Tracking movements of an endangered bird using mark-recapture based on DNA-tagging

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Keywords

Abstract

1   Knowing the location and movements of individuals at various temporal and spatial scales is an
2   important facet of behaviour and ecology. In threatened populations, movements that would en-
3   sure adequate genetic flow and long term population viability are often challenged by habitat
4   fragmentation. It is also in those endangered populations where capturing and handling indi-
5   viduals to equip them with transmitters or to obtain tissue samples may present additional logist-
6   ical challenges. DNA-tagging, i.e. individual identification of samples obtained via non-invasive
7   approaches, can reveal certain movement patterns. We used faecal material genetically as-
8   signed to individuals to indirectly track movements of a large-bodied, endangered forest bird,
9   Cantabrian capercaillie (*Tetrao urogallus cantabricus*), for three consecutive mating seasons.
10   We identified 127 individuals, and registered movements of 70 of them (22 females, 48 males).
11   Most movements were relatively short for capercaillie, mostly concentrated around display
12   areas. We did not find differences in movement distances between females and males within
13   mating seasons, or between them. Several longer, inter-valley movements up to 9.9 km of plani-
14   metric distance linked distant display areas, showing that both females and males of Cantabrian
15   capercaillie were able to move through the landscape, complementing previous studies on gene
16   flow. Those longer movements may be taking birds outside of the study area, and into historical
17   capercaillie territories, which still include substantial forest cover. Tracking animals via DNA tag-
18   ging, particularly those on endangered populations, showed clear advantages like non-intrusive-
19   ness and potential for sample sizes much larger than via direct handling. However, it also
20   misses out on direct observation and natural history, which would provide key information like
21   social status and timing of movements.

Introduction

22   The study of movement patterns at various temporal and spatial scales provides basis for un-
23   derstanding behaviour, ecology and, ultimately, aspects of the conservation status of most an-
24   imals (Börger, Dalziel, & Fryxell, 2008). Some animal movements are tightly associated to their
25   specific habitat requirements, and in those cases navigating unfamiliar and unsuitable habitats
26   might increase risk exposure, compromising survival (Yoder et al. 2004; Bonte et al. 2012). As
27   consequence, the loss and fragmentation of habitat that affects most terrestrial ecosystems
28   (e.g. Watson et al. 2018) may result in appearance of dispersal barriers, which affect population
29   dynamics and gene flow via reduced connectivity (Ricketts 2001; Caplat et al. 2016). Indeed,
30   habitat loss and fragmentation of previous distribution ranges may yield smaller, subdivided
31   populations, if the loss of connectivity results in less frequent movements, and limits effective
32   dispersal. Those subdivided populations are more vulnerable to stochastic events that could re-
33   strict their probability of survival (Lens et al., 2002).

34   The combination of the species' movement ability and the presence and shape of remnant hab-
35   itat fragments together with the characteristics of the surrounding matrix, determine the species'
36   responses to landscape changes. Thus fine-scale movement behaviour of species of conserva-
37   tion interest should be incorporated in conservation planning and management, particularly
38   when habitat restoration is feasible (Lechner et al., 2015). Yet, such dataset are not easy to ob-
39   tain, and tend to be replaced by assumptions and simplifications (e.g. Southwell et al. 2008) de-
40   rived from data from other populations, or similar species. However, movements are often par-
41   tially determined by landscape characteristics, and by distinct selective pressures on different
42   populations (Baguette et al. 2013), so it is not always safe assuming that populations of a given
43   species would show equivalent movement patterns throughout their distribution range. For in-
44   stance, the established knowledge on a species' behaviour and habitat requirements may have
45   been obtained from parts of its distribution range less affected by habitat loss and fragmenta-
46   tion. Yet, in fragmented and peripheral areas of a distribution range, the quality of what may ap-
47   pear as secondary habitat is possibly key for the species' survival (Channel and Lomolino 2000;
48   Blanco-Fontao et al. 2010). This is particularly general for those areas within a species' range
49   where dispersal movements depend on fine-scale structural elements, acting as stepping
50   stones (Lechner et al. 2015).

51   We studied movements of an endangered forest bird, Cantabrian capercaillie *Tetrao urogallus*
52   *cantabricus*, living at the southern edge of the species range, under the influence of Atlantic cli-
53   mate (Olson et al. 2001; Cervellini et al. 2020). This capercaillie population declined severely
54   from its known historical range in the last third of the 20th century (Pollo et al. 2005; Storch et
55   al. 2006), and its viability appears compromised (Bañuelos et al. 2019). It has been recently lis-
56   ted as critically endangered in Spain (Ministerio para la Transición Ecológica 2018). Therefore,

57   to study them, it was advisable to use minimally intrusive techniques, like tagging of individuals
58   based on their DNA, left behind in shed tissues or scats. DNA tagging, where the repeated oc-
59   currence of a genotype is a direct indicator of movement, has been used to study movements at
60   various spatial and temporal scales (Palsbøll et al. 1997; Palsbøll 1999). It allows monitoring a
61   wider representation of the variability of individuals in a population, albeit with with fewer obser-
62   vations per individual than direct tracking techniques.

