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Research article

Estimating capercaillie *Tetrao urogallus* population size in Scotland from annual leks and counts of broods over the period 2010–2020

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The population size of capercaillie *Tetrao urogallus* in Scotland was estimated from annual counts of males at 151 known spring lek sites and 45 counts of males, females and their broods in August during the period 2010–2020, combined with published survival estimates. Population size declined from an estimated 580 birds (95% CL: 462–698) in 2011 to 304 (239–369) in 2020 and the extinction probability was 23% after 25 years, 95% after 50 years and 100% after 100 years. Removing mortality associated with collisions against fences lowered extinction probabilities to 0, 3 and 40% respectively, emphasizing fence removal as a management priority. Greatest declines occurred in Deeside and Donside, Morayshire and Ross-shire and Perthshire and Trossachs. In the Badenoch and Strathspey stronghold, where an estimated 83% of males remain, numbers of occupied leks and lekking males have decreased in the last five years and are associated with reduced breeding success over the last 10 years. Our estimates of population size are only half that derived from the last official national survey in winter 2015/2016. We discuss possible reasons for this difference including underestimates from lek-based surveys linked to male detection probabilities. Finally, we recommend improvements to the current annual monitoring scheme, including repeat counts at leks and use of novel remote acoustic devices and restoration of annual brood counts in remaining key forests.

Keywords: breeding success, extinction probability, forest, national survey

Introduction

The western capercaillie *Tetrao urogallus* (hereafter capercaillie) is the largest and most sexually size dimorphic of the family Tetraonidae, inhabiting old stand forests of the boreal and temperate zones of the Western Palearctic. Large and recent declines in abundance, have resulted in capercaillie's status changing from a hunted gamebird to a protected species that is red-listed in many parts of central and western Europe (Storch

2007), including the Black Forest in Germany (Coppes et al. 2016, Dopper et al. 2021) and the French Pyrenees (Bal et al. 2021). In Scotland, extinction in the late eighteenth century was followed by successful reintroductions in the 1830s (Lever 1977) and now capercaillie are chiefly associated with older stands of scots pine *Pinus sylvestris* (Picozzi et al. 1992) in the Scottish Highlands. Causes of decline include large-scale intensified forest management (Wegge and Rolstad 2011), associated increases in predator numbers (Baines et al. 2016, Kammerle et al. 2017), changes in weather patterns (Moss et al. 2001, Wegge and Rolstad 2017, Coppes et al. 2021) and, in Scotland, collisions with fences erected to exclude red deer *Cervus elaphus* to help promote forest regeneration (Baines and Summers 1997). Similar man-made wires and cable hazards in Norway and the Pyrenees are associate with deaths of capercaillie and other grouse species (Bevanger 1995, Bal et al. 2021). Declines are often associated with reduced breeding success (Jahren et al. 2016), which can vary in relation to weather at hatch, larval food for chicks and predation (Wegge et al. 2022).

In Scotland, capercaillie numbers and range have declined since the mid-1970s (Moss 1994). A first national survey in Scotland, based on transects walked in winters 1992–1994, estimated 2200 birds (Catt et al. 1998). A further decline to 1073 birds had occurred by 1998/1999 (Wilkinson et al. 2002), with successive estimates between 2003 and 2015 suggesting a fluctuating population of 1000–2000 birds, with no significant overall trend (Wilkinson et al. 2018). These population estimates have large confidence intervals due to few observations and variations in encounter rates, leading to non-significant differences in estimated population size between successive surveys. The −51% decline between surveys (1994–2016) is however the highest long-term population decrease for a bird species in Scotland (Scottish Natural Heritage 2019).

The decline has occurred despite land managers deploying multiple conservation interventions including predator control, habitat management and marking and removing fences, with associated monitoring to help inform effects of management on status and to better understand mechanisms underpinning declines. Monitoring measures include annual counts of males attending leks and counts of females and their broods within sample forests to estimate breeding success (Baines et al. 2004, 2016), the demographic stage thought to be driving the recent Scottish decline (Moss et al. 2000).

