WILDLIFE BIOLOGY

Research article

Tracking movements in an endangered capercaillie population using DNA tagging

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Wildlife Biology
2024: e01121
doi: 10.1002/wlb3.01121
Subject Editor: Yuehua Sun
Editor-in-Chief: Ilse Storch
Accepted 28 November 2023

Knowing the location and movements of individuals at various temporal and spatial scales is an important facet of behavior and ecology. In threatened populations, movements that would ensure gene flow and population viability are often challenged by habitat fragmentation. Also in those endangered populations capturing and handling individuals to tag them, or to obtain tissue samples, can present additional challenges. DNA tagging, i.e. non-invasive individual identification of samples, can reveal movement patterns. We used fecal material genetically assigned to individuals to indirectly track movements of a large-bodied, endangered forest bird, Cantabrian capercaillie (*Tetrao urogallus cantabricus*). We wanted to know how the birds were using the fragmented forest landscape, and whether they showed fidelity to display areas. We used multi-event capture–recapture models to estimate fidelity to display areas among three consecutive mating seasons. We identified 127 individuals, and registered movements of 22 females and 48 males. Most observed movements were as expected relatively short, concentrated around display areas. We did not find differences in movement distances between females and males within mating seasons, or between them. Fidelity to display areas among seasons was 0.62 (± 0.12 SE) for females and 0.77 (± 0.07 SE) for males. The best CR model suggested no sex or season effects. Several longer movements, up to 9.9 km, linked distant display areas, demonstrating that Cantabrian capercaillies were able to move between different parts of the study area, complementing previous studies on gene flow. Those longer movements may be taking birds out of the study area, and into historical capercaillie territories, which still include substantial forest cover. The non-invasive DNA tagging approach provided a much larger sample size than would have been feasible with direct tracking. Lack of information on the social status of individuals, and timing of movements, are some disadvantages of DNA tagging.

Keywords: DNA-tagging, grouse, multi-event CR models, *Tetrao urogallus cantabricus*, tracking movements

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Introduction

The study of movement patterns at various temporal and spatial scales provides basis for understanding behaviour, ecology and, ultimately, aspects of the conservation status of most animals (Börger et al. 2008). Some animal movements are tightly associated to their specific habitat requirements, and in those cases navigating unfamiliar and unsuitable habitats might increase risk exposure, compromising survival (Yoder et al. 2004, Bonte et al. 2012). As a consequence, the loss and fragmentation of habitat that affects most terrestrial ecosystems (Watson et al. 2018) can result in appearance of dispersal barriers, which affect population dynamics and gene flow via reduced connectivity (Ricketts 2001, Caplat et al. 2016). Habitat loss and fragmentation can yield smaller, subdivided populations, if the loss of connectivity results in less frequent movements, and limits effective dispersal. Those subdivided populations are more vulnerable to stochastic events that could restrict their probability of survival (Lens et al. 2002).

The combination of the species' movement ability, and the configuration of remnant habitat fragments and the surrounding matrix, determine the species' responses to landscape changes. Thus fine-scale movement behaviour of species of conservation interest should be incorporated in conservation planning and management, particularly when habitat restoration is feasible (Lechner et al. 2015). Yet, such dataset are not easy to obtain, and tend to be replaced by assumptions and simplifications (Southwell et al. 2008) derived from data from other populations, or similar species. However, movements are often partially determined by landscape characteristics and distinct selective pressures on different populations (Baguette et al. 2013), so it is not always safe assuming that populations of a given species would show equivalent movement patterns throughout their distribution range. For instance, the established knowledge on a species' behaviour and habitat requirements may have been obtained from parts of its distribution range less affected by habitat loss and fragmentation. Yet, in fragmented and peripheral areas of a distribution range, the quality of what can appear as secondary habitat is possibly key for the species' survival (Channel and Lomolino 2000, Blanco-Fontao et al. 2010). This is particularly true for those areas within a species' range where dispersal movements depend on fine-scale structural elements, acting as stepping stones (Lechner et al. 2015).

