio at display areas because dominant capercaillie males monopolize copulations and can mate with several females in their territory (Johnsgard 1983; Wegge and Larsen 1987; Watson and Moss 2008); however male-biased spring sex ratios have been previously reported in a Swiss capercaillie population (Mollet et al. 2015). As our estimates of abundance during the mating season reflect the proportion of females that could potentially mate, they indicate a male-biased operational sex ratio (Weir et al. 2011; Székely et al. 2014). Sex-ratio was less biased in the gross super-population N_{Sgross} , which takes into account also birds not available at the time of sampling. We also found that more females than males entered each year the sample population (higher female B_{gross} and β), and seemingly disappeared before the mating season. Such higher entry of females is consistent with reports of female-biased autumn brood sex-ratio in other capercaillie populations (Wegge 1980, Moss & Oswald 1985); followed by lower female survival through the winter, it could then result in balanced or male-biased adult sex-ratios in the mating season.

We found that apparent survival ϕ was much lower for females (Fig. 3). We were particularly interested in evaluating sex-specific demographic parameters because in populations that require conservation or, more generally, management it is relevant understanding intra-population partitioning (Durell 2000). We chose mark-recapture models that estimate survival because it usually drives population dynamics in vertebrates with strong reproductive investment and a single reproductive event per year (e.g. Lande 1988; Sæther and Bakke 2000). Besides, both theory and previous empirical data pointed to females as drivers of grouse population dynamics: parameters related to reproduction and female mortality have the highest impact on population viability (Hannon and Martin 2006), and female survival can be particularly important in polygynous species like capercaillie (Grimm and Storch 2000; Moss et al. 2006). In our case, lower female apparent survival appeared compensated by higher female turnover, i.e. higher probability that females from the super-population entered the sampled population, and higher number of female gross entries B_{gross} . Indeed, realized population growth rates λ were positive for both females and males (Fig. 3).

We were not surprised of finding sex-specific survival, given the marked sexual dimorphism and segregation of reproductive roles in capercaillie (Johnsgard 1983). However, interpreting the

implications of such sex-specific survival is not straightforward. Our female apparent survival was lower than expected from records in the literature, both in capercaillie (Wegge et al. 1987; Moss et al. 2000; Watson and Moss 2008; Augustine et al. 2019) and in the comparably large and sexually dimorphic sage grouse *Centrocercus urophasianus* (Johnson and Braun 1999). But with few exceptions published records of grouse vital rates or territory use have been mostly obtained by directly following with great effort a comparatively smaller number of tagged individuals, whose fate is often well known (e.g. Storch 1997; McNew et al. 2012). Mark-recapture models on the other hand estimate apparent survival, which does not differentiate deaths from movement of individuals in or out of the sampled population (e.g. Sandercock 2003). Thus non-invasive mark-recapture models can provide data with relative ease from a much higher number of individuals than actual captures, and might be the only ones feasible in rare and threatened populations, but interpretation of results against existing reference values should be cautious. It seems timely to foster non-intrusive methods of monitoring (Augustine et al. 2019) and better understanding of their specific sources of variation (Marucco et al. 2011, 2012).

One possible caveat of studies like ours would be that different sectors of the population were not equally represented, as can happen even with more direct methods and in more conspicuous species like imperial eagles (Katzner et al. 2011), or bearded vultures (Margalida et al. 2011). We sampled during the mating season because then both males and females visit display areas, although they do not necessarily use them alike: females do not display and show more sporadic presence, and subordinate or non-breeding males might remain at the periphery, waiting for their chance (Wegge and Larsen 1987; Storch 1997; Watson and Moss 2008). Nonetheless all of them regardless of sex, temperament or social status should be emptying their guts often due to their folivorous diets (Sedinger 1997). And using feces and shed feathers as source of DNA should not introduce biases like avoidance of the observer or response to an initial mark (see also Miller et al. 2005; Jacob et al. 2010). To evaluate potential sampling bias we can use probabilities of recapture estimated in the models (Prévot-Julliard et al. 1998; Marucco et al. 2012): In single-season models we got enough recaptures of both males and females to get reliable estimates for small populations (Miller et al. 2005). In addition, probabilities of recapture in our open-population models were in the range of those found in other mobile vertebrates (e.g. Bradshaw et al. 2003, Sandercock 2003). And what is more important, probabilities of recapture were similar for males and females, and remained consistent through sampling events (Fig. 3 and Table 3). They did not appear to have a confounding effect on estimates of sex-ratio or sex-specific apparent survival.

