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Research article

Improving population size estimation at western capercaillie leks: lek counts versus genetic methods

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The western capercaillie *Tetrao urogallus*, hereafter capercaillie, is the largest galliform bird present in the boreal and montane forests of the Western Palearctic. Precise and accurate methods for estimating the number of individuals and/or their densities are crucial for the proper management of its free-ranging populations. However, obtaining reliable estimates of the abundance of populations of wild species and, particularly, of birds is not a simple task. In the case of lek-mating birds such as capercaillie, surveys are traditionally based on lek counts, that is, counts of calling males present in their mating areas: the leks. This study was carried out on the Pyrenees at six capercaillie leks where two different lek counting approaches were performed: hide-based and walk-based. The results were compared with those obtained from an estimate of minimum population size (MPE) derived from genotyping all faeces samples found in the lek area, and with a population size estimate derived from a genetic mark-recapture model ($\hat{N}$) of each capercaillie lek. The results of $\hat{N}$ were used to estimate the detection rate (D) of both lek count approaches. Our results show that traditional lek counts do not detect all male capercaillies since the detection rate was 0.34 (95% CI: 0.26–0.43) for hide- and 0.56 (95% CI: 0.43–0.68) for walk-based lek counts. Our results suggest that the walk-based lek counts were more efficient than the hide-based ones, providing more accurate results compared to the $\hat{N}$ estimate. The combination of non-invasive sampling with genetic mark-recapture model was found to be the most reliable method for obtaining the $\hat{N}$ of leks given that traditional lek counts underestimate the number of capercaillie and, furthermore, can cause disturbance to the species at these sites.

Keywords: detection rate, genetic mark-recapture model, microsatellites, non-invasive genetic sampling, population size

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Introduction

The western capercaillie *Tetrao urogallus* (hereafter capercaillie) is the largest galliform bird present in the boreal and montane forests of the Western Palearctic. It is regarded as an umbrella species for these habitats since its presence correlates with a high diversity of other birds and mammals (Suter et al. 2002, Pakkala et al. 2003). Several molecular markers, mitochondrial, microsatellites and other nuclear markers have been described for this species for more than 20 years (Segelbacher et al. 2000, Lucchini et al. 2001). This allowed different studies on genetic diversity, habitat fragmentation and phylogeny, among others (Segelbacher et al. 2000, 2008, Lucchini et al. 2001, Rutkowski et al. 2017). More recently, many other studies have used these markers for studies on population size and sex-dispersal patterns (Jacob et al. 2010, Pérez et al. 2011, Mollet et al. 2015, Bañuelos et al. 2019, Zeni et al. 2023).

The distribution of the capercaillie is homogeneous and the species is fairly abundant across much of its boreal range (Segelbacher et al. 2003), however in western Europe its distribution is more fragmented and restricted to isolated mountain ranges such as the Pyrenees, Central Massif (France) and Cantabrian mountains (Spain) (de Juana 1994, Storch 2000, Segelbacher et al. 2003, BirdLife International 2016). The subspecies *T. u. aquitanicus* is endemic to the Pyrenees, where it is present from 900 to 2400 m a.s.l. It is flexible in its choice of forest type and is found in both deciduous forests *Fagus sylvatica* on the Atlantic side of this mountain chain and in coniferous forests (*Pinus mugo uncinata*, *P. silvestris* and *Abies alba*) on the Mediterranean side (Ménoni et al. 2004, Storch 2007). In the Pyrenees, capercaillie leks are distributed regularly with inter-lek distances of approximately 1.5–2 km (Ménoni 1991, Mossoll-Torres and Menoni 2006) and on average 2–3 males are usually counted in each lek (Robles et al. 2006). The mating system of the capercaillie is midway between that of the black grouse *Lyrurus tetrix*, which is only territorial at leks, and that of more territorial forest grouse species such as the ruffed grouse *Bonasa umbellus*, whose males have separate territories (Watson and Moss 2008). Capercaillie leks vary in size from 0.2 to 8 ha in the Pyrenees (Catusse 1993). Cocks remain a few metres away from each other and the whole lek is structured around the dominant male that attracts most hens (Watson and Moss 2008).

The first references to capercaillie monitoring techniques date back to the 1960s, when several methodologies, mainly based on transect surveys (on foot, by snowmobile or even by plane), were developed in European Nordic countries for estimating the number of individuals of this species (Rajala 1966, Couturier and Couturier 1980). Currently, in central and western Europe, surveys are based on lek counts performed early in the morning from hides placed in the centre of the lek, which we refer to as hide-based lek counts (Catusse and Novoa 1983, OGM 2017, Abrahams 2019, Aleix-Mata et al. 2019, Baines and Aebischer 2023). These lek counts are conducted in a very similar way in all areas in which the capercaillie is present. However, there is also a variant that is walk-based and consists of walking around the lek site making stops to listen for capercaillie males. This approach is recommended for small leks or if there is an indication that the lek might have changed its location (Canut et al. 2006, OGM 2017).

Lek counts are commonly used for monitoring galliform species and are based on male displays (Sands and Pope 2010, Aleix-Mata et al. 2019, Baines and Aebischer 2023, Shyvers et al. 2023). Leks are the mating areas where females attend to mate, after which they leave the area (Höglund and Alatalo 1995) and return to their nesting habitat, usually about 300 m from the lek site in the Pyrenees (Ménoni 1997) or about 700 m in the Bavarian Alps (Storch 1997). Due to this behaviour, the chance of detecting females in lek counts is about half that of males (Storch 1997, Watson and Moss 2008, Mollet et al. 2015). Therefore, leks are not the best place for estimating female numbers with direct counts (Canut et al. 2006), so estimates based on lek counts are not representative of the whole population (Storch 1997, Wegge et al. 2005, Mollet et al. 2015, Aleix-Mata et al. 2019). Moreover, young and sub-adult males (< 2–3 years old), which are thought to represent half of the male population (Watson and Moss, 2008), position themselves on the periphery of the lek. Consequently, these individuals have lower chances to be detected compared to calling males. Therefore, lek counts underestimate the number of individuals of this species (Gullion 1981, Storch 2007, Jacob et al. 2010, Mollet et al. 2015, Lentner et al. 2018), moreover some authors suggest that the results of these counts are highly variable (Abrahams 2019, Aleix-Mata et al. 2019). Although, as for other lek species, it is important to have standardised field protocols for these counts in order to compare results (Johnson and Rowland 2007, Monroe et al. 2016), to date no comparative studies of hide- and walk-based approaches have ever been undertaken for capercaillies.

Precise and accurate methods for estimating the number of individuals in an area are crucial for addressing population status and trends, as well as for management purposes (Shea 1998, Williams et al. 2002, Monroe et al. 2016). This is especially relevant for game species when deciding hunting quotas, implementing and/or evaluating management measures, or quantifying the impact of hunting on population sustainability (Greenwood and Robinson 2006, Franceschi et al. 2014). However, obtaining reliable estimates of the population size of wild species – and, in particular, birds – is not always a simple task (Bibby 2004, Buckland et al. 2008). Abundance estimates of avian species by point-counts (e.g. hide-based lek counts) also require an estimate of the detection probability (Kissling et al. 2006, Sólymos et al. 2013) to increase accuracy (Ménoni et al. 2014, Calenge et al. 2022). It is also a key parameter in order to estimate site occupancy, local extinction probabilities and analyse the relation between abundance and detection (Mackenzie et al. 2003, Kéry and Schmidt 2008, McCarthy et al. 2013, Baines and Aebischer 2023). Indeed, the estimation and standardisation of this parameter should allow for comparisons to be made with the estimates of the number of individuals obtained using

other methodologies or in other areas (Farnsworth et al. 2002, Kissling et al. 2006, Wilkinson et al. 2018). However, it should be noted that the standardisation of detection probability is specific to each methodology.