63   The remnant distribution range of Cantabrian capercaillie includes some relatively large patches
64   of forest and shrubland above the treeline, the latter being especially relevant for females with
65   broods (Bañuelos et al. 2008). Yet, these habitats are embedded in a patchwork of disturbed
66   landscape, including former forest clearings and burns in various states of secondary succes-
67   sion, pastures, roads, villages, and industrial activities like mountaintop mining; several known
68   display areas are less than 500 meters from the edge of those mining operations. We wanted to
69   know how capercaillie moved in such landscape, and whether they would show regular, relat-
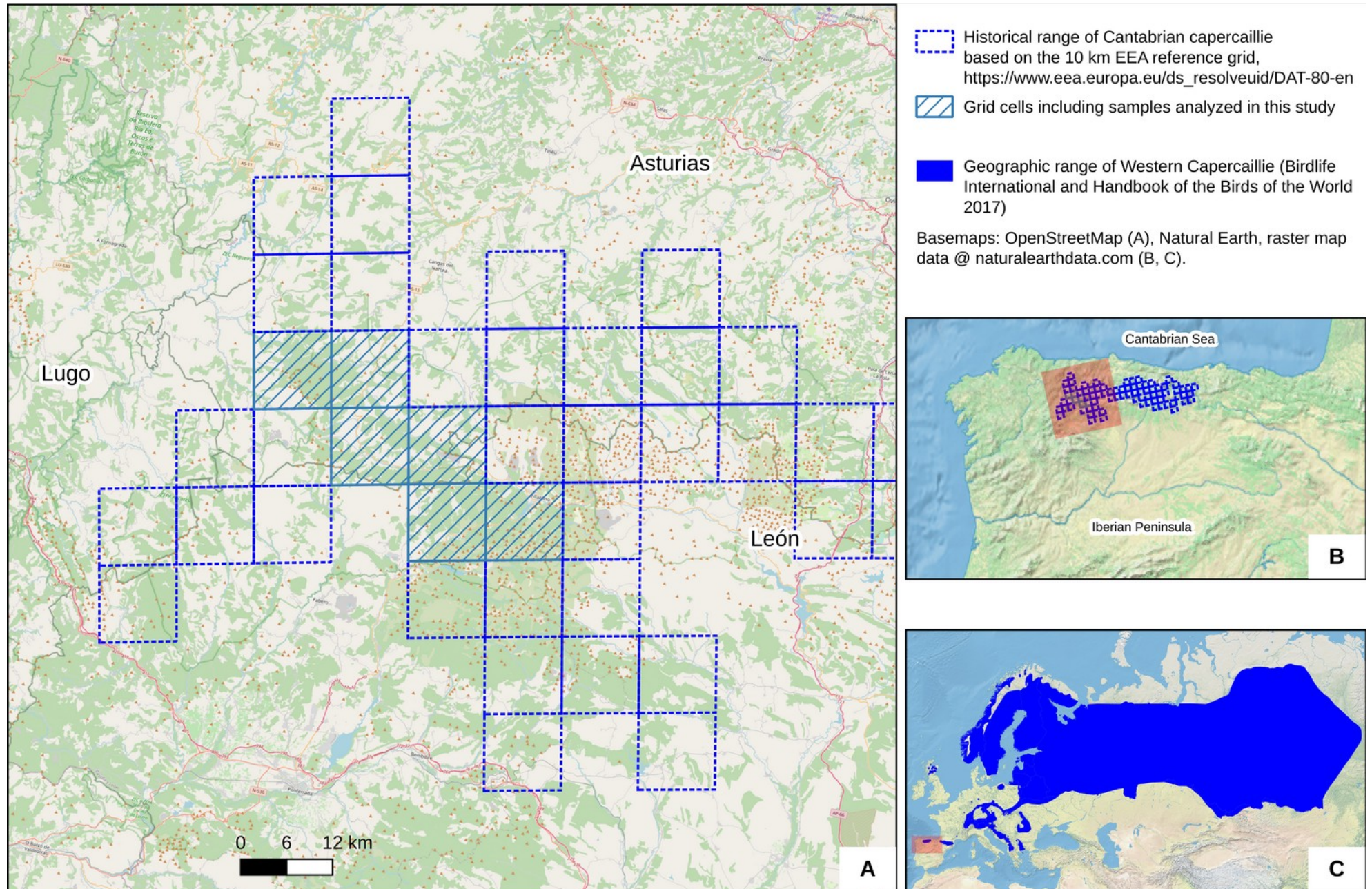70   ively long movements.

Methods

Field survey

71   The study area (Fig. 1) lays within the region of broadleaf forests under Atlantic influence (e.g.
72   Olson et al. 2001). The area is rugged, with elevation ranging from 450 to 2000 m a.s.l. Larger
73   patches of relatively old forest are restricted to the higher slopes of the mountain range, mirror-
74   ing a widespread pattern of landscape configuration related to human impacts (Sandel and
75   Svenning 2013).