We studied movements of an endangered forest bird, Cantabrian capercaillie *Tetrao urogallus cantabricus*, tracking individuals based on their DNA, left behind mostly in faeces. With such DNA or genetic tagging (Palsbøll et al. 1997, Lamb et al. 2019), where the repeated occurrence of a genotype is a direct indicator of movement, we wanted to reveal movements during and among display seasons while using a minimally intrusive approach. The study area included relatively large patches of forest and shrubland above the treeline, the latter being especially relevant for females with broods (Bañuelos et al. 2008). Yet, these habitats are embedded in a matrix of disturbed landscape, including former forest clearings, burns in various states of secondary succession, and mountaintop mining. We hoped DNA tagging would yield enough recaptures to check whether capercaillie showed the expected lek fidelity during and among display seasons (Watson and Moss 2008), but also if they were able to move among distinct valleys of the remaining range, and across disturbed habitat.

Material and methods

Population, study area, and field survey

Cantabrian capercaillie lives at the southern edge of the species range (Rodríguez-Muñoz et al. 2007), under the influence of Atlantic climate (Olson et al. 2001). The population declined severely from its known historical range in the last third of the 20th century (Pollo et al. 2005, Storch et al. 2006), and its viability appears compromised (Bañuelos et al. 2019). It has been recently listed as critically endangered in Spain (Ministerio para la Transición Ecológica 2018).

The study area (Supporting information) is rugged, with elevation ranging from 450 to 2000 m a.s.l. Forest cover is about 46%. Larger patches of relatively old forest are restricted to the higher slopes of the mountain range, separated by valleys that concentrate most human population and activities, mirroring a widespread pattern of human impact on the landscape (Sandel and Svenning 2013). Those forest patches harbour the lekking areas where capercaillies gather in the mating season. Such Spring gatherings facilitate obtaining enough droppings or feathers as source of DNA. Sampling would be much harder at other moments of the seasonal cycle, when the birds are more dispersed, and the use of habitat by females and males overlaps less (Bañuelos et al. 2008).

During the mating seasons (mid-March to early June) of 2009, 2010 and 2011 we visited 62 previously known capercaillie leks (Morán-Luis et al. 2014, Bañuelos et al. 2019 for further details). Those reference locations of leks, 'cantaderos' in Spanish, stem from the former period of capercaillie hunting in Spring (Rodríguez-Muñoz et al. 2015). Of those leks, 83% showed signs of capercaillie presence at some point since year 2000, the rest had apparently been unused. We considered that those 62 historical lek locations corresponded to 53 display areas because in some instances lek separation seemed too small (411 to 802 m), and samples were found continuously under forest cover. We also had in mind that display in capercaillie does not conform to the classical notion of leks (Wegge et al. 2013).

Using leks as reference, two people surveyed forest patches for 2 to 3 h. Areas where we did not find signs of capercaillie presence were surveyed again 2–3 weeks later. The position of each sample was recorded with a GPS (± 5 m) and was later incorporated into a GIS. To minimize redundant samples and the risk of oversampling the same individual, we selected samples based on a minimum distance of 25 m from others with similar appearance (i.e. we weighed in freshness,

size, shape and apparent content) in the case of droppings, or from the same sex in the case of feathers. Droppings were stored in tubes with silica-gel in the field, and were kept frozen at −20°C until DNA extraction. Feathers were kept dry at room temperature.

DNA tagging and movements

We aimed at obtaining individual genotype profiles using nine microsatellite markers (five previously developed for *Tetrao urogallus*, TUD2, TUD4, TUD5, TUT1, TUT3, Segelbacher et al. 2000, and four developed for the closely related *Tetrao tetrix*, TTD2, TTD6, BG10, BG15, Caizergues et al. 2001, Piertney and Höglund 2001), and a specific primer developed for sex assignment for Cantabrian capercaillie (Pérez et al. 2011). We included in the Supporting information details of methods of DNA extraction and amplification, molecular sexing, validation of genotype profiles, and genotyping errors. To ensure genotype reliability, we double-checked each genotype profile. We kept only those samples for which at least six microsatellite loci amplified correctly, and which rendered an unequivocal consensus genotype (Morán-Luis et al. 2014, Bañuelos et al. 2019).