Alternatively, methods based on non-invasive genetic sampling can be used to estimate the minimum number of capercaillies present at a lek (minimum population estimate, MPE) and have been shown to detect more than twice the number of male capercaillies than conventional hide-based lek counts (Jacob et al. 2010, Aleix-Mata et al. 2019). In addition, genetic mark-recaptures models can provide reliable estimates of population sizes (Solberg et al. 2006, Lampa et al. 2015, Woodruff et al. 2020, Schoenecker et al. 2021, Shyvers et al. 2023). To obtain better estimates, models for closed populations (Otis et al. 1978, Huggins 1989) are currently being adapted and implemented with maximum likelihood estimators (Lonsinger et al. 2019) or using Bayesian methods (Kéry and Royle 2015, Schoenecker et al. 2021). Other authors develop 'Capwire' a model based on the frequencies of captured individuals to infer the population size (Miller et al. 2005) which has been used on capercaillie (Bañuelos et al. 2019). The application of this type of model to non-invasive samples (hair, feathers and faeces) is increasing in many mammal (Mowat and Strobeck 2000, Lampa et al. 2015, Woodruff et al. 2020, Schoenecker et al. 2021) and bird (Rösner et al. 2014, Shyvers et al. 2019, 2023) species. Recently, several studies using statistical models based on spatial genetic mark-recapture methods have been carried out on capercaillies to estimate population sizes (Morán-Luis et al. 2014, Mollet et al. 2015, Augustine et al. 2019, Bañuelos et al. 2019). However, the estimates obtained with these models have not yet been directly compared with the results of the lek counts.

The present study is a continuation of the research conducted by Aleix-Mata et al. (2019) using the same field and laboratory protocols. The field methodology employed here is consistent with the previous study; however, our analysis includes the results of three faecal-sampling collections from each lek, instead of only two. In their study, Aleix-Mata et al. (2019) concluded that the genetic method is a viable alternative to traditional lek counts, provides more accurate estimates and causes less disturbance to capercaillies. In this study, the inclusion of three faecal collections allowed us to go a step further and use genetic mark-recapture models (Mollet et al. 2015, Augustine et al. 2019, Shyvers et al. 2023) to estimate the male population size of each monitored lek. Moreover, we applied an additional counting approach involving a walk around the lek, which requires fewer observers, and is commonly used in the Pyrenees (Canut et al. 2006, OGM 2017). It should be noted that this counting method is compared with other methods for the first time in this study.

In line with the existing literature, our results take into account the fact that traditional methods do not allow for the detection of all capercaillies at a lek. However, by comparing with the estimations of the genetic mark-recapture models of each lek, we aim to determine the degree of underestimation associated with each lek-counting approach and explore possibilities for improvement. Thus, we compared four methodologies used to estimate the number of male capercaillies at leks: 1) hide-based lek counts, 2) walk-based lek counts, 3) minimum population estimates (MPE) and 4) M_0 genetic mark-recapture model, the latter two conducted using a non-invasive genetic sampling procedure. The aim of this study was to compare and analyse the estimates of male capercaillie numbers obtained with each of these methodologies to propose ways of improving estimation methods and calculating detection rates, the latter a key parameter for characterising population trends and persistence probabilities.

Material and methods

Study area

The study was carried out in the French and Andorran Pyrenees at six active capercaillie leks: five in Ariège, France (42°38′–42°53′N, 1°11′–1°56′E) and one in Andorra (42°27′N, 1°26′E) (Fig. 1). The leks were selected using criteria such as accessibility and safety (no dangerous cliffs or steep hillsides). We also ensured that the selected leks were representative of Pyrenean capercaillie leks in terms of forest type, altitude and orientation. The selected leks were situated at 1400–2100 m a.s.l. in deciduous and coniferous forests, where 1–9 male capercaillies are usually counted. During the study, nine surveys were carried out in the springs of 2016–2019 (Table 1). Each survey was conducted over three days: on the first two days lek counts were carried out and capercaillie faeces were collected, while on the third day (a maximum of five days after the first day) only faeces collection was performed (Table 2). All leks had been monitored in advance to ensure that the calling peak had been reached; the presence of females, calling activity and male behaviour were used to determine the optimal moment to perform the surveys (Canut et al. 2006, Watson and Moss 2008, Haysom 2013, Aleix-Mata et al. 2019, Coppes et al. 2021, Baines and Aebischer 2023).

Hide- and walk-based lek counts

During each survey, two lek counts were carried out simultaneously at the same lek on the same day, using two different approaches: hide-based and walk-based lek counts. As recommended, all lek counts were performed by experienced observers in favourable weather conditions (i.e. absence of wind or precipitation) to maximise the possibility of detecting capercaillies (Abrahams and Denny 2018, Lentner et al. 2018). Counts were carried out at the peak of male calling activity at each lek (6–27 May in our case), with a maximum of three days between the two counts (Table 2).

Observers performing the hide-based lek counts arrived at the lek the previous afternoon (before 18:00) and set up the hide where they were to spend the night (Haysom 2013, Calenge et al. 2022). Depending on the lek size, counts were performed from one, two or four hides, all positioned in the central activity area of the lek, previously determined by the