76   Capercaillie gather at lekking areas in the mating season, thus making it more feasible to obtain
77   sufficient droppings or feathers than at other times, when the birds are more dispersed and the
78   habitat use of females and males is distinct (Bañuelos et al. 2008). We visited areas including
79   62 previously known capercaillie leks during the mating seasons (mid-March to early June) of
80   2009, 2010 and 2011 (Morán-Luis et al. 2014; Bañuelos et al. 2019 for details). Those reference
81   locations of leks derived in fact from the period of capercaillie hunting during the mating season,
82   which extended for much of the 20th century (Rodríguez-Muñoz et al., 2015).

Figure 1. Study area

Historical range of Cantabrian capercaillie based on the 10 km EEA reference grid, https://www.eea.europa.eu/ds_resolveuid/DAT-80-en

Grid cells including samples analyzed in this study

Geographic range of Western Capercaillie (Birdlife International and Handbook of the Birds of the World 2017)

Basemaps: OpenStreetMap (A), Natural Earth, raster map data @ naturalearthdata.com (B, C).

83   Of those leks, 83% showed signs of capercaillie presence at some point since year 2000; the
84   rest had apparently been previously unused. The study area includes several largely forested
85   areas with capercaillie presence, separated by valleys where human population and activity are
86   mostly concentrated. Forest cover in the study area averaged 46%

87   Using the location of each lek from previous reports as reference, two people surveyed those
88   forest patches for 2-3 h. Locations where we did not find signs of capercaillie presence were
89   surveyed again 2-3 weeks later. The position of each sample was recorded with a GPS (± 5m)
90   and was later incorporated into a GIS. To minimize redundant samples and the risk of over-
91   sampling the same individual, we selected samples based on a minimum distance of 25 m from
92   others with similar appearance (i.e. we weighed in freshness, size, shape and apparent content)
93   in the case of droppings, or from the same sex in the case of feathers. Droppings were stored in
94   tubes with silica-gel in the field, and were kept frozen at -20ºC until DNA extraction. Feathers
95   were kept dry at room temperature. We assigned samples to *display areas* instead of the histor-
96   ical leks used as reference because in some instances lek separation seemed an artifact, par-
97   ticularly considering that capercaillie display do not conform to the classical lek notion (Wegge
98   et al. 2013).

DNA tagging and movements

99   We aimed at obtaining individual genotype profiles using nine microsatellite markers (five previ-
100   ously developed for *Tetrao urogallus*, TUD2, TUD4, TUD5, TUT1, TUT3, Segelbacher et al.
101   2000; and four developed for the closely related *Tetrao tetrix*, TTD2, TTD6, BG10, BG15, Ca-
102   izergues et al. 2001, Piertney and Höglund 2001), and a specific primer developed for sex as-
103   signment for Cantabrian capercaillie (Pérez et al. 2011). Details of methods of DNA extraction
104   and amplification, molecular sexing, validation of genotype profiles and genotyping errors, were
105   detailed in Bañuelos et al. (2019). To ensure genotype reliability, we double-checked each gen-
106   otype profile. We kept only those samples for which at least six microsatellite loci amplified cor-
107   rectly, and which rendered a reliable and unequivocal consensus genotype (Morán-Luis et al.
108   2014, Bañuelos et al. 2019).

109   We recorded the repeated finding of capercaillie genotypes (hereafter *recaptures)* in success-
110   ively processed samples. Note that the initial observation of an individual does not necessarily
111   imply its first presence in a lek, as scats cannot accurately be dated in this context. We used in-
112   dividuals recaptured at least once for subsequent movement analyses. We focused particularly
113   on the maximum planimetric distance between recaptures of each individual, both within each
114   single mating season of 2009, 2010 and 2011, and between each mating season and the sub-
115   sequent ones. We coded those recaptures as philopatric if they occurred within the same dis-
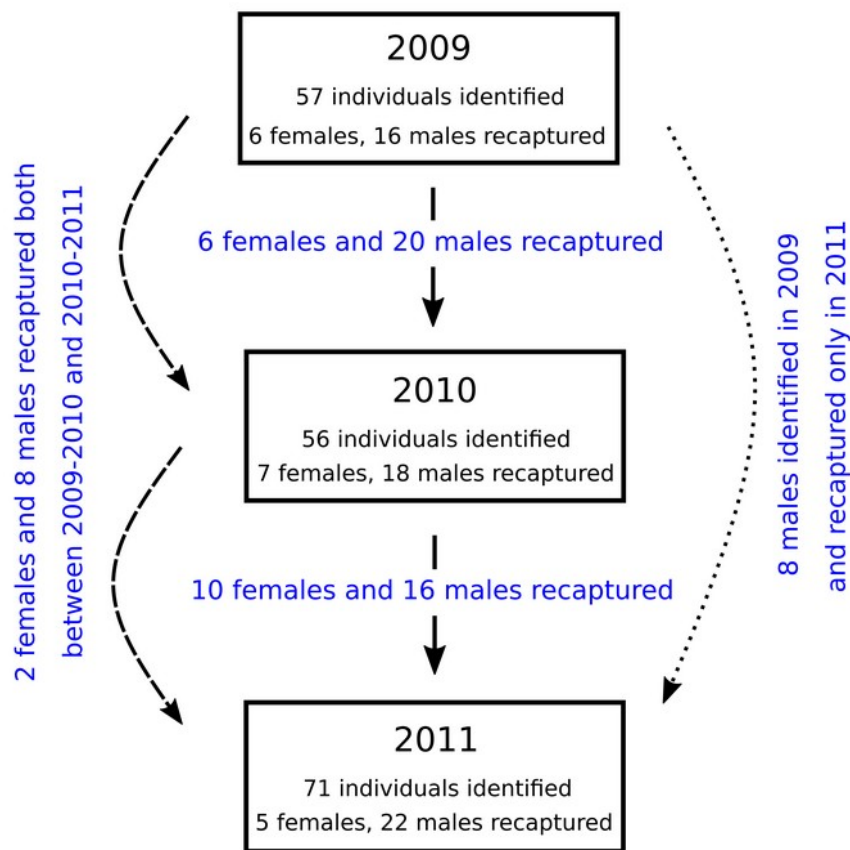116   play area.