We recorded the repeated finding of capercaillie genotypes (hereafter 'recaptures') in successively processed samples. Note that for samples collected during any single season, the initial observation of an individual does not necessarily imply its first presence in a lek, as scats cannot accurately be dated in this context. To get estimates of individual movements, we measured the maximum planimetric distance between any two recaptures of each individual, both within and between mating seasons. We coded those recaptures as philopatric if they occurred within the same display area.

Multi-event capture–recapture approach to estimate site fidelity among seasons

We analysed capture–recapture data from the three subsequent mating seasons using a multi-event approach (Pradel 2005, Lagrange et al. 2014, Cayuela et al 2017), considering that we were not focusing particularly on the specific display areas. This approach can be best applied to studies in which sites may be considered as equivalent, allowing then a drastic reduction in the number of estimated parameters. Movement of animals between different locations is quantified, while accounting for imperfect detection and potential differences between groups (in our case, males and females), and eventually, in time. This approach allows obtaining estimates of survival and site fidelity rates simultaneously, besides recapture probabilities.

We used the annual probability of remaining in the same display area for two successive mating seasons as a measure of site fidelity. We assigned 'site fidelity' to those birds that were found at the same display area at time t and t + 1. We assigned 'non-fidelity' to birds that changed display areas between years. For birds visiting more than one display area per mating season, we assigned 'site fidelity' to those birds found in the same display areas at time t and t + 1.

In a previous study (Bañuelos et al. 2019) we had estimated several demographic parameters of this population, using the same dataset (except for 7 individuals that were genotyped later to complete the sample) and several modelling approaches (namely Jolly–Seber POPAN, Pradel, and Cormack–Jolly–Seber models). Among others, we estimated apparent survival and probability of recapture, taking into account the potential variation as a function of sampling occasion (i.e. time) and sex. That study suggested that there were differences in survival between sexes, and that probability of recapture was similar for males and females. Those parameters remained relatively constant through the three field occasions. In this study we have built a new model to estimate interannual site fidelity, based on those previous results. We evaluated the potential influence of sex and sampling occasion in site fidelity rates. Models were built and fitted using maximum-likelihood methods implemented in program E-SURGE ver. 2.2.3 (Choquet et al. 2009). E-SURGE does not manage missing data, so we excluded for this analysis 6 individuals that could not be sexed. We selected models using the Akaike Information Criterion, considering overdispersion and small sample size (QAICc). We considered that two models were equivalent when they differed by less than two units (Anderson and Burnham 1999). Details of model description and implementation are included in the Supporting information.

Results

We found 127 capercaillie individuals (genotypes) in the study area: 48 females, 73 males, and 6 individuals that could not be sexed. Those capercaillies were the minimum number of individuals present in the area during the study. Individual identifications were derived from DNA extracted and amplified correctly in 422 samples, out of an initial set of 752 samples.

We found capercaillies in 35 display areas, which included 47 reference lek locations. In two of those display areas we did not find males. The maximum number of females per display area was 4 (median = 1), and the maximum number of males per display area was 7 (median = 2), not coincident with the display area with most females.

Seventy of the above capercaillies, 22 females (46%) and 48 (66%) males, were recaptured at least once. We recaptured 53 individuals within any single mating season, and 49 individuals between mating seasons (Fig. 1).

Most recaptures occurred within 500 m of the initial observation, both within (median = 297 m) and between mating seasons (median = 483 m; Fig. 2, 3). Distributions were highly skewed, including a few relatively long-distance movements (Fig. 3, 4). There were no differences between females and males in recapture distances within mating seasons (Wilcoxon rank sum test, W = 497, p = 0.947), or between mating seasons (Wilcoxon rank sum test, W = 375, p = 0.701). Maximum recapture distances were larger between mating seasons (Wilcoxon rank sum test, W = 2804, p = 0.01).