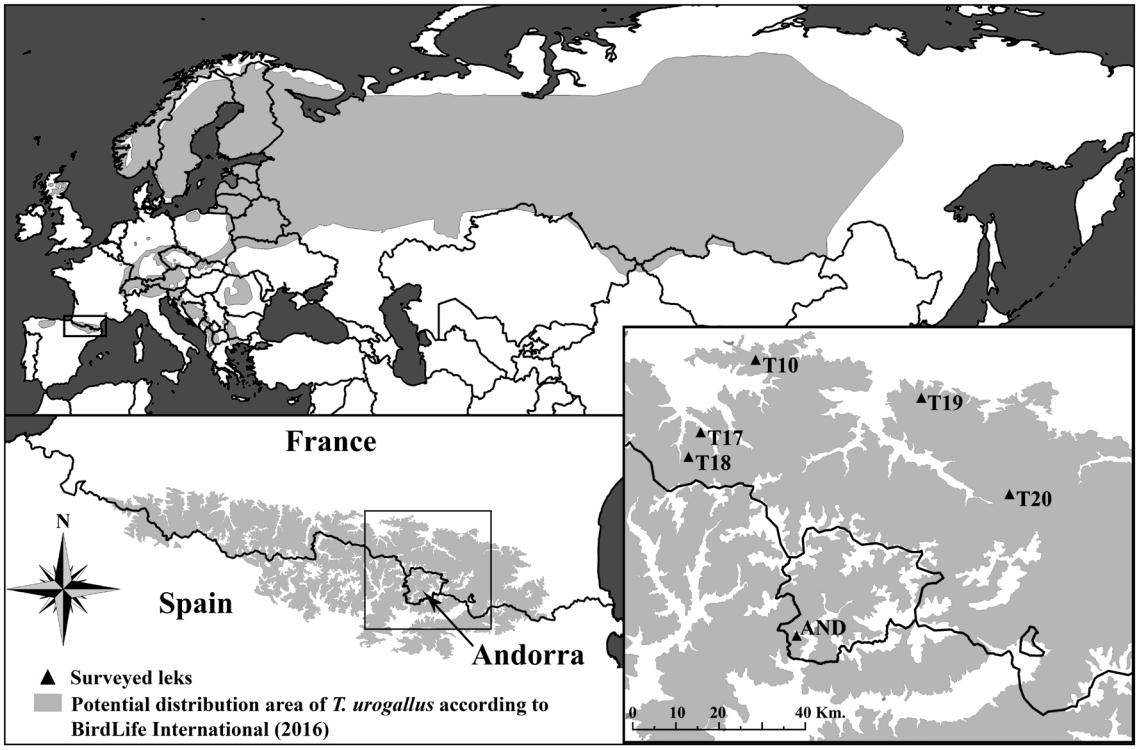

Figure 1. Map of the potential distribution area of *Tetrao urogallus* and the surveyed leks. Five of the surveyed leks were located in Ariège (France) and one in Andorra.

position of capercaillie droppings and tracks in the snow (Aleix-Mata et al. 2019) (Table 2). Counts started early the following morning whilst still dark (around two hours before sunrise) and finished around 1.5 h after sunrise; during this period the observer(s) counted all the capercaillies they heard or saw (Catusse and Novoa 1983, Canut et al. 2006, Haysom 2013, OGM 2017, Calenge et al. 2022). For the surveys 2016-1 and 2018-1, the results of the hide-based lek counts were the same as for the surveys 2016-2 and 2018-1 performed during the previous study (Aleix-Mata et al. 2019).

The walk-based lek counts were performed by a single experienced observer with good knowledge of the lek area, as the walk took place very early in the morning without artificial light to avoid disturbing the capercaillies. During the walk, the observer conducted regular listening stops and counted all the capercaillies they heard or saw (Canut et al. 2006, OGM 2017). After detecting a capercaillie the observer took all the necessary precautions to avoid disturbing it and continued the count.

To be able to compare the results obtained with these two approaches (hide- and walk-based), the counts were performed simultaneously and, as recommended, repeated twice a year, usually on consecutive days (Catusse and Novoa 1983, Watson and Moss 2008, Aleix-Mata et al. 2019). In surveys performed with more than one hide, after each count observers pooled their observations by comparing the hour and the place of all locations of each male to exclude potential double counts and determine the number of males present at the lek. For hide- and walk-based lek counts, the final number of capercaillie males detected during a survey was taken as the maximum number of males detected by each approach during one of the two days of lek counts (Aleix-Mata et al. 2019).

Non-invasive sampling and genetic analysis to establish the minimum population (MPE)

During each survey three non-invasive collections of faeces were also performed. The first two were carried out after

Table 1. Monitoring period and physical characteristics of the studied leks.

Lek	Years monitored	Average altitude (m)	Average slope orientation	Type of forest	No. of capercaillies usually counted
T10	2018	1400	N	Deciduous	2–3
T17	2016	1600	NW	Deciduous	1–2
T18	2016	1550	N	Deciduous	1–2
T19	2016	1400	N	Deciduous	8–9
T20	2016–2017	1800	NE	Coniferous	4–6
AND	2017–2019	2100	NE	Coniferous	1–3

T#: Ariège leks; AND: Andorran lek.

Table 2. Number of male capercaillies directly counted during the hide- and walk-based lek counts, data and estimates based on non-invasive genetic surveys: number of male samples, MPE (minimum population estimate), $\hat{N}$ and 95% credible interval (CI) for M_0 model.

Survey	Lek	Year	Sampling date (in May)[a]	No. of hides	No. of capercaillies hide-based counts	No. of capercaillies walk-based counts[b]	No. of male samples	MPE (capercaillies detected)[c]	$\hat{N}_{M0}$ (95% CI)
2016-1	T17	2016	06/07/08	1	1	1	15	3	4 *(3-6)*
2016-2	T18	2016	06/07/08	1	0	1	10	2	3 *(2-5)*
2016-3	T19	2016	11/12/16	4	5	7	106	9	10 *(9-12)*
2016-4	T20	2016	18/20/22	2	5	6	69	6	7 *(6-9)*
2017-1	T20	2017	20/21/22	2	2	4	40	5	6 *(5-7)*
2017-2	AND	2017	23/27/28	1	1	np	47	7	8 *(7-9)*
2018-1	AND	2018	17/18/19	1	1	np	21	2	3 *(2-3)*
2018-2	T10	2018	26/27/29	2	2	np	35	2	3 *(2-5)*
2019-1	AND	2019	20/23/25	1	1	np	27	5	6 *(5-9)*

[a]Underlined dates: lek counts and faeces collection; the non-underlined date corresponds to the third faeces collection.
[b]np: not performed.
[c]The sum of capercaillies detected is greater than the number of capercaillies genotyped (31), in fact the lek T20 and the lek AND were surveyed for more than one year, and some capercaillies were detected in different years (Supporting information).

finishing the lek counts and the third on a day with no lek count no more than five days after the first count (Table 2). To avoid disturbance, faeces were always collected later in the day once the calling activity had finished to ensure that the capercaillies had left the lek (Bañuelos and Quevedo 2008, Morán-Luis et al. 2014). To compare the lek counts and the results based on the non-invasive genetic sampling, faeces were collected in an area that was equivalent to the lek count area. Faeces were collected in a pre-established area within a 200-m radius around the hide(s), which corresponds to the maximum detection distance of capercaillies (Moss and Lockie 1979, Couturier and Couturier 1980). Faeces were collected by walking parallel transects (25-m apart) along contour lines; the coordinates of each sample were recorded with a GPS (Aleix-Mata et al. 2019). Whenever possible, to ensure similar sampling efforts, the same people carried out each faeces collection each time. As recommended, only fresh faeces were collected, which were then stored in silica gel at −20°C until analysis (Jacob et al. 2010, Aleix-Mata et al. 2019, Bañuelos et al. 2019). In the surveys 2016-1 and 2018-1, the first two faeces collections correspond to those presented in the previous study (Aleix-Mata et al. 2019): surveys 2016-2 and 2018-1 in which 13 and 30 faeces were collected, respectively. During the third faeces collection, three and 15 supplementary faeces were collected (surveys 2016-1 and 2018-1, respectively), which were new samples that had not previously been analysed.

Faecal DNA extraction was performed using the Qiamp Fast DNA stool Mini kit (Quiagen); the recommendations to avoid cross-contamination were followed (Beja-Pereira et al. 2009, Lampa et al. 2013). Each batch of extractions (n = 24) was performed in an isolated area of the laboratory and a period of 24 h was respected before a new DNA extraction or PCR amplification was performed. The working area and the equipment used to handle the samples were washed with 20% bleach solution before a new sample was processed. In addition, DNA extractions and PCR amplifications (control PCRs, genotyping and sexing PCRs) were carried out in different rooms in the laboratory and filter tips were used in all processes. The extracted DNA was conserved at +4°C until performing the PCRs.