Results

117 We found 127 capercaillie individuals (genotypes) in the study area: 48 females, 73 males, and

118 6 individuals that could not be sexed. Those capercaillies were the minimum number of individu-

119 als present in the area during the study. Individual identifications were derived from DNA extrac-

120 ted and amplified correctly in 422 samples, out of an initial set of 752 samples.

121 We found capercaillies in 35 display areas, which included 47 historical lek locations. In two of

122 those display areas we did not find males. The maximum number of males per display area was

123 7, with a median of 2. The maximum number of females per display area was 4 – not coincident

124 with the display area with most males – and the median was 1.

125 Seventy of the above capercaillies, 22 females (46%) and 48 (66%) males, were recaptured at

126 least once. We recaptured 53 individuals within any single mating season, and 49 individuals

127 between mating seasons (Fig. 2).

Figure 2. Scheme of recaptures

128 Scheme of capercaillie individuals identified and recaptured per season (boxes), recaptured in
129 consecutive seasons (solid arrows), and recaptured between seasons.

2009
57 individuals identified
6 females, 16 males recaptured

6 females and 20 males recaptured

2010
56 individuals identified
7 females, 18 males recaptured

10 females and 16 males recaptured

2011
71 individuals identified
5 females, 22 males recaptured

2 females and 8 males recaptured both between 2009-2010 and 2010-2011

8 males identified in 2009 and recaptured only in 2011

131   Most recaptures occurred within 500 m of the initial observation, both within and between mat-
132   ing seasons (Fig. 3, 4). Distributions were highly skewed, including a few relatively long-dis-
133   tance movements (Fig. 4, 5). Table 1 shows descriptive statistics of maximum distances of re-
134   capture of each individual.