Given the low precision, high costs and infrequency (once every six years) of the national surveys, it has been suggested that greater use of annual lek and brood counts could be made to derive annual population estimates to help guide conservation actions (Wilkinson et al. 2018). Here we consider the value of these data collected during the last 10-years, used alongside published estimates of adult and juvenile survival (Moss et al. 2000), to derive such estimates. We suggest improvements to monitoring efforts that may provide more robust estimates to better complement future national surveys.

Material and methods

Lek counts

Capercaillie are polygamous, with males displaying together at traditional lek sites in spring to attract females (Hjorth 1970). Here, older males occupy exclusive territories close to the lek centre, with younger males around the periphery (Storch 1997). Counts of males attending all the 151 known leks in Scotland were made across four Scottish regions, Deeside/Donside, Moray and Ross-shire, Perthshire and Trossachs and Badenoch and Strathspey from 2010 to 2019 (Fig. 1). Within that period, males were recorded at 110 leks, with the number of attended leks varying from 79 to 100 per annum. No leks were surveyed in 2020 following human lockdown restrictions due to the SARS-COV-2 virus.

Counts followed standardised methods (Picozzi et al. 1992, Scottish Natural Heritage 2013) and typically comprised one visit in either the second half of April or first week of May between 04:00 and 08:00 GMT, when bird activity peaked (Abrahams 2019). Observers were positioned in hides or vehicles before daylight to minimise disturbance. The total number of observers used for surveys has been broadly consistent across the last 10 years. The number of observers deployed per lek varied in relation to male aggregation, males attending and topography from one observer on leks with up to five males spread over even terrain to three or four observers on larger leks with 10 or more males on uneven ground. If multiple observers were used, each viewed a different sector of the lek. After lekking had been completed, observers compared data to agree a total number of males. If count validation was needed, this was done by looking for trampled faeces or cast feathers indicating stances of individual males. All males seen or heard were recorded regardless of whether they were exhibiting lekking behaviour. Prior to 2019, the presence of signs (males' feathers or faeces) was recorded as male presence even if none were seen. Leks could subtly move positions between years, often in response to forest management. To ensure that these were not missed, the general area was searched in March or early April to find signs and to subsequently position hides accordingly.

The number of occupied leks, together with the total attending males, were summed for each region in 2011 and 2016, to compare with the geographical distribution of lekking males encountered during the national surveys in the previous two winters (Ewing et al. 2012, Wilkinson et al. 2018), and in spring 2019. The number of attending males (lek sizes) were assigned into four categories (one male, 2–4, 5–7 and > 7 males), compared for 2010 and 2019 and differences tested using a Chi-squared contingency table.

Counts were not possible at all leks in all years, and it is likely that some leks were unknown in 2010. To account for these missing data, a Poisson regression in a generalised linear model (GLM) framework was used to predict lek and year terms from existing data. The number of males at each lek in each year was the response variable and lek and year were factors (categorical variables). This allowed interpolation of