To evaluate the yield of the DNA extracted and to discard samples with highly degraded or low quantities of DNA, we performed a control PCR (Aleix-Mata et al. 2019). For this purpose, the primers TU-Cont-F [5′-CTGGGGTCATTAGGCAGAGC-3′] and TU-Cont-R [5′-TGCGTGTGTGCAGAGATAGG-3′] targeting the capercaillie locus TUD7 (Segelbacher et al. 2000) were designed, which gave an amplified fragment of 300 base pairs (bp). The PCR was performed on 13 µl of reaction mix with 5 µl of template DNA, 6.5 µl of Type-it Microsatellite PCR Kit (Qiagen) and 0.2 µM of each primer. The PCR conditions were as follows: initial denaturation at 95°C for 5 min; 35 cycles for 30 s at 92°C, 90 s at 55°C and 30 s at 72°C; and a final extension of 30 min at 60°C. PCR amplicons were resolved in 1% agarose gels and the DNA samples with no amplification of the 300-bp fragment were discarded. A negative control was included in each PCR.

DNA samples with positive and specific amplification in the control PCR were genotyped using a set of 12 microsatellites (Aleix-Mata et al. 2019): seven described by Segelbacher et al. (2000) (TUD1, TUD2, TUD3, TUD4, TUD5, TUT1, TUT3) and five by Piertney and Höglund (2001) (BG10, BG12, BG15, BG16, BG18). To sex the DNA samples, two primer pairs were used: 1) PU and P8mod specific to capercaillies, which amplify the sex-linked marker chromodomain-helicase-DNA-binding protein (CHD) (Pérez et al. 2011); and 2) a USP1 specific forward primer (Ogawa et al. 1997) and our designed primer USP-New [5′-CAGCTTTCCCCTGGAGATAGAG-3′], which amplified specifically in females a 214-bp fragment of the WPG pseudogene from the chromosome W. To genotype and sex the samples we used three multiplex-PCRs: Mix 1: TUD4, TUT3, TUD3, TUT1, USP1, USP_New; Mix 2: TUD1, TUD2, TUD5; Mix 3: BG10, BG15, BG16, BG18, BG12, TUD6, PU, P8mod. Each multiplex was performed on 13 µl of reaction mix with 5 µl of template DNA, 6.5µl of Type-it Microsatellite PCR Kit (Qiagen) and 0.1–0.2 µM

of each primer. PCR conditions were as follows: initial denaturation at 95°C for 5 min; 30 cycles for 30 s at 92°C, 90 s at 60°C (Mix 1 and 2) or at 55°C (Mix 3), and 30 s at 72°C; and a final extension of 30 min at 60°C. Each multiplex-PCR was performed with a negative control. Genetic Analyzer 3500 and GeneMapper Software ver. 4.1 (Applied Biosystems) were used to determine the alleles, both provided by the technical services (CICT) of the University of Jaén (Spain).

As recommended, we used the multiple-tube approach for the DNA genotyping of the faecal samples (Navidi et al. 1992, Taberlet et al. 1996, Beja-Pereira et al. 2009, Lampa et al. 2013). We used three replicates simultaneously and established a consensus genotype for each sample. We considered the sample to be homozygous for a locus if the same allele was found in at least two replicates and no other allele was present; otherwise, we considered a sample to be heterozygous if the same two different alleles at a locus were present in at least two replicates. If the same allele was observed in all three replicates but an additional allele was present in one replicate, the locus was noted as 00/aa. In this case, we were sure of one allele but there may have been another that had not been amplified correctly (allele dropout) or it may have been a false allele. Loci that did not meet these three categories were considered to be 'non-genotyped' and noted as 00/00. A quality index (QI), similar to those described by Miquel et al. (2006), was calculated as described by Aleix-Mata et al. (2019). For further analyses, samples with a QI of less than 0.6, with four or more loci that had not amplified correctly (noted 00/00), or were suspected of being contaminated, were discarded. We used computer algorithms to discard genotyping errors and to identify the different genotypes of individuals (Beja-Pereira et al. 2009), and Gimlet ver. 1.3.3 (Valière 2002) to check for genotyping errors and to regroup samples from the same individual. The consensus genotypes of each sample were compared with each other, identical genotypes were considered as belonging to the same individual. In cases of one or two non-matching alleles between two samples, the genotypes of the samples were checked and, if the non-matching alleles could be explained by a PCR failure (i.e. allele dropout or false allele), they were assigned to the same individual. To perform this analysis, we used the option of 'Regroup genotypes' in Gimlet ver. 1.3.3 (Valière 2002) and we followed the recommendations of Lampa et al. (2013). The probabilities of identity (P_{ID}) (Waits et al. 2001) were calculated with Cervus ver. 3.0.7 (Field Genetics; Marshall et al. 1998). Finally, with MICRO-CHECKER ver. 2.2.3 (Van Oosterhout et al. 2004) we checked for potential errors, while with Gimlet ver. 1.3.3 (Valière 2002) we calculated the matching probabilities of the genotypes for each male. We used information from the matching algorithm to determine the number of males detected in each lek and year, which corresponds to the minimum population estimate (MPE). These data were used to perform the genetic mark-recapture model, performed in the R environment (www.r-project.org) (next section).

Genetic mark-recapture models to estimate the male population size ($\hat{N}$) and detection rate (D)

The estimation of the capercaillies' male population size ($\hat{N}$) of each lek was carried out by applying the genetic mark-recapture model to the genetic data. As for the MPE, only male samples were used when estimating the $\hat{N}$. We estimated the male capercaillie population size of each lek using genetic mark-recapture model that assumed closed populations. The field methodology met this assumption since it was performed on five consecutive days outside the hatching period. The mark-recapture genetic model was performed in the R environment (www.r-project.org) using a script analogous to the one provided by Kéry and Schaub (2012) to fit the Otis M_0 model (Otis et al. 1978). We used the Bayesian approach of this classical M_0 model, in which the model is implemented in JAGS code (Plummer 2003) using data augmentation (Kéry and Schaub 2012, Chapter 6.2.1). This model estimated the detection probability on all three sampling occasions based on the assumption that all individuals in each sampling session have equal detection probabilities (Otis et al. 1978, Kéry and Schaub 2012; see Supporting information for more details).

Once the $\hat{N}$ had been obtained using the statistical model described above, we used these results to estimate the detection rate (D) of the lek count approaches. The parameter was estimated for each survey on the basis of Eq. (1) of Kéry and Schmidt (2008) as:

$$D = \frac{n}{\hat{N}}$$

where n is the number of males directly counted during the hide- and walk-based approaches, and $\hat{N}$ the population size estimated by the model M_0.