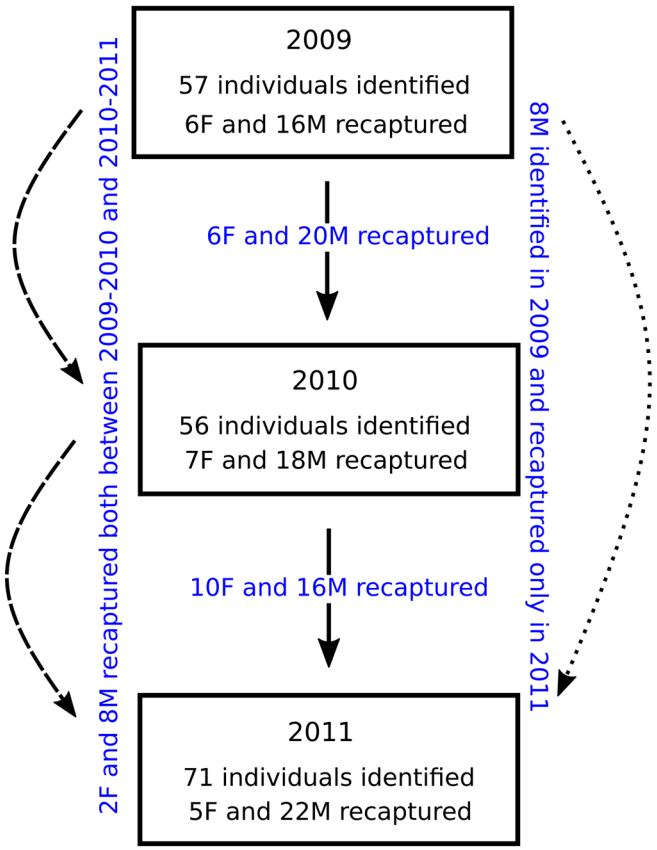

Figure 1. Scheme of recaptures including numbers of capercaillie individuals identified and recaptured per season (boxes), recaptured in consecutive seasons (solid arrows), and recaptured between seasons. 'F' and 'M' stand for female and male, respectively.

The farthest recapture within any mating season was that of a male that moved 7.6 km between two major valleys of the study area (Fig. 4, male 13). The farthest recapture between mating seasons was that of a female re-identified in 2011 at 9.9 km from her previous location in 2010 (Fig. 4, female 19). That female visited different display areas each spring, changing sub-basins of the study area.

About one quarter of the recaptured birds (23% of females, 32% of males) visited more than one display area at some point. There were no differences between females and males in the proportion of recaptures registered in display areas different from the initial ($X^2 = 0.08$, df = 1, $p = 0.78$ within mating seasons; $X^2 = 1.47$, df = 1, $p = 0.23$ between mating seasons).

Most birds that visited more than one display area during a single mating season were found at 2 different ones (3 females, 10 males); only one male was recaptured at 3 different display areas. These non-philopatric recaptures during the mating season occurred essentially between display areas located within sub-basins of the study area. We also found a coincident, non-philopatric 3.5 km movement of a female and a male in the mating season of 2010 (Fig. 4, individuals 61 and 65). A notable outlier to the pattern just described was male 13, which moved in 2011 between two major