Figure 3. Pattern of philopatric movements within mating seasons

135   Example of the short movements that where the norm in a mating season. Symbols show loca-
136   tions of 4 capercaillie males (circles) and 2 females (squares) at a display area in 2009. Lines
137   show idealized tracks as minimum concave polygons for each individual. White stars mark the
138   reference location of two areas historically considered as leks. Basemap: aerial image from the
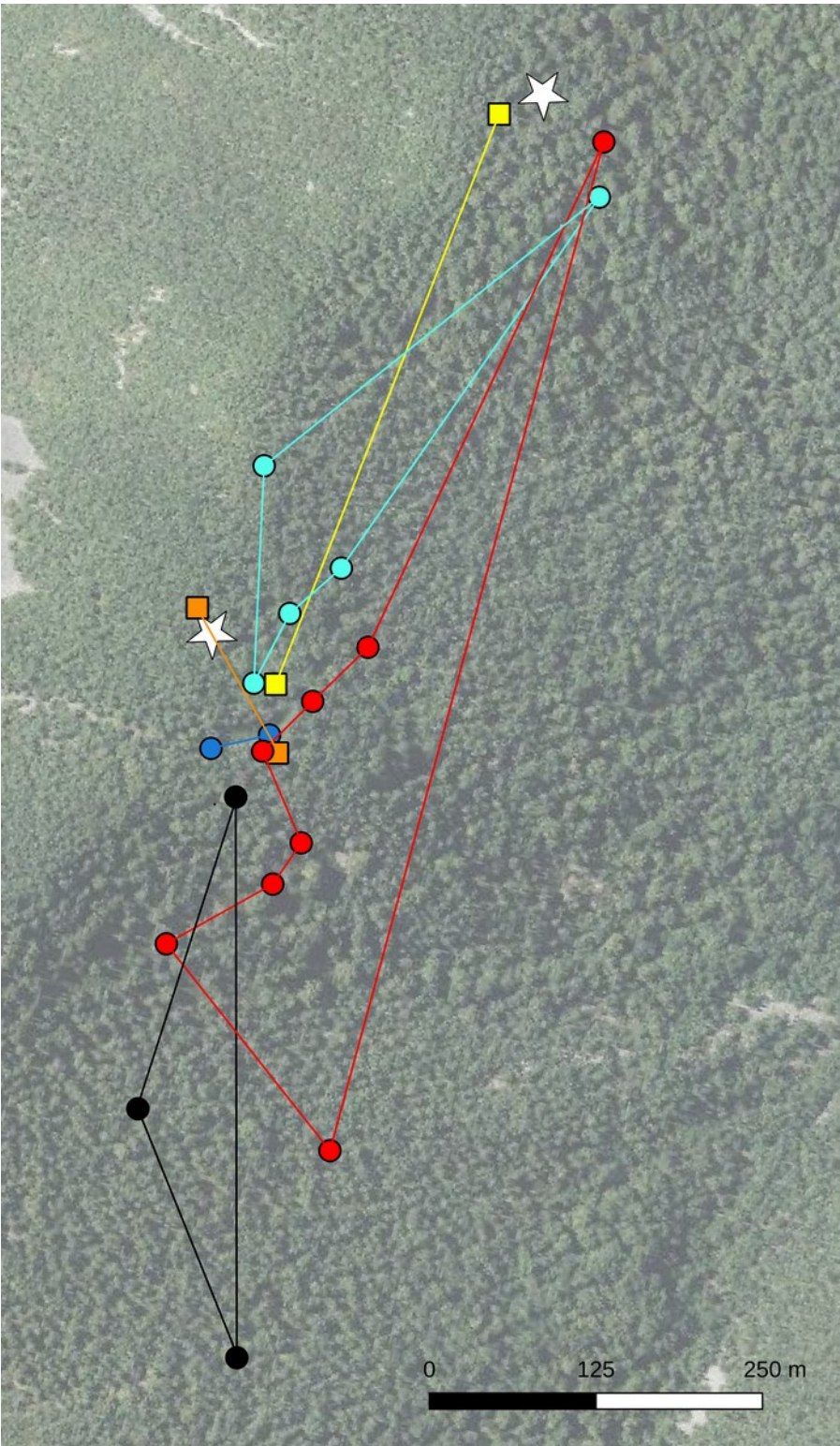139   Spanish Geographic Institute (https://pnoa.ign.es).

Table 1. Descriptive statistics of maximum distances of recapture (m) of each individual

Period	Sex	Recaptures	Median	Median absolute deviation	Range
Within mating seasons	female	18	297	252	63 - 3443
	male	56	297	341	29 - 7618
Between mating seasons	female	16	483	599	59 - 9895
	male	44	486	460	51 - 7673

140   There were no significant differences between females and males in maximum recapture dis-

141   tances within mating seasons (Wilcoxon rank sum test, W = 497, p = 0.947), or between matin

142   seasons (Wilcoxon rank sum test, W = 375, p = 0.701). Maximum recapture distances were lar-

143   ger between mating seasons (Wilcoxon rank sum test, W = 2804, p = 0.01).

144   The farthest recapture within any mating season was that of a male that moved 7.6 km between

145   two major valleys of the study area (Fig. 5, male 13). The farthest recapture between mating

146   seasons was that of a female re-identified in 2011 at 9.9 km from her previous location in 2010

147   (Fig. 5, female 19). That female visited different display areas each spring, changing sub-basins

148   of the study area.

149   In terms of philopatry, 79 % of male recaptures and 83% of female recaptures within mating

150   seasons occurred at the same display area. 73 % of male recaptures and 56 of female recap-

151   tures between mating seasons occurred at the same display area.

152   About one quarter of the birds (32% of males, 23% of females) visited more than one display

153   area at some point. There were no differences between females and males in the proportion of

154   recaptures registered in display areas different from the initial (X^2 = 0.08, df = 1, p = 0.78 within

155   mating seasons; X^2 = 1.47, df = 1, p = 0.23 between mating seasons).