Comparison of the different methodologies

Friedman's non-parametric test (Wayne 1990) was used to compare the results of the four methodologies used to estimate the number of male capercaillies at leks and to detect significant differences between them. We conducted multiple pairwise comparisons after Friedman's test using the Durbin–Conover test (Conover 1999). The Durbin–Conover test provides p-values and adjusted p-values following the Benjamini–Hochberg correction to minimize false discovery rates. The detection rates (D) obtained with each lek count approach were compared using Friedman's non-parametric test (Wayne 1990). We also performed a Spearman correlation test to prove the relation between the number of capercaillies detected from the two lek counts approaches and the $\hat{N}$ obtained from the M_0 model.

Results

The comparison between the four methodologies used to estimate the number of male capercaillies at leks were generally significant (Friedman's test: $\chi^2 = 14.43$; df = 3; p-value = 0.0023).

Lek counts

During the study period, we conducted 28 counts at the six leks (Table 2). For surveys 2017-2, 2018-1, 2018-2 and 2019-1, the walk-based lek count was not performed due to the impossibility of obtaining technical support (i.e. trained observers) on the required days. During the total of 18 hide-based and 10 walk-based lek counts, 18 and 19 male capercaillies were detected, respectively (Table 2). In survey 2016-2, no capercaillies were detected (neither seen nor heard) during the two repetitions of the hide-based lek count, although one capercaillie was detected on the walk-based lek count. In the surveys for which the counts were performed with both approaches (2016-1, 2016-2, 2016-3, 2016-4 and 2017-1), the hide-based lek count detected fewer individuals than the walk-based lek count (Table 2, Fig. 2). Combined data from these surveys indicates that the total number of males detected coincided with the walk-based lek counts, with the exception of the 2016-3 survey, when a single male was missed by the walk-based lek count (Table 2). To summarise, the walk-based approach detected up to twice as many more capercaillies as the hide-based one (Table 2, Fig. 2). The Durbin–Conover's test showed that the difference in the numbers of male capercaillies detected with these two approaches is significant (p-adj < 0.001, Table 3).

Non-invasive genetic sampling

For the non-invasive genetic sampling, 505 faeces samples were collected during the nine surveys performed between 2016 and 2019. All collected samples were analysed, of which 415 (82.2%) were sexed and genotyped with a quality index, QI ≥ 0.6; the negative PCR controls gave no amplified product. Of these 415 samples, 370 samples were from males and 45 from females. Only the male samples were used to perform the analyses. The analyses of the genotyping error performed with Gimlet ver. 1.3.3 (Valière 2002) detected 154 allelic dropouts and seven false alleles for the 13 320 amplified loci (i.e. 370 samples × 12 loci × 3 replicates), corresponding to 1.15 and 0.052%, respectively (Supporting information). Based on the results generated by Gimlet ver. 1.3.3 (Valière 2002) and visual inspections, 31 male capercaillies were genotyped. The probabilities of identity considering unrelated or sibling individuals were $P_{(ID)} = 7.1 \times 10^{-9}$ and $P_{(ID)sib} = 3.7 \times 10^{-4}$, respectively; two different males differ in at least three different loci. The average QI for male faeces used for the analysis was 0.93, which represents a very good quality for this kind of sample. The analysis performed of the genotypes of 31 genotyped male capercaillies with MICRO-CHECKER ver. 2.2.3 (Van Oosterhout et al. 2004) detected no genotyping errors at any locus or any evidence of scoring errors due to stuttering, large allelic dropouts or null alleles (Supporting information). The matching probabilities calculated with Gimlet ver. 1.3.3 (Valière 2002) were very low (Supporting information). One locus, TUT3, exhibited no variation in any of our samples and so the results of the analysis are based on 11 microsatellites (Supporting information).

Table 3. Significant pairwise comparisons between the four methodologies used to estimate the number of male capercaillies at leks using the Durbin–Conover test and the Benjamini–Hochberg correction via adjusted p-value.

Comparison	Statistics	p-value	p-adj
H-based vs W-based	5.19	< 0.001	2.2×10^{-4}
H-based vs MPE	10.39	< 0.001	4.7×10^{-7}
H-based vs $\hat{N}_{M0}$	16.74	< 0.001	6.6×10^{-9}
W-based vs MPE	5.19	< 0.001	2.2×10^{-4}
W-based vs $\hat{N}_{M0}$	11.54	< 0.001	2.2×10^{-7}
MPE vs $\hat{N}_{M0}$	6.35	< 0.001	5.5×10^{-5}

H-based: hide-based lek count; W-based: walk-based lek count.

Minimum population estimate (MPE)

The lek T20 and the lek AND were surveyed for two and three years, respectively, hence some male capercaillies genotyped

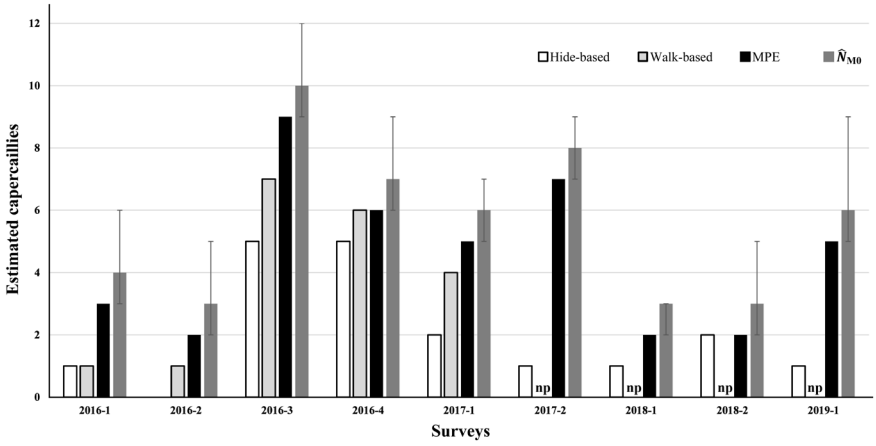

Figure 2. Number of capercaillies obtained by surveying with each method. For the $\hat{N}$ obtained with M_0 the associated CI (95%) is represented by bars. In the surveys 2017-2, 2018-1, 2018-2 and 2019-1 the walk-based approach was not performed (np). MPE: minimum population estimate.

were detected in more than one survey(Supporting information). Therefore, the sum of the MPE (capercaillies detected) from each survey is greater than the number of capercaillies genotyped (31). The MPE were higher than those obtained in the lek counts for 89 and 80% of the surveys performed by hide- and walk-based lek counts, respectively (Table 2). The MPE were twice as high as the males counted with the hide-based lek counts and were also higher (30%) than the males counted with walk-based lek counts (Table 2, Fig. 2) and the Durbin–Conover's test showed significant differences in both comparisons (p-adj < 0.001, Table 3). The MPE was only the same as the hide-based lek count for the 2018-2 survey and the same as the walk-based lek count for the 2016-4 survey (Table 2).

Population size ($\hat{N}$) and detection rate (*D*)

The $\hat{N}$ values obtained with the statistical model using the 370 male samples are shown in Table 2. The $\hat{N}$ obtained with M_0 model were 22% (CI 95%: 0–58%) higher than the MPE at each lek (Table 2) and the Durbin–Conover's test showed significant differences (p-adj < 0.001, Table 3).