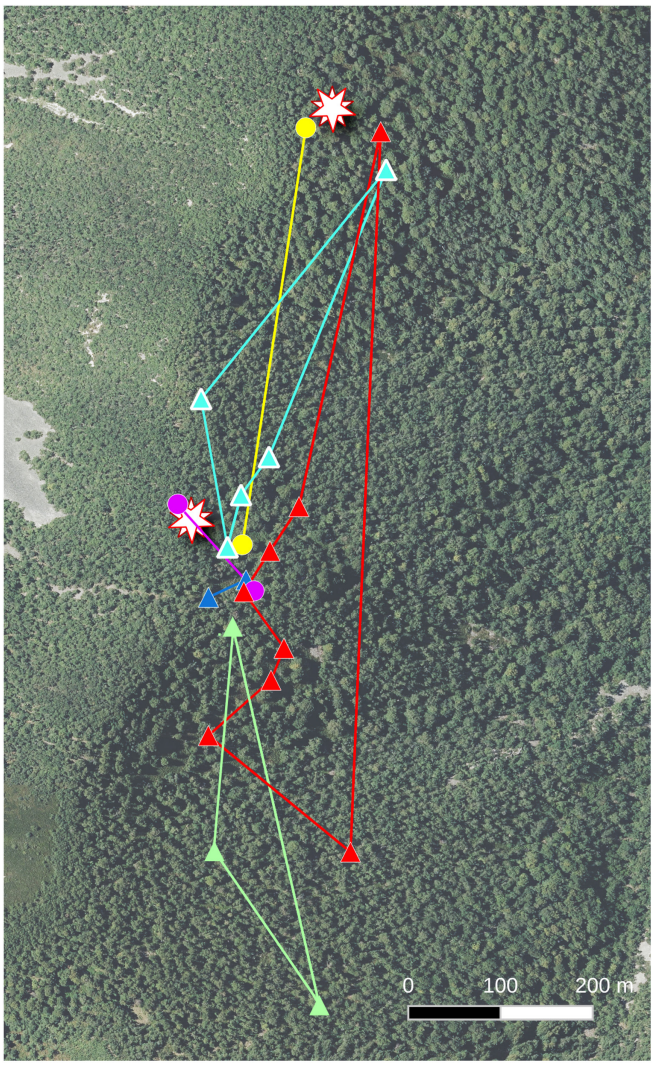

Figure 2. Example of the short movements that were the norm in a mating season. Symbols show locations of 4 capercaillie males (triangles) and 2 females (circles) at a display area in 2009. Lines show idealized tracks as minimum concave hulls for each individual. Stars mark the reference location of two areas historically considered as leks. Basemap: aerial image from the Spanish Geographic Institute (https://pnoa.ign.es).

valleys separated by deforested terrain in southern exposure, and other human-modified terrain.

Most birds changing display areas between mating seasons were recaptured at 2 different ones (5 females, 8 males), with just 1 female and 2 males recaptured at 3 different display areas. These recaptures also occurred mostly within major valleys, although there were three recaptures bridging sub-basins. Interestingly, two of them from 2009 to 2010, and 2010 to 2011, belonged to the same 'travelling' male 13 referred above (Fig. 4).

In terms of probability, the fidelity to display areas among seasons was estimated at 0.62 (± 0.12 SE) for females and 0.77 (± 0.07 SE) for males by the multi-event CR approach. The best model for interannual site fidelity suggested no effect

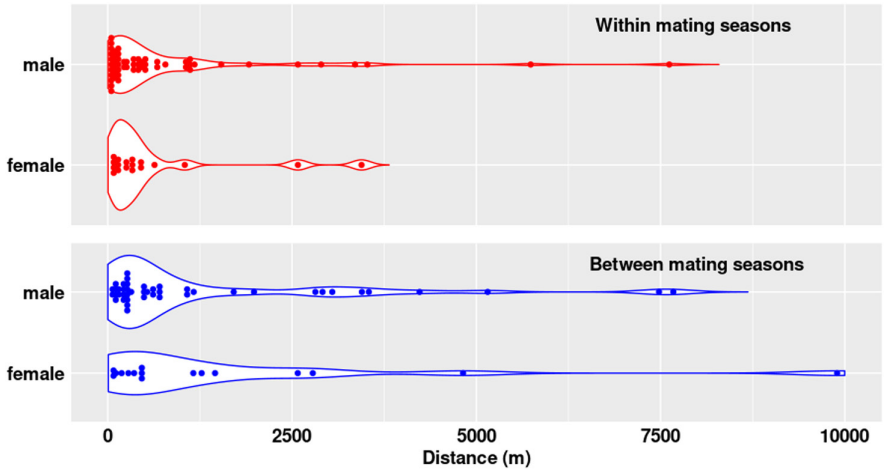

Figure 3. Violin plots (data points plus a probability density) showing the frequency distribution of maximum planimetric distance of recaptures (m) for each capercaillie individual, both within and between mating seasons.