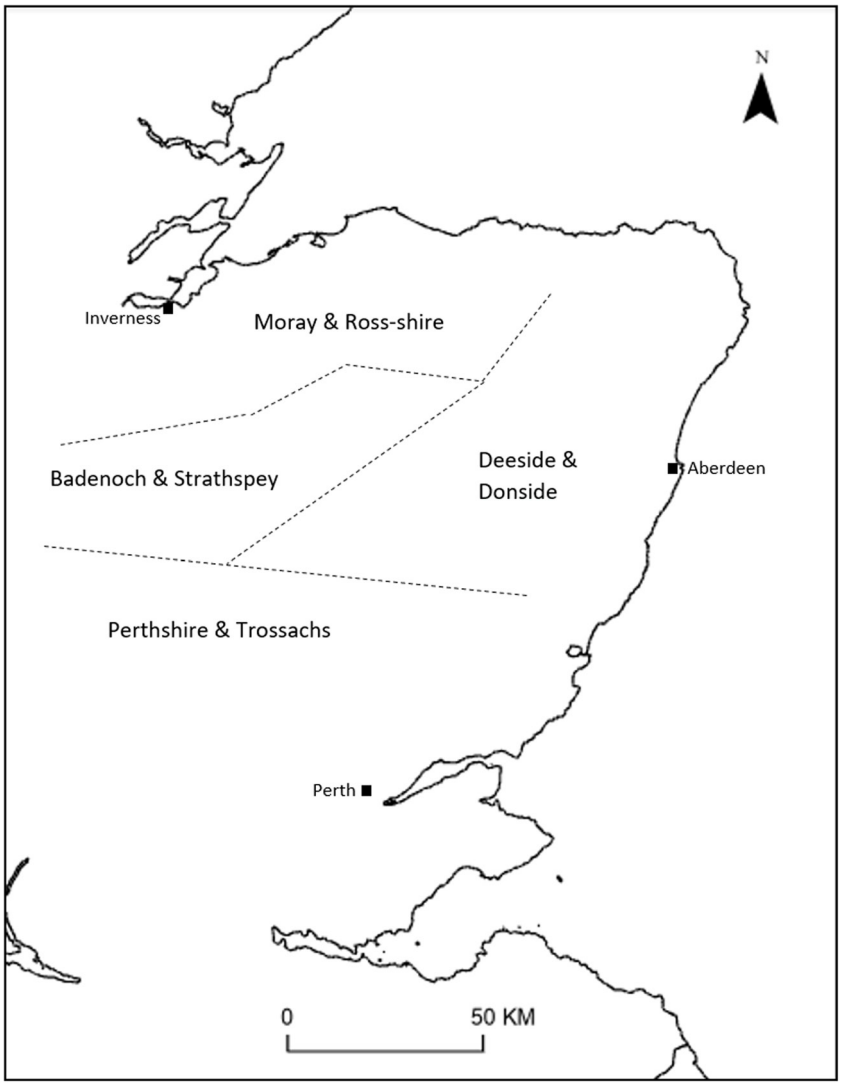

Figure 1. Map showing the four regions of northeast Scotland within which all known capercaillie lek sites were located.

missing data values and prediction of the annual total of males with 95% confidence limits (CL). This approach was however limited by not allowing for lek colonisation–extinction dynamics. It assumed that leks discovered mid-way through the study period existed at the start of the period and that no leks had become extinct before they were detected.

Brood counts

Up to five forests, all in Badenoch and Strathspey, were searched annually in August from 2010 to 2020 using trained dogs to locate birds. Areas searched varied between forests from 7.2 to 11.0 km^2. Observers, usually the same three across years, walked the same parallel transects 100 m apart each year along pre-agreed compass directions, whilst encouraging their dogs (one dog worked per observer at any one time) to search the ground between the transects. For further details see Baines et al. (2004). Any direct risks from dogs to chicks were minimised by using only experienced dogs and dog handlers. For example, in over 30 years of conducting counts of capercaillie broods, author DB had no chicks killed or injured by his dogs. Risks associated with disturbing and dispersing broods were minimised by not surveying in late-afternoons or evenings, thus allowing adequate time for any broods dispersed by the survey to gather before dusk. Radio-tracking studies, e.g. Fletcher and Baines (2020), verified that if broods were disturbed, members readily gathered to reform broods.