Conclusions

While keeping in mind the inherent uncertainty of the non-intrusive but indirect method that we used, sex ratios notably biased towards males, higher female turnover, and seemingly low female apparent survival were salient aspects of our study. We believe that the fate of adult females of Cantabrian capercaillie deserves priority in further monitoring and evaluation of conservation actions. Besides, the

whole population requires close and continuous monitoring. Precisely scarce and elusive populations like Cantabrian capercaillie could benefit from a combination of snapshot monitoring and multiple season estimates of vital rates, based on DNA-tagging and mark-recapture models. Both estimates and interpretation require sampling designs that consider intra-population partitioning, and both extended and consistent monitoring. The latter is essential to narrow the confidence intervals of estimates, and to help distinguishing short-term fluctuations and population trends (e.g. McCain et al. 2016).

Conflict of Interest: The authors declare that they have no conflict of interest.

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Table 1. Description of parameters.

N_{min}	Individuals identified each spring by means of DNA-tagging.
N_{cap}	Single-season estimates of population size obtained via CAPWIRE models. Estimates were based on N_{min} and the scheme of individual recaptures.
N_{popan}	Estimates of population size based on multiple-season, open-population models (POPAN formulation of Jolly-Seber models).
N_{Sgross}	Gross super-population size: estimate of the total number of individuals that entered the sampled population between the first and last sampling occasion.
N_{Snet}	Net super-population size: as above, but tallying only individuals that were in the study area during at least one sampling occasion.
φ	Apparent survival: probability of individuals surviving between sampling occasions t and $t+1$. In CJS models it takes into account only identified (marked) individuals, whereas in <i>POPAN</i> models it includes both identified and unidentified individuals.
p	Probability of recapture of individuals alive in sampling occasion $t+1$ that were identified in t . Probability of capture at t in the case of POPAN and Pradel models.
β	Probability that an individual from the super-population N_{Snet} enters the population between t and $t+1$.
B_{net}	Net new entries. Individuals that entered the population between t and $t+1$.
B_{Sgross}	Gross new entries. As above plus individuals that entered between two sampling occasions but either emigrate or die before being subject to capture at $t+1$.
λ	Realized population growth rate.

Table 2. Minimum number of individuals, and estimates of population size of Cantabrian capercaillie. N_{min} is the number of identified individuals, i.e. the minimum number of individuals; N_{cap} and N_{popan} are estimates of population size corresponding to single-season closed population models and open-population models, respectively. Superscripts beside 95% confidence intervals of N_{cap} indicate cases when a partitioning method was required as an additional step in the analysis to account for further presence of singletons and frequently captured individuals in the dataset (PART; Pennell et al. 2013).

		Samples	Encounters per individual (median)	N_{min}	N_{cap}	N_{popan}
2009	All	136	1.98	57	104 (92-142) ^{part}	
	Males	98	2.15	35	56 (47-81) ^{part}	47 ± 8 (32-62)
	Females	34	1.78	19	35 (23-59)	29 ± 9 (12-46)
2010	All	131	1.80	56	101 (84-136) ^{part}	
	Males	92	2.03	31	43 (38-62) ^{part}	56 ± 7 (42-70)
	Females	36	1.63	22	49 (36-87)	31 ± 7 (16-45)
2011	All	141	2.10	67	115 (99-157)	
	Males	103	2.28	45	73 (60-97)	63 ± 10 (44-82)
	Females	37	1.72	21	42 (32-72)	32 ± 8 (15-48)

Table 3. Model selection for Cormack-Jolly-Seber (CJS), POPAN, and Pradel models of apparent survival (ϕ), re-encounter probability (p), probability of entry (β), and realized population growth rate (λ). For each model we include the number of parameters (K), the Akaike Information Criterion corrected for small sample size (AIC_c), delta AIC_c , and AIC_c weights (w_i). We dropped or adjusted¹ those models with confounding parameter estimation. We ranked models according to their AIC_c values, and included only those with delta $AIC_c < 4$. Subscripts: c = constant; sex = distinct between males and females; time = changes among sampling events.