When comparing the number of capercaillies detected with the two lek count approaches (hide- and walk-based) and the $\hat{N}_{M0}$ obtained from the genetic data, it is obvious that lek count methods detect fewer male capercaillies than those identified by non-invasive genetic sampling (Fig. 2). $\hat{N}_{M0}$ was, respectively, 2.8 and 1.6 times higher than the results for the hide- and walk-based lek counts. For these comparisons the p-adj of the Durbin–Conover's test was < 0.001, showing a significant difference in the number of capercaillies detected (Table 3). The relation between the male capercaillies detected by the lek count approaches (hide- and walk-based) and the $\hat{N}$ obtained from the M_0 model are represented in Fig. 3. The Spearman corelation test showed insignificant correlation between the number of male capercaillies detected by hide-based lek count and the $\hat{N}_{M0}$ (r = 0.53, p-value = 0.134). For the number of male capercaillies detected by walk-based lek count and the $\hat{N}_{M0}$ the Spearman correlation test showed a very strong and significant correlation (r = 0.97, p-value = 0.004).

The *D* of the hide-based lek counts was half that of the walk-based lek counts, on average 0.34 (95% CI: 0.26–0.43) and 0.56 (95% CI: 0.43–0.68), respectively (Table 4). The results of the Friedman's test show that this difference is significant (Friedman's test $\chi^2 = 4$; p-value = 0.045).

Discussion

To the best of our knowledge, this is the first time the results of the two lek counting approaches commonly used in the Pyrenees, as well as a population model based on genetic sampling, have been compared. These methodological considerations are crucial for improving the accuracy of monitoring aimed at estimating the size of capercaillie populations.

Lek counts

An analysis of the number of capercaillies detected using the two lek count approaches shows that the walk-based lek counts detect more male capercaillies (46%) than the hide-based lek counts (Table 2, Fig. 2). Similar differences have been previously described for other bird species when comparing data from fixed points and transect counts (Nijman 2007, Golding and Dreitz 2016). It has been reported that, when calling activity is low, as may occur with capercaillies, counts made from a fixed point detect fewer individuals than on a transect (Nijman 2007). Hence, calling activity could be a factor explaining the observed difference between the two approaches. In addition, the position of the observer inside the hide could have a negative effect on the number of males detected. Indeed, the background noise generated by the hide,

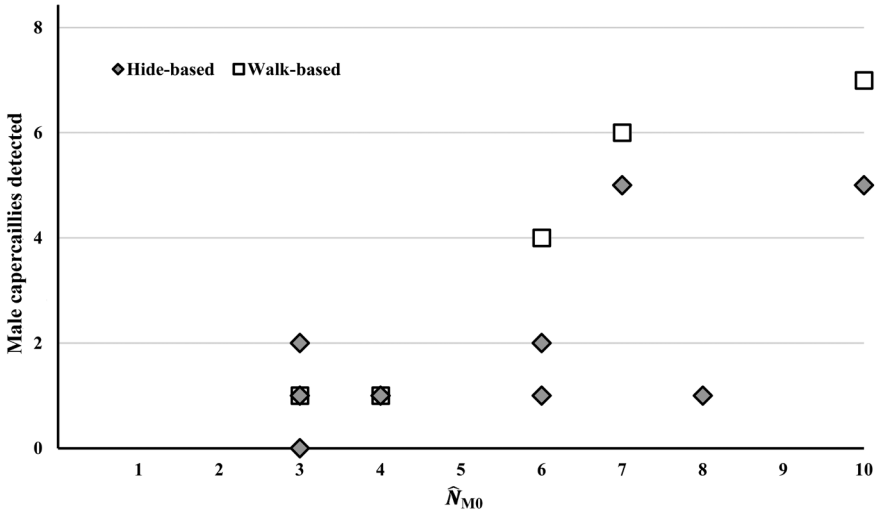

Figure 3. Comparison between the number of male capercaillies detected during lek counts with the $\hat{N}$ obtained from the M_0 model.

Table 4. Comparison of the $\hat{N}$ obtained with the results of the lek counts, and the detection rate (D) for each survey estimated with the M_0 model.

		Hide-based count			Walk-based count	
Survey	$\hat{N}_{M0}$ (95% CI)	No. of males	No. of hides	D_{M0} (95% CI)	No. of males	D_{M0} (95% CI)
2016-1	4 *(3-6)*	1	1	0.25 *(0.16-0.33)*	1	0.25 *(0.16-0.33)*
2016-2	3 *(2-5)*	0	1	0.00 *(0.00-0.00)*	1	0.33 *(0.20-0.50)*
2016-3	10 *(9-12)*	5	4	0.50 *(0.41-0.55)*	7	0.70 *(0.58-0.77)*
2016-4	7 *(6-9)*	5	2	0.71 *(0.55-0.83)*	6	0.85 *(0.66-1)*
2017-1	6 *(5-7)*	2	2	0.33 *(0.28-0.40)*	4	0.66 *(0.57-0.80)*
2017-2	8 *(7-9)*	1	1	0.13 *(0.11-0.14)*	–	–
2018-1	3 *(2-3)*	1	1	0.33 *(0.33-0.50)*	–	–
2018-2	3 *(2-5)*	2	2	0.67 *(0.40-1)*	–	–
2019-1	6 *(5-9)*	1	1	0.17 *(0.11-0.20)*	–	–

which could hinder the hearing and locating of the capercaillie displays, may explain the observed differences between the approaches. It is assumed that environmental noise such as wind, other singing and calling birds and even noise generated by the observers themselves (i.e. their clothes and headgear) may interfere with observers' performances and reduce the number of detected individuals (Johnson and Rowland 2007, Simons et al. 2007, Koper et al. 2015, Sadoti et al. 2016, Abrahams and Denny 2018). Another explanation for the differences in the approaches could be the behaviour of young and sub-adult males, which tend to remain on the periphery of the lek (Watson and Moss 2008) and are therefore more likely to be detected by the walk-based approach.

Overall, given the number of observers involved in both approaches and the number of detected capercaillies, the walk-based approach was found to be more efficient than the hide-based one. Comparing the five surveys in which both approaches were performed, 10 observers from hides detected only 13 capercaillies (1.3 capercaillies/observer), while 19 were detected by five walking observers (3.8 capercaillies/observer) (Table 2). Despite the advantage that walk-based lek counts have over hide-based lek counts, the former approach is still complex to implement because it needs to be performed by experienced observers with good knowledge of the area around the lek.

Non-invasive genetic sampling

The literature demonstrates that the use of faeces as a source of genetic material is becoming increasingly common given that it provides accurate population estimates for a great variety of species and terrains, and is non-invasive and easy to perform (Lampa et al. 2015, Schoenecker et al. 2015, Shyvers et al. 2019, Woodruff et al. 2020, Schoenecker et al. 2021, Zemanova 2021). Our analyses of the 370 samples (faeces) genotyped 31 male capercaillies. Different individuals were separated by at least three loci, so the risk of artificially increasing the number of individuals due to genotyping errors was very low; the $P_{(ID)sib}$ value obtained was within the recommended range (Waits et al. 2001, Beja-Pereira et al. 2009, Latorre-Cardenas et al. 2020). In fact, the $P_{(ID)}$ values were lower than the values obtained by other studies of capercaillies using a similar panel of microsatellites (Morán-Luis et al. 2014, Bañuelos et al. 2019). Moreover, the policy of discarding samples with a QI < 0.6, as well as samples with more than four 'non-genotyped' loci (noted 00/00), enabled us to rule out samples with potential errors or contaminations (Miquel et al. 2006). The followed protocols including contamination prevention, low-quality sample screening and consensus genotype generation allowed us to minimise and detect possible errors (Beja-Pereira et al. 2009, Lampa et al. 2013). Hence, the methodology applied during the laboratory work and the microsatellite panel used were sufficiently powerful to discriminate individual male capercaillies with certainty and avoid ghost individuals in our data.