Combining all years, 792 females with 503 chicks were observed during 45 counts. Approximately two-thirds of Scottish females breed in their first spring (Moss et al. 2006, Fletcher and Baines 2020). Distinguishing between females that had bred but failed and those who did not breed was not possible, hence all females seen were included when estimating breeding success. GLM Poisson regressions, adjusted for overdispersion, were used to model breeding success (chicks per female) in relation to the factors 'forest' and 'year' and then separately over time with 'year' as a linear covariate. Furthermore, 531 males were also observed from 32 counts

in four forests, allowing estimation of adult sex ratios. Of the 503 chicks, 247 were sufficiently old to be reliably sexed and 100 of these were male chicks. Sex ratios of both chicks within broods and adults within counts were modelled as binomial regressions, with the number of males, either chicks in each year or adults on each count, as the response variable, the number of sexed chicks or sexed adults seen as the binomial totals, and 'year' as a, explanatory factor. Neither the sex ratio amongst chicks nor that amongst adults differed between years and mean sex ratios with their SEs, weighted by the number of male chicks (or adults) that were sexed in each year, were calculated for chicks and adults across the full 11-year period.

Population estimation and extinction probability

The population parameter estimates used in the estimation of population size and the modelling steps (below) are summarised in Table 1, together with standard errors or confidence limits and source data/references. Survival rates were higher in the absence of fences (Moss et al. 2000), so our modelling considered a scenario with fences and a scenario with no fences, to explore the sensitivity of population modelling outputs to variation in survival rates. Published adult and juvenile survival rates were over three months, so adult rates were raised to a power of 4 to cover a full year, and juvenile ones to a power of 8/3 to cover eight months (September–April). Capercaillie population size on 1 May for each of the years 2011–2020 was estimated using as a start point the mean of the predicted number of adult males P_t^M attending leks in each of the previous years (t). The number A_{t+1}^M of adult males surviving to year $t+1$ was estimated by multiplying the males attending leks in year t by the annual adult survival rate $(s_A)^4 = 0.72$. The number F_t of females in May of year t was estimated by multiplying the number of lekking males in year t by the mean adult female-to-male ratio of $r_A = 1.15$. Doing so assumes that all males encountered during brood surveys were breeders, i.e. that all first-year males recruited to leks; this is a best-case scenario as delayed recruitment gives more time for young birds to die before they attend a lek. Multiplying the number of females in May by the annual adult survival rate $(s_A)^4$ gave the number A_{t+1}^F of adult females surviving to year $t+1$.

The number of yearlings alive on 1 May in year $t+1$ was estimated starting from the number of females in May of year t. To account for female mortality between May and brood counts at the start of August, F_t was multiplied by the 3-month survival rate $s_A = 0.92$. The result was multiplied by the mean number c_t of chicks per female in year t to give the number of chicks in August, which was corrected for a four-weekly poult survival rate $s_P = 0.89$ to give the number of juveniles surviving to 1 September, which in turn was multiplied by the 8-month juvenile survival rate $(s_J)^{8/3} = 0.63$ to give the number Y_{t+1} of yearlings alive on 1 May in year $t+1$. Yearlings were added to the numbers of surviving adult males and females to model a total number of capercaillie N_{t+1} in year $t+1$. The male population size in year $t+1$, M_{t+1}, was similarly modelled using the number of male yearlings estimated by multiplying Y_{t+1} by the proportion m of male chicks in broods. These operations are summarised below in equation form (Eq. 1–5):

$$A_{t+1}^M = P_t^M \left(s_A\right)^4 \quad (1)$$

$$A_{t+1}^F = P_t^M r_A \left(s_A\right)^4 \quad (2)$$

$$Y_{t+1} = P_t^M r_A s_A c_t s_P \left(s_J\right)^{8/3} \quad (3)$$

$$N_{t+1} = A_{t+1}^M + A_{t+1}^F + Y_{t+1} \quad (4)$$

$$M_{t+1} = A_{t+1}^M + mY_{t+1} \quad (5)$$

The 95% confidence intervals around the estimate Y_{t+1} were obtained by randomising each parameter 1000 times in accordance with its distribution. The predicted annual numbers

Table 1. Parameter estimates (means (SE)) used in modelling the annual population size of capercaillie in Scotland (2011–2020).