156   Most birds that visited more than one display area during a single mating season were found at

157   2 different ones (3 females, 10 males); only one male was recaptured at 3 different display

158   areas. These non-philopatric recaptures during the mating season occurred essentially between

159   display areas located within sub-basins of the study area. We also found a coincident, non-

160   philopatric 3.5 km movement of a female and a male in the mating season of 2010 (Fig. 5, indi-

161   viduals 61 and 65). A notable outlayer to the pattern just described corresponded to the male

162   13, mentioned above, which in the mating season of 2011 moved between two major valleys,

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

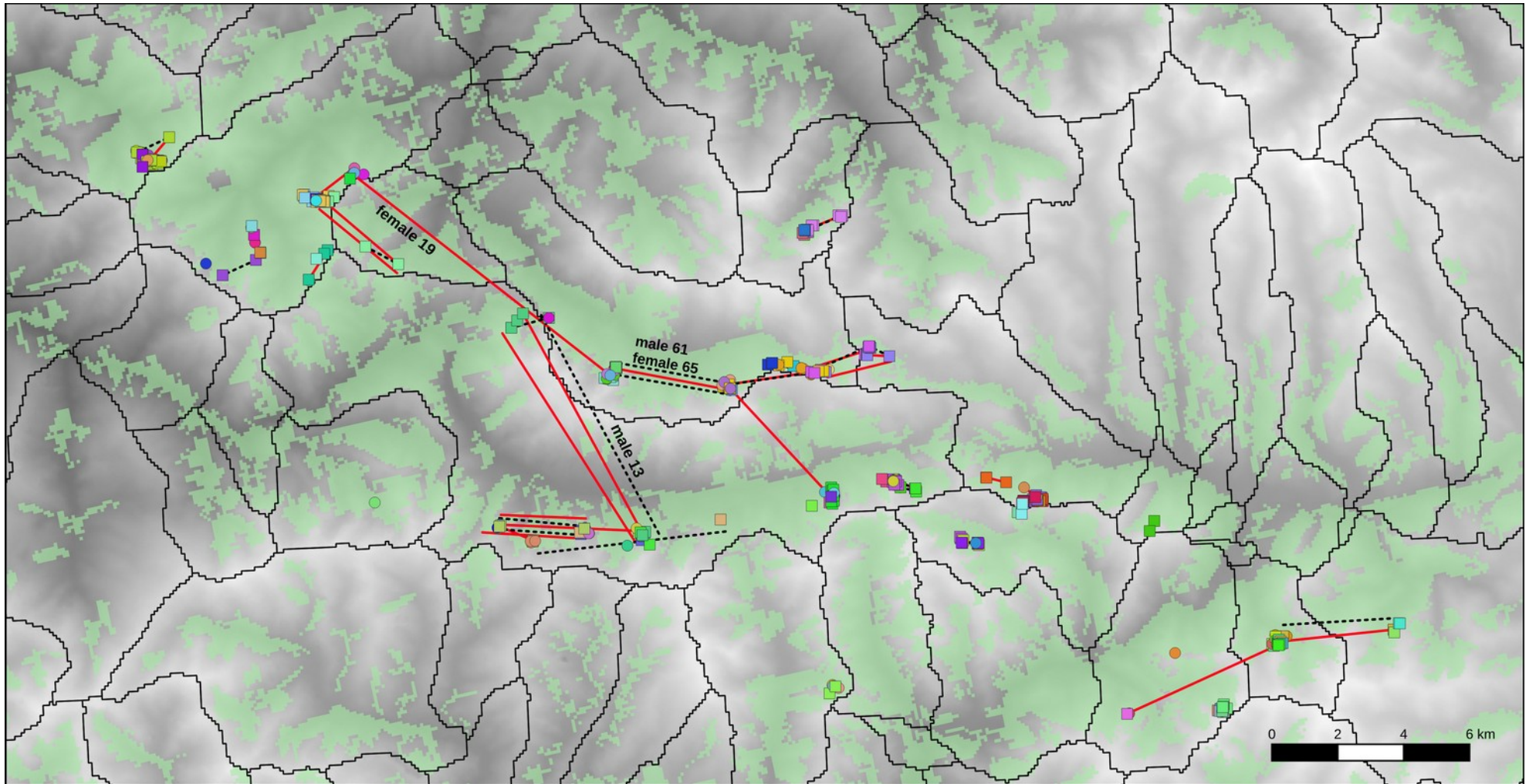## Figure 4. Distance of recaptures

164   Violin plots (data points plus a probability density) showing frequency distribution of maximum
165   planimetric distance of recapture (m) for each capercaillie individual, both within and between
166   mating seasons.
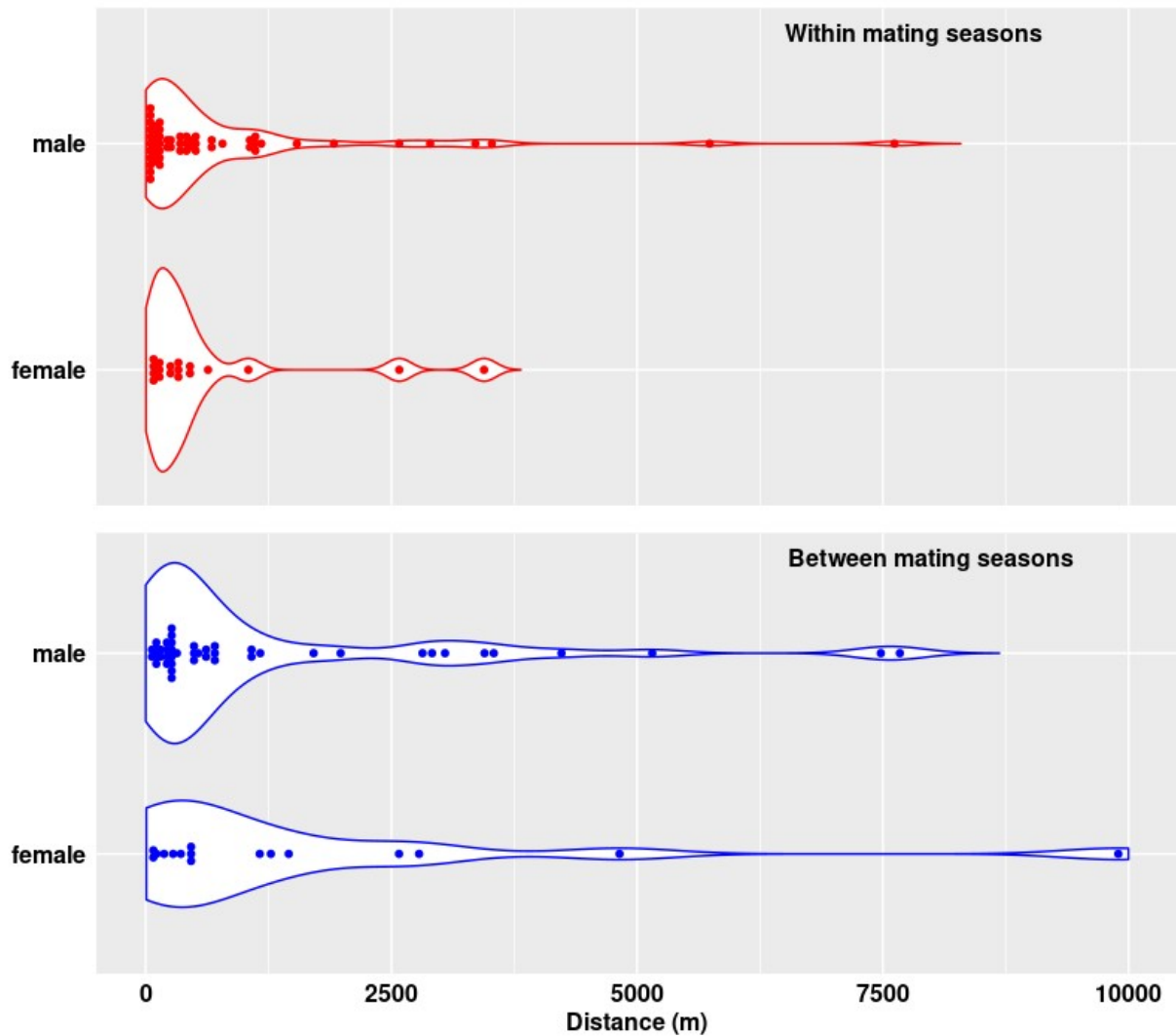
167   Most birds shifting display areas between mating seasons were recaptured at 2 different ones
168   (5 females, 8 males), with just 1 female and 2 males recaptured at 3 different display areas.
169   These recaptures also occurred mostly within major valleys, although there were three recap-
170   tures bridging sub-basins. Interestingly, two of them from 2009 to 2010, and 2010 to 2011, be-
171   longed to the same 'travelling' male 13 referred above (Fig. 5).

Figure 5. Non-philopatric recaptures and movements

172   Squares and circles show DNA-tagged male and female capercaillie, respectively. Lines show maximum straight line movements between recaptures of ca-
173   percaillie genotypes within (solid red) and between (dashed black) mating seasons. Overlapping movements were slightly displaced for clarity. Polygons show