of sex (Table 1). Yet the results include uncertainty about the effect of sex and time on site fidelity, since models with and without sex and/or time as covariates yield very close estimates in terms of AIC ($\Delta i < 2$ units, Table 1). Estimates of recapture were 0.62 ± 0.10 SE (males and females pooled). Estimates of apparent survival were 0.53 ± 0.11 SE and 0.89 ± 0.10 SE for females and males, respectively.

Discussion

Our DNA-based recaptures of capercaillie allowed us obtaining individual detection histories (sensu Lamb et al. 2019), which provided data on the use of space of individuals of this endangered population, which have been previously, and surprisingly, lacking. Surveying display areas during three consecutive breeding seasons, we found relatively high capercaillie fidelity to display areas, but also rarer, much longer movements.

Birds tended to remain in one display area in spring, although a quarter of the individuals did visit two or three display areas. In males, the latter seemed consistent with expected exploratory movements into other male territories (Wegge et al. 2013). Overall the prevalence of short movements in the mating season agrees with previous studies in capercaillie (Wegge and Larsen 1987, Gjerde et al. 2000),

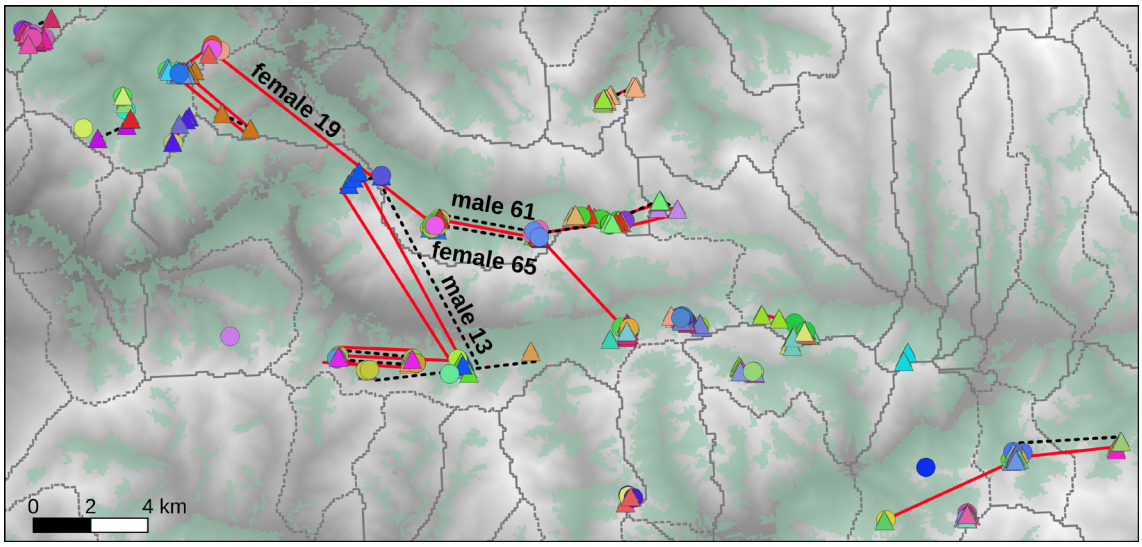

Figure 4. Triangles and circles show DNA-tagged male and female capercaillie, respectively. Lines show maximum straight line movements between recaptures of capercaillie genotypes within (solid red) and between (dashed black) mating seasons. Overlapping movements were slightly displaced for clarity. Polygons show landscape sub-basins* over a digital elevation model of the study area, where lighter hues indicate higher elevation (range 357 to 2094 m a.s.l.). Light-green shading indicates forest patches (Corine Land Cover ver. 2012). *Ministerio para la Transición Ecológica y el Reto Demográfico (https://www.miteco.gob.es/en/cartografia-y-sig/ide/descargas/agua/cuencas-y-subcuencas.aspx).