Minimum population estimate (MPE)

MPE was higher than numbers of male capercaillies detected by the hide- and walk-based lek counts (Fig. 2), which agrees with the results of the preliminary study (Aleix-Mata et al. 2019). These differences are due to the fact that non-invasive genetic sampling allows all male capercaillies at a lek, both calling and non-calling (i.e. young birds, sub-adults, adults exhibiting predator-avoidance behaviour and subordinate males) to be detected; by contrast, silent males can only be detected during lek counts if they are visible (not too far away, not hidden behind vegetation or by the terrain) (Storch 1997, Wegge et al. 2003, Mollet et al. 2015, Sadoti et al. 2016, Aleix-Mata et al. 2019, Cayuela et al. 2019). Other authors also note that traditional lek count methods do not permit the detection of single displaying males (Bibby et al. 2000). Therefore, our results support the idea that traditional lek counts only detect a part of the population (Storch 1997, Wegge et al. 2005, Mollet et al. 2015, Aleix-Mata et al. 2019, Shyvers et al. 2023).

In this study we performed three sample collections to estimate the MPE, although in the preliminary study only two sample collections were analysed (Aleix-Mata et al. 2019). Comparing the surveys of the lek T17 and the lek AND – respectively, 2016-1 and 2018-1 – with surveys 2016-2 and 2018-1 in the preliminary study (Aleix-Mata et al. 2019), we can see that the MPE was the same as that of the 'genotyped males': three for the survey 2016-1/2016-2 and two for the survey 2018-1 (Table 2, Table 1 in Aleix-Mata et al. 2019). In these cases, the third sample collection did not allow us to detect more males. However, the probability of detecting

faeces of capercaillies was very variable (Mollet et al. 2015) and it is possible to miss some of them; therefore, a third sample collection was necessary for applying the genetic mark-recapture models with more confidence.

The estimation methods using non-invasive genetic sampling have certain advantages over the traditional lek counts. They allow the detection of females and identification of individuals from one year to the next, thereby providing additional demographic information (e.g. sex ratios and survival rates) (Mondol et al. 2009, Augustine et al. 2019, Bañuelos et al. 2019, Shyvers et al. 2023). Furthermore, the target population is much less disturbed by the collection of faeces than by lek counts (Bañuelos and Quevedo 2008, Jacob et al. 2010, Abrahams 2019, Aleix-Mata et al. 2019, Zemanova 2021). In Scandinavia, as well as in the Bavarian Alps, it has been reported that during the daytime male capercaillies are located at a distance of more than 250 m (Wegge et al. 2003) and even 376–779 m – depending on the age class – (Storch 1997) from the centre of the lek. Therefore, we can assume that our faeces collection minimised disturbance as it was performed within a 200-m radius around the hide (centre of the lek) in silence during daytime, after the capercaillies had left the lek. A similar faeces collection protocol as used in our study has been used with another endangered population of capercaillies with no reported problems of disturbance (Morán-Luis et al. 2014).

In both lek count approaches, the reliability of the results depends on the ability to detect the peak in calling activity (Catusse and Novoa 1983, Canut et al. 2006, Watson and Moss 2008, Haysom 2013, Abrahams 2019, Aleix-Mata et al. 2019, Coppes et al. 2021). However, it has been observed in other lekking species that counting at the peak of activity does not guarantee the detection of all males at a lek (Johnson and Rowland 2007), which highlights the limitations of this traditional method. Moreover, direct counts do not provide any error estimate. Although lek counts provided biased population estimations, due to fluctuations in the number of males in the lek during the day and the season (Franceschi et al. 2014, Abrahams 2019, Aleix-Mata et al. 2019), these types of counts can provide an index of abundance if appropriately validated, and can allow monitoring of lek occupancy.

$\hat{N}$ of the leks

To estimate the number of individuals from the genetic data generated by the non-invasive genetic sampling, statistical analyses using genetic mark-recapture models are recommended (Beja-Pereira et al. 2009, Lampa et al. 2013, Mollet et al. 2015, Cayuela et al. 2019, Schoenecker et al. 2021). The model used generated a robust estimate of the true population size for closed populations (Woodruff et al. 2020). Moreover, the social harem structure of capercaillies increases the detection probability of faeces during sample collection, thereby increasing the analytic precision (Perry et al. 2012, Schoenecker et al. 2021). In fact, the $\hat{N}$ obtained from the M_0 model using the genetic data has a low 95% credible interval (CI), which is evidence of the sensitivity of the estimate (Fig. 2, Table 2).

The $\hat{N}$ estimation was larger than the MPE based on the non-invasive genetic sampling method (Fig. 2, Table 2) and agrees with previous capercaillie studies (Jacob et al. 2010, Rösner et al. 2014, Mollet et al. 2015, Bañuelos et al. 2019). In fact, we cannot rule out the possibility that faeces from a bird present in the lek was not collected and so non-invasive genetic sampling may also underestimate the population size (Aleix-Mata et al. 2019). The M_0 model takes this into account and provides an estimate of $\hat{N}$ (Mollet et al. 2015, Woodruff et al. 2020, Schoenecker et al. 2021), which explains why 22% more capercaillies were estimated with this method than those detected using non-invasive genetic sampling alone. This result is in line with the study by Bañuelos et al. (2019). Although these authors have estimated it with a different model, they found that the data of the individuals genotyped were 16% lower than the birds present during the mating season.

The $\hat{N}$ obtained by the M_0 model was 2.8- and 1.6-times higher, respectively, than the number of males counted by the hide- and walk-based lek count approaches (Fig. 2). The results for $\hat{N}_{M0}$ reinforce the idea that traditional lek counts underestimate the males at a lek, as has previously been reported (Jacob et al. 2010, Lentner et al. 2018, Aleix-Mata et al. 2019).

Lek counts approaches versus genetics methods

In this work, $\hat{N}_{M0}$ was used to calculate the detection rate (D) for the two different lek count approaches, a parameter which, although different, can approximate the detection probability. In fact, we have not taken into account the availability of males to estimate D: this parameter is affected by the presence of the target species in the count area and the duration of the count (Kéry and Schmidt 2008). However, as we sampled spots where all males tend to gather (the leks), and given the duration of the counts (about 1.5 h), we can assume male availability equal to 1 (during the counts), and the $\hat{N}_{M0}$ estimated as a reliable estimate of true $\hat{N}$. Therefore, considering the $\hat{N}$ obtained from the M_0 model to be true, the probability of detection of each count should be close to the D obtained, considering the 95% CI associated with each estimate (Table 4). Our results show that the hide-based lek counts had a detection rate that was half that of the walk-based lek counts detection rate (Table 4), which coincides with results previously reported by Golding and Dreitz (2016). This is more likely to occur in small leks, i.e. where there are usually few individuals. In fact, in capercaillie, the song rate was significantly correlated with the number of displaying males in a lek, and with displaying activity (Laiolo et al. 2011, Abrahams 2019) so it should be easier to detect capercaillies when song rate is high. Hence, it is important to consider this fact when monitoring capercaillie populations in the Pyrenees, as most leks consist of very few individuals (Robles et al. 2006).