174   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.). *Ministerio para la
175   Transición Ecológica y el Reto Demográfico [https://www.miteco.gob.es/en/cartografia-y-sig/ide/descargas/agua/cuencas-y-subcuencas.aspx]

Discussion

176   Surveying display areas during three consecutive breeding seasons, we tracked different caper-
177   caillie individuals in space and time. DNA-tagging recaptures provided a view of the use of
178   space of individuals of this endangered population that we did not previously have. We found
179   high capercaillie fidelity to display areas, but also rarer and much longer movements. Birds ten-
180   ded to remain in one display area in spring, although a quarter of the individuals did visit 2 or 3
181   display areas. In males, the latter seemed consistent with expected exploratory movements into
182   other males' territories (Wegge et al. 2013). Overall the prevalence of short movements in the
183   mating season agrees with previous studies in capercaillie (e.g. Wegge and Larsen 1987,
184   Gjerde et al. 2000), and more broadly in lekking grouse species (Cross et al. 2017). However,
185   we expected that in this endangered population, inhabiting a fragmented forest landscape, fe-
186   males visited several leks in spring due to low availability of males, as suggested in the case of
187   inter-lek movements of females in the Alps (Storch 1997). Overall, the observed pattern of
188   movement within mating seasons implies that individuals used several historically recognised
189   leks, in a pattern that reminded of the exploded leks notion (Wegge et al. 2013). Many of those
190   registered leks may in fact be merged into fewer display areas, at least in terms of planning sur-
191   vey design and efforts.