Parameter	Value	Source
Predicted males at leks (May), P_t^M	Back-transformed mean (SE or 95% CL)	Lek database (Cairngorms Capercaillie Project)
Adult sex ratio (females/males May), r_A	1.15 (0.05)	Brood counts 2010–2019, Ewing et al. 2012, Wilkinson et al. 2018
Proportion of males in broods, m	0.41 (0.02)	Brood counts 2010–2019
Chicks per female, c_t	Annual mean (SE)	Brood counts 2010–2019
Four-week poult survival rate (Aug–Sep), s_P*	0.89 (0.75–0.96)	Moss et al. 2000
Three-month juvenile survival rate (including fence deaths), $s_{J,f}$*	0.84 (0.75–0.90)	Moss et al. 2000
Three-month juvenile survival rate (without fence deaths), $s_{J,nf}$*	0.92 (0.86–0.97)	Moss et al. 2000
Three-month adult survival rate (including fence deaths), $s_{A,f}$*	0.92 (0.88–0.95)	Moss et al. 2000
Three-month adult survival rate (without fence deaths), $s_{A,nf}$*	0.94 (0.93–0.95)	Moss et al. 2000

*Assumed to be the same for males and females.

of males and the annual number of chicks per hen were assumed normal on the logarithmic scale, with means and variances derived from the underlying statistical models. The adult sex ratio and proportion of male chicks were assumed normal with variance equal to SE^2. Survival rates, which Moss et al. (2000) had estimated through logistic regression, were assumed normally distributed on the logistic scale (for a parameter s with 95% confidence limits s_L and s_U, the mean on the logistic scale was logit(s) and the variance estimated as $([\text{logit}(s_U) - \text{logit}(s_L)]/2/z_{0.975})^2$). We back-transformed values of parameters randomised on a non-arithmetic scale, then repeated the modelling steps with the randomised parameters to generate 1000 estimates of population size. From these we calculated standard errors and took the 95th percentiles as 95% confidence limits. We compared the modelled male population size in year $t+1$ with the predicted number of males derived from annual lek counts using correlation and assessed the slope of the relationship using principal axis regression to allow for error in both quantities.

Population extinction probabilities were calculated using the package ULM ver. 6.0 (Legendre and Clobert 1995) and a population model matching the one described above. At each time step (year), the model generated a set of demographic parameters obtained from the estimates and standard errors given in Table 1; the number of chicks per hen was assumed normally distributed on the logarithmic scale, with mean and standard deviation obtained from the logarithms of the annual values in Table 3. We then applied Eq. 1–5 where P_t^M was replaced by M_t. Initial conditions (number of adult and yearling males) were taken from the modelled number of males in 2020, averaged across the values estimated from survival rates with and without mortality from collisions with fences. As extinction probability after a given time interval goes down as population size increases, we repeated the process with more conservative initial conditions corresponding to the greater numbers recorded during the last national survey in winter 2015/2016 (Wilkinson et al. 2018). The survey estimated 483 males, which was adjusted for four months of mortality between the January mid-point of the survey and May 2016 by multiplying by $1/[j_{2016}\ (s_J)^{-4/3} + (1 - j_{2016})\ (s_A)^{-4/3}]$, where j_{2016} is the modelled proportion of yearling males in May 2016. The result was projected forward to 2020 using the ratio of modelled number of males at leks in 2020 to the number of males at leks estimated from counts in 2016 as a scale factor, then splitting the result pro rata between adults and yearlings as per previous initial conditions. We incorporated demographic stochasticity by modelling the fate of individuals probabilistically according to the year's set of parameters and their distributions (cf. Table 1). The probability of extinction after 25, 50 and 100 years was determined by running each model 10 000 times and evaluating the percentage of times that the total number of individuals at the start of the breeding season dropped to one.