Moreover, it is important to note that D is not constant for all leks due to factors such as the number of males, which can vary greatly from one lek to another, the method of estimation used and also other factors affecting lek counts

(Kéry and Schmidt 2008, Sadoti et al. 2016, Abrahams 2019, Aleix-Mata et al. 2019, Baines and Aebischer 2023). In fact, for the lek T20 (surveys: 2017-1 and 2018-2) and the lek AND (surveys: 2017-2, 2018-1 and 2019-1), *D* varied between surveys (Table 4).

Our results of *D* are quite different from the detection probability estimated by Calenge et al. (2022), who have estimated the male capercaillie population size in the French Pyrenees using hierarchical models based on data from lek counts performed from hides. These authors estimated a detection probability for one observer from a hide of 0.53 (80% CI: 0.50–0.55). With our approach the detection rate obtained for the hide-based lek count was lower 0.34 on average (95% CI: 0.26–0.43, Table 4). Taking only the data for leks for which the hide-based lek count was performed by just one observer (2016-1; 2016-2; 2017-2; 2018-1; and 2019-1), the detection rate was even lower at an average of 0.17 (95% CI: 0.15–0.24, Table 4). These differences may be due to the fact that these authors only estimate the adult male capercaillie population in leks (males > 2 years old) (Calenge et al. 2022). However, the genetic method used allows us to estimate all male capercaillies at a lek, both calling and non-calling. Therefore, the lek count detection rate obtained (*D*) refers to all male capercaillies of the lek. In the future, studies using extended M_0 models applied to non-invasive genetic data should study the variables that have the most important effects on the detection rate or, even better, on the probability of detection in order to normalise estimates of lek counts.

By comparing the number of male capercaillies detected during the lek count approaches with the $\hat{N}_{M0}$ estimated it has analysed if the lek counts results are reliable and are well correlated with this estimate (Fig. 3). We can observe that the results of the walk-based lek count are strongly correlated to the $\hat{N}$ estimated with the M_0 model. This indicates that, although this approach detects fewer individuals than the genetic mark-recapture model, the results obtained are in accordance with the capercaillies estimated with the M_0 model. However, in the case of the hide-based lek count, the results are not correlated. In fact, they can differ considerably from one method to another, as is the case for the 2017-1, 2017-2 and 2019-1 surveys (Table 2, Fig. 2). Therefore, the counts carried out with the walk-based approach are more reliable than the hide-based approach to determine the number of male capercaillies in a lek.

Management implications

The number of males attending leks can be affected by the date, time of day, weather conditions and the presence of predators, among other factors (Walsh et al. 2004, Johnson and Rowland 2007, Franceschi et al. 2014), all of which will affect results based on the direct detection of individuals such as lek counts. However, techniques based on non-invasive genetic sampling are not affected by these factors and, if combined with genetic mark-recapture models, population sizes can be determined (Woodruff et al. 2020, Schoenecker et al. 2021).

Our results indicate that the best method for estimating capercaillie numbers is the genetic mark-recapture model applied to non-invasive genetic data followed, in order, by non-invasive genetic sampling alone (which can determine the MPE), the walk-based lek count and, finally, the hide-based lek count.

If the hide-based lek count is chosen, it is necessary to bear in mind that the detection rate (i.e. the ratio between lek-counted capercaillies and those estimated by the genetic mark-recapture model) of this method is very low: 0.34 (Table 4). When applying the walk-based approach, the detection rate rose to 0.56 (Table 4). This method is more cost-efficient as it involves fewer observers, counts more birds and is better suited to determine the number of male capercaillies in a lek. However, it is more invasive and complicated to perform, so it should only be used under certain circumstances and only by experienced observers with a good knowledge of the lek area (Canut et al. 2006). In any case, as recommended in several works, whichever lek count approach is chosen (hide- or walk-based), all counts must be carried out at the peak of calling activity and under favourable weather conditions.

Non-invasive genetic sampling has advantages over traditional lek counts as it is less intrusive and less disturbing (Jacob et al. 2010, Aleix-Mata et al. 2019, Zemanova 2021). It allowed us to determine that the MPE corresponds to 82% of males at a lek (Table 2). The accuracy of population size estimates could be greater if genetic mark-recapture models are applied. Another very important advantage is that this method is not affected by the behaviour or the calling activity of the capercaillies (Aleix-Mata et al. 2019). However, genetic analyses that require this method need appropriate infrastructure (a genetics laboratory including clean-room facilities) in which to perform analyses, which can make its implementation difficult. Furthermore, it must be taken into account that the cost of this method is higher than for lek counts, but does provide more information and is a non-invasive method (Aleix-Mata et al. 2019).

The results of the detection rate of the lek count approaches could help us to compare results with other methods. In fact, in other areas of the capercaillies' range, a monitoring method based on distance sampling (Buckland et al. 2001) is performed in winter (outside the mating season). This is the case in Scotland for example, where capercaillies are detected and counted along line transects and the population size is estimated every six years (Wilkinson et al. 2018); however, this methodology is difficult to apply in mountain areas.

Conclusions

Traditional lek counts, commonly used to estimate population sizes (hide-based lek counts), underestimate population sizes and gather imperfect indices of abundance and/or occupancy. Our results suggest that the hide-based lek counts only detect one-third of capercaillies at a lek, while walk-based lek counts detect two-thirds. In addition, the results obtained with walk-based lek counts are better correlated with the $\hat{N}$ estimated.

More comparative studies of different estimation methods are needed to garner more information from fieldwork and make better use of available resources to obtain more accurate estimates (Cagnacci et al. 2013, Monroe et al. 2016). Monitoring agencies and other organisations should choose which methods and indicators to use for species management in accordance with their logistical and economic possibilities, but should always bear in mind the limitations of each method. Our results, as well as those of other comparative studies, will help in improving and updating current estimation/prediction models for population sizes and trends. This is especially relevant in the case of an emblematic galliform bird such as the Pyrenean capercaillie that requires sustainable management.

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Author contributions

Gaël Aleix-Mata: Conceptualization (lead); Data curation (equal); Funding acquisition (lead); Methodology (lead); Writing – original draft (equal); Writing – review and editing (equal). **Antonio J. López-Montoya**: Formal analysis (lead); Writing – review and editing (equal). **Pascal Lapébie**: Writing – original draft (equal). **Evelyn Marty**: Methodology (equal). **Pierre Mourieres**: Methodology (equal); **Jesús M. Pérez**: Conceptualization (equal); Writing – review and editing (equal). **Antonio Sánchez**: Conceptualization (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/jav.03176.

Data availability statement

The analyses reported in this article can be reproduced using the data provided by Otis et al. (1978), Kéry and Schaub (2012, Chapter 6.2.1) and the Supporting information, and are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.95x69p8tc (Aleix-Mata et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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