			K	AIC_c	Delta AIC_c	w_i	¹ Adjustments applied to models with non-estimable parameters (see Methods)
<i>Cormack-Jolly-Seber</i>							
ϕ_{sex}	p_c		3	177.8	0.0	0.602	
ϕ_{sex}	p_{time}		4	179.8	2.0	0.220	
$\phi_{sex \cdot time}$	p_c		5	180.8	3.0	0.133	
<i>POPAN</i>							
ϕ_{sex}	p_c	β_{sex}	7	216.4	0.00	0.485	
ϕ_{sex}	p_c	$\beta_{sex \cdot time}$	8	217.9	1.52	0.226	β_{males} time-invariant
ϕ_{sex}	p_{time}	β_{sex}	8	218.0	1.56	0.221	$p_{2009} = p_{2010}$
<i>Pradel</i>							
ϕ_{sex}	p_c	λ_c	4	419.4	0	0.166	
$\phi_{sex \cdot time}$	p_c	λ_c	6	419.5	0.13	0.156	
ϕ_{sex}	p_c	λ_{time}	5	419.5	0.17	0.152	
ϕ_{sex}	p_c	$\lambda_{sex \cdot time}$	7	420.2	0.87	0.107	
$\phi_{sex \cdot time}$	p_c	λ_{time}	7	420.2	0.88	0.107	
ϕ_{sex}	p_c	λ_{sex}	5	420.5	1.12	0.095	
$\phi_{sex \cdot time}$	p_c	λ_{sex}	7	421.5	2.12	0.057	
ϕ_{sex}	p_{time}	λ_c	6	421.7	2.31	0.052	
ϕ_{sex}	p_{time}	λ_{sex}	7	423.1	3.75	0.025	
$\phi_{sex \cdot time}$	p_c	$\lambda_{sex \cdot time}$	9	423.3	3.94	0.023	

Fig. 1. Geographic range of Western Capercaillie (BirdLife International and Handbook of the Birds of the World, 2017; Robinson projection). The black polygon in the lower-left corner corresponds to a coarse-scale, historical range of the Cantabrian population; the center of the dashed cross corresponds to the one in the inset, zoomed map of the study area. The latter is based on a minimum convex polygon including all sampled display areas. Shaded polygons indicate forest cover $\geq 10\%$.