192   Despite the prevalence of philopatric movements, non-philopatric recaptures over much longer
193   distances showed that both females and males of Cantabrian capercaillie were able to move
194   regularly through the landscape at ecological time scales. These results complement previous
195   data on gene flow and thus longer time scales, which showed that there was no genetic subdivi-
196   sion among individuals living in relatively distant sub-basins of the landscape (Fameli et al.
197   2017). We did not find longer movements by females, despite that previous studies showed fe-
198   males dispersing farther, and moving more frequently between mating seasons (Segelbacher et
199   al. 2008; Watson and Moss 2008).

200   Our study was focused on relatively small-scale movements. Studies that explicitly attempted to
201   cover dispersal would in principle obtain much lower recapture rates, but would also identify
202   longer movement events (Koenig et al. 1996; Cross et al. 2017). It is conceivable that year-
203   round movements would be longer than those we detected in the mating season (Saniga 2006,
204   Zizas et al. 2012). Possibly those would also be directed towards alternative habitats (e.g. Wat-
205   son and Moss 2008), and could take birds outside of the study area, which is nested among his-
206   torical capercaillie territories (Fig. 1). Thus, those historical territories, which today could be per-
207   ceived as peripheral but which include substantial forest cover, should also be protected and
208   monitored, as an objective for the potential recovery of the Cantabrian capercaillie population.

209   A related question is where were the birds that we did not recapture. Some of them were likely
210   in the same area, and were not detected in our fieldwork, as reflected by mark-recapture mod-
211   els of population dynamics (Bañuelos et al. 2019). But there are other, non-exclusive possibilit-
212   ies. We had previously found that females showed higher turnover in the study area, and yiel-
213   ded less recaptures (Morán-Luis et al. 2014; Bañuelos et al. 2019). Those results could be re-
214   lated to lower female survival, but also to more frequent dispersal events that remained un-
215   detected in our sampling schemes. It is possible that birds kept dispersing outside of the study
216   area, which we selected for its consistent capercaillie presence in the recent decades. Data
217   from Russian capercaillie populations suggested that younger birds switched an area of primary
218   habitat for lower quality, logged neighbouring patches, due to competition with dominant adults,
219   and some returned later as adults (Borchtchevski 1993). An equivalent pattern of sources and
220   sinks in capercaillie local populations has been described in the Bavarian Alps (Segelbacher et
221   al. 2003). We speculate that a similar process could be taking place in our study area, which in-
222   cludes higher forest cover and quality than the adjacent landscape (Quevedo et al. 2006). How-
223   ever, evaluating that idea would require regular, formal surveying efforts, and we are not aware
224   of any. Capercaillie management in the Cantabrian Mountains has paid little if any attention to
225   forest patches outside the historically known display areas. Moreover, as the presence of caper-
226   caillie in spring declined in historically known territories, attention has been placed on a sub-
227   sequently smaller fraction of those, without monitoring formerly used forests, or potential new
228   locations.

Ups and downs of studying movements with DNA tagging

229   Comparing different aspects of tracking animals based on DNA-tagging vs. direct tracking is not
230   straightforward, yet we saw both pros and cons of DNA-tagging: We identified 127 individuals,
231   and registered movements for 70 of them. Such indirect tracking thus provided a much larger
232   sample size of *tagged* individuals distances than could possibly be obtained by a standard re-
233   search team working with endangered birds, and under standard Spanish research funding. In
234   addition, DNA-tagging based on scats is a non invasive technique, particularly suited to individu-
235   als of endangered populations, for which handling stress would be a serious problem (Gibson et
236   al. 2013; Blomberg et al. 2018). Results may also be less influenced by behavioral bias, like
237   avoidance of the observer, or response to handling and initial mark (Miller et al. 2005; Biro and
238   Dingemanse 2009; Garamszegi et al. 2009).

239   On the other hand, what we gained in number of individuals identified, we certainly missed in
240   the number of data points per individual. Present-day GPS tracking technology could provide a
241   much larger datasets, thus allowing detailed inferences (e.g. de Gabriel Hernando et al. 2020).
242   Another shortcoming is that using DNA-tagging based on shed tissues or scats it is not possible

243   detailing the sequence of the initial and subsequent "captures"; thus it is not possible tracing

244   precise movement paths. In addition, we lack direct information on the natural history of the

245   "tagged" birds. We lacked for instance important individual information like age and social

246   status; aspects that would have been useful to interpret whether the registered movements

247   were dispersive or exploratory. Or to check whether results were biased to adult males. Such

248   bias is certainly possible, because the presence of subordinate males may be more difficult to

249   detect in spring (Wegge and Larsen 1987), even though we had it in mind, and included as

250   much surveyed terrain as possible in the periphery of reference lek locations.

Acknowledgments

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