Table 1. Candidate models of annual survival (φ), site fidelity (f) and recapture (r) probabilities for Cantabrian capercaillie *T. urogallus cantabricus*. Number of parameters in the model (K), deviance (D), Akaike's information criterion values amended for overdispersion and corrected for sample size (QAICc), QAICc differences (Δi). Subscripts in the parameters φ, f, r, indicate the potential effects considered for each model.

	Model	K	Deviance	QAICc	Δ_i	W_i
(1)	φ_{sex}, f, r	4	234.86	243.10	0.00	0.35
(2)	φ_{sex}, f_t, r	5	233.48	243.84	0.74	0.24
(3)	φ_{sex}, f_{sex}, r	5	233.72	244.08	0.98	0.21
(4)	φ_{sex}, f_{sex+t}, r	6	232.66	245.16	2.06	0.12
(5)	φ_{sex}, $f_{sex.t}$, r	7	232.47	247.14	4.04	0.04
(6)	φ, f, r	3	244.13	250.27	7.17	<0.01

and more broadly in lekking grouse species (Cross et al. 2017). However, we expected that in this endangered population, inhabiting a fragmented forest landscape, females visited several leks in spring due to low availability of males, as suggested in the case of inter-lek movements of females in the Alps (Storch 1997). Overall, the observed pattern of movement within mating seasons implies that individuals used several historically recognised leks, in a pattern that reminded of the exploded leks notion (Wegge et al. 2013). Many of those registered leks can be merged into fewer display areas, at least in terms of planning survey design and efforts. Fig. 2 included an example of two registered leks that we treated as a single display area.

Despite the prevalence of philopatric movements, both raw data and CR analysis indicate that non-philopatric movements are relevant, with some uncertainty regarding differences between sexes and mating seasons. Some of those non-philopatric movements occurred over relatively long distances, showing that both females and males of Cantabrian capercaillie were able to move through the landscape at ecological time scales, possibly contributing to demographic connectivity (sensu Lowe and Allendorf 2010). Our results also complement previous data on genetic connectivity and thus longer time scales, which found no genetic subdivision among individuals living in relatively distant sub-basins of the landscape (Fameli et al. 2017). We did not find longer movements by females, which would be expected according to direct tracking in other populations (Watson and Moss 2008). Previous studies of differential dispersal by females analysed through genotyping feathers or faeces showed disparate results (Mäki-Petäys et al. 2007, Segelbacher et al. 2008). However, our small sample size of longer movements (Fig. 3) prevents further discussion. Studies looking at movements in larger areas relative to the animals' home range would in principle obtain lower recapture rates, but would also identify longer movement events (Koenig et al. 1996, Cross et al. 2017). It is conceivable that year-round movements would be longer than those we detected in the mating season (Saniga 2006, Zizas et al. 2012). Possibly those undetected movements would also be directed towards alternative habitats (Watson and Moss 2008), and could take birds outside of the study area, which is nested among historical capercaillie territories (Supporting information).