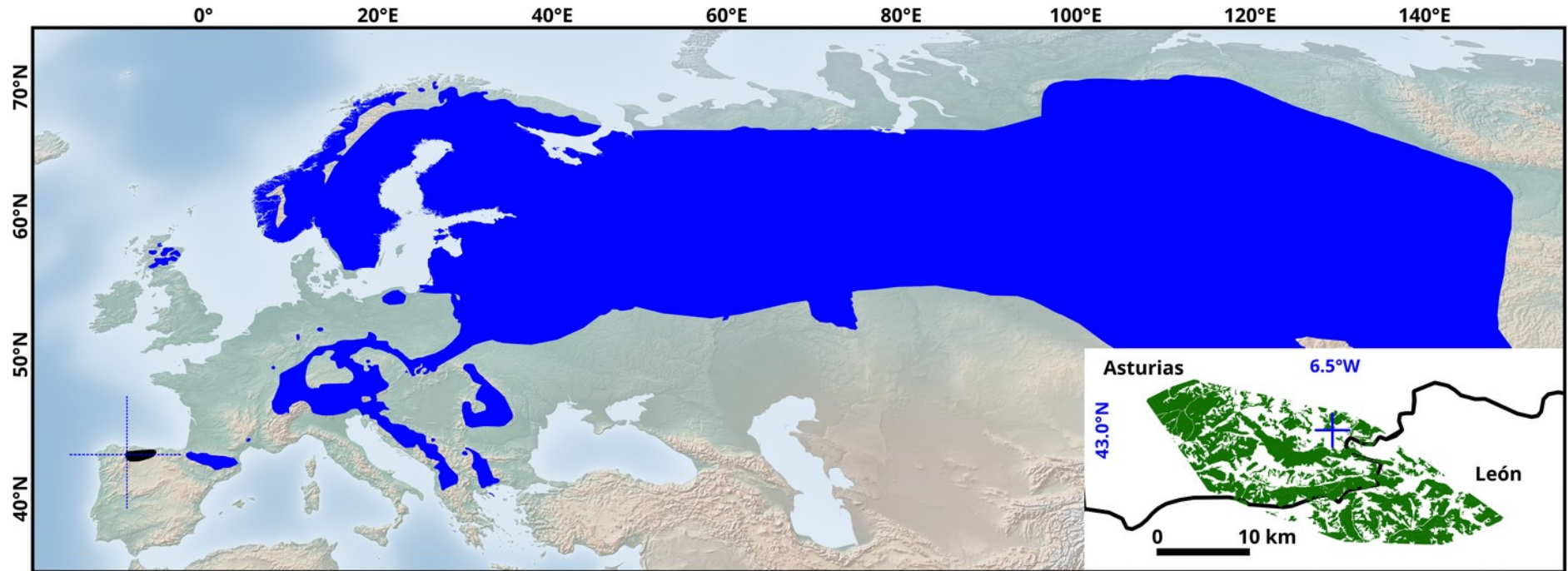


Fig. 2. Parameters considered and their position in the mark-recapture modeling scheme Super-population (N_s), or birds that entered the sampled population between the first and last sampling occasion; apparent survival (ϕ); probability of (re) capture of individuals (p); probability of individuals entering the population from the super-population (β); entries to the population (B); realized population growth rate (λ); individuals identified by DNA-tagging during each survey (N_{min}); single-season closed-population estimates of population size obtained via CAPWIRE models (N_{cap}); estimates of population size based on multiple-season open-population models (N_{popan}).

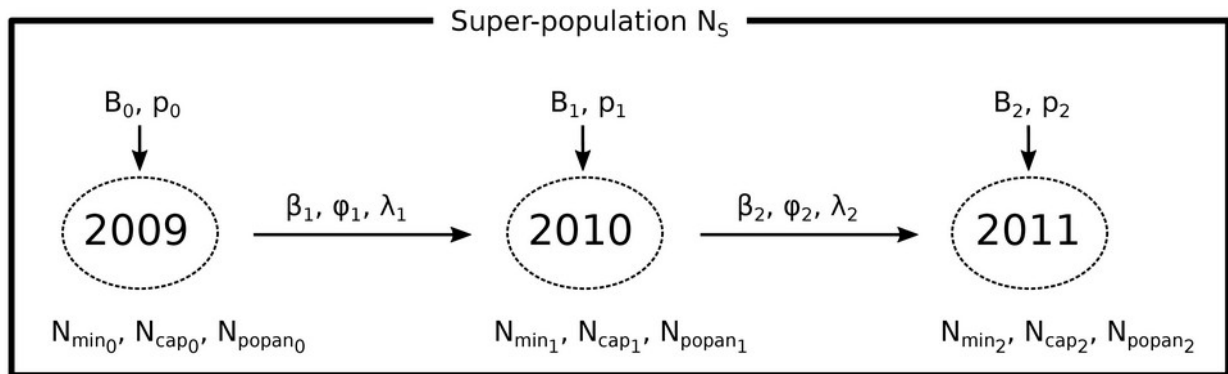


Fig. 3. Sex-specific demographic parameters of Cantabrian capercaillie derived from mark-recapture models. All panels show mean parameter values and 95% confidence intervals for male (solid) and female (dashed) capercaillie. Inset JS, Pr and CJS stand for Jolly-Seber POPAN, Pradel and Cormack-Jolly-Seber models, respectively. Apparent survival (ϕ) was estimated in CJS, POPAN and Pradel models. Probability of recapture (p): although the three model types deal with survival and recapture, they are not identical; CJS models used only marked animals whereas JS POPAN and Pradel models used both marked and unmarked. CJS gives a probability of recapture between occasions t and $t+1$, while JS POPAN and Pradel give a probability for each sampling event, which sometimes is termed "probability of capture". β is the probability that an individual from the super-population (N_{snet}) entered the sampled population between t and $t+1$. Realized population growth rate λ was estimated in Pradel models.