A related question is where were the birds not captured or recaptured during our surveys? Some of them were likely in the same area, and were not detected, as reflected by mark-recapture models of population dynamics (ca 20% females and 12% males, according to the 'net superpopulation size' – N_{Snet}, i.e. the estimated number of individuals present in the study area at least during one spring between 2009 and 2011, Bañuelos et al. 2019). But there are other, non-exclusive, possibilities. We had previously found that females showed higher turnover in the study area (Morán-Luis et al. 2014, Bañuelos et al. 2019). Those results could be related to lower female survival, but also to more frequent dispersal events that remained undetected in our sampling schemes. It is possible that birds kept dispersing outside of the study area, which we selected for its consistent capercaillie presence in the recent decades. Data from Russian capercaillie populations suggested that younger birds left areas of primary habitat for lower quality, logged neighbouring patches, due to competition with dominant adults; some of those birds returned later as adults to the undisturbed habitats (Borchtchevski 1993). An equivalent pattern of sources and sinks in capercaillie local populations has been described in the Bavarian Alps (Segelbacher et al. 2003). We speculate that a similar process could be taking place in our study area, which includes higher forest cover and quality than the adjacent landscape (Quevedo et al. 2006). We found movements of birds up to 9 km within the study area. It is conceivable that similar movements may be pointing towards other areas, including historical capercaillie territories, which might be part of a source–sink dynamic in the population. However, evaluating that idea would require regular, formal surveying efforts, and we are not aware of any. Capercaillie management in the Cantabrian Mountains has paid little if any attention to forest patches outside the historically known leks. Moreover, as the presence of capercaillie in spring declined in historically known territories, attention has been placed on a subsequently smaller fraction of those, without monitoring formerly used forests, or potential new locations.

Comparing tracking animals based on DNA tagging versus direct tracking is not straightforward (Lamb et al. 2019), and probably those approaches are better viewed as complements rather than substitutes. We saw both pros and cons of DNA tagging: We identified 127 individuals, and registered movements for 70 of them, based just on their scats. Such indirect tracking thus provided a much larger sample size of individuals than could possibly be obtained by a standard research team working with endangered birds, under standard Spanish research funding. In addition, DNA tagging based on scats is a non invasive technique, particularly suited to individuals of endangered populations, for which handling stress should be particularly considered (Gibson et al. 2013, Blomberg et al. 2018). It has proved effective in our case, and we expect that its use as a monitoring method will gain traction for other endangered or elusive animals (Zemanova 2021). Results may also be less influenced by behavioral bias,

like avoidance of the observer, or response to handling and initial mark (Miller et al. 2005, Garamszegi et al. 2009).

An important shortcoming of looking at movements through DNA tagging based on shed tissues or scats is the lack of information on the sequence of 'captures' with samples from the same sampling period. It is not possible tracing precise movement paths, nor using the wealth of analytical methods developed for direct tracking of movements, and home ranges (Getz et al. 2007, Horne et al. 2007). It does allow to obtain crude measures of range use, for instance using minimum concave polygons to plot idealized tracks (Fig. 2). Another shortcoming, a trade-off for the number of individuals identified, is the number of data points per individual, which could be much larger using present-day GPS tracking technology (de Gabriel Hernando et al. 2020). Using DNA tagging we also missed important individual information like age and social status; aspects that would have been useful for instance to interpret whether the registered movements were dispersive or exploratory.

Acknowledgements – We thank Alberto Fernández-Gil, Bea Blanco Fontao, and Rolando Rodríguez Muñoz for their help in designing and conducting field surveys. Eduardo González, Víctor Rodríguez, and Damián Ramos helped with the fieldwork, and Jose Carral helped with field logistics. Alberto Fameli greatly helped fine-tuning lab methods, and Leticia Viesca Lombardía helped analyzing individual genotypes. The suggestions by an anonymous reviewer improved substantially the analytical approach of the manuscript. We acknowledge the permits granted by the environmental authorities of Asturias and León, required to survey capercaillie mating areas.

Funding – The study was funded by grants IB08-158 (FICYT, Asturian Government) to MJ Bañuelos and CGL2010-15990 (MICINN, Spanish Government) to MJ Bañuelos and M Quevedo. Mario Quevedo was partially supported by grant AYUD/2021/51261 (FICYT, Gobierno del Principado de Asturias, FEDER) to S. Suárez-Seoane.

Author contributions

María-José Bañuelos: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (equal). **María Morán-Luis**: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (lead); Project administration (supporting); Resources (equal); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (supporting). **Patricia Mirol**: Conceptualization (supporting); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (lead); Resources (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Mario Quevedo**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (lead).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01121.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b8gtht7kh (Bañuelos et al. 2023).

Supporting information

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

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