Results

Counts of males at leks

The number of observed leks increased across years from 79 in 2010 to 100 in 2019 but tended to plateau at 95–100 leks from 2014 onwards (Fig. 2a). The annual predicted number of males showed an overall decline during the 10-year period ($F_{1,8} = 7.92$, $p = 0.023$) at a rate of 2.9% (± 1.0 SE) per annum, particularly in the period 2015–2019 when year-on-year reductions occurred. There were regional differences in the extent of decline with numbers of males approximately halving between 2010 and 2019 in Deeside and Donside and Morayshire and Ross-shire, reducing to one male only in Perthshire and Trossachs, but showing an apparent increase, before falling again, in Badenoch and Strathspey (Table 2). In 2010, Badenoch and Strathspey hosted 68% of males attending leks, which had increased to 85% and 83% in 2016 and 2019 respectively.

The mean number of males observed per lek decreased from 2.7 in 2010 and 2011 to 1.8 in 2019 ($F_{1,8} = 12.04$, $p = 0.008$). Lek sizes changed between 2010 and 2019 (Chi-squared = 12.28, df = 3, $p = 0.006$), with leks attended by one male only almost doubling from 29% to 55%, smaller leks (2–4 males), reducing from 47% to 20% and larger leks (5–7 and > 7 males combined) averaging 8% across both years (Table 3).

Counts of females and broods

Breeding success (11-year forest mean chicks per female) varied non-significantly, from 0.52 to 0.98 between the five forests ($F_{4,30} = 2.55$, $p = 0.059$). Data from within forests in the same year were combined to give annual estimates of breeding success for Badenoch and Strathspey. Breeding success differed 25-fold between-years, being highest in 2010 (1.24 chicks per hen) and lowest in 2020 (0.05) ($F_{10,30} = 7.35$, p

Table 2. Numbers of capercaillie lek sites visited, those occupied (Occ) and the total (and percentage) of displaying males in each of five Scottish regions in the spring following the last two national surveys in 2009/2010 and 2015/2016, and in 2019. Regional breakdowns of the national survey estimates are provided from Ewing et al. (2012) and Wilkinson et al. (2018).

		2010		2009–2010	2016		2015–2016	2019	
Region	Leks	Occ	Males	%	Occ	Males	%	Occ	Males
Deeside and Donside	16	12	20 (9%)	10	10	12 (5%)	5	7	11 (6%)
Morayand Ross-shire	26	17	38 (18%)	10	16	20 (9%)	12	14	18 (10%)
Perthshire and Trossachs	6	6	10 (5%)	5	2	2 (1%)	0	1	1 (1%)
Badenoch and Strathspey	62	33	143 (68%)	75	46	194 (85%)	83	38	145 (83%)
Total	110	68	211	1285	74	228		60	175

Table 3. The number of males attending leks (lek sizes) at 68 leks in 2010 and 60 leks in 2019.

Year	1 male	2–4 males	5–7 males	> 7 males
2010 (n = 68)	20 (29%)	32 (47%)	10 (15%)	6 (9%)
2019 (n = 60)	33 (55%)	12 (20%)	11 (18%)	4 (7%)

< 0.001) (Table 4). An apparent decline in breeding success of 0.07 (0.03 SE) chicks per female per annum over the period neared significance ($F_{1,9} = 5.00$, $p = 0.055$) and was significant when 2021 was included (0.24 chicks per female) ($F_{1,10} = 6.39$, $p = 0.030$). The weighted mean proportion of male chicks in August at 0.41 (0.02 SE) differed significantly from parity and was identical to the 0.41 (CL: 0.36–0.46) described by Moss et al. (2000). The proportion of adults seen on brood counts that were males did not differ between years ($F_{9,17} = 1.09$, $p = 0.42$) and over the 11 years averaged 0.49 or a sex ratio of 1.04 females per male. Equivalent values were 1.20 females per male observed along winter transects by Ewing et al. (2012) and 1.20 females per male derived from distance sampling from winter transects by Wilkinson et al. (2018). The average of these three values 1.15 (0.05 SE) females per male was used in subsequent calculations.

Population estimation

Each year, the modelled population size was calculated from the number of males predicted from counts in the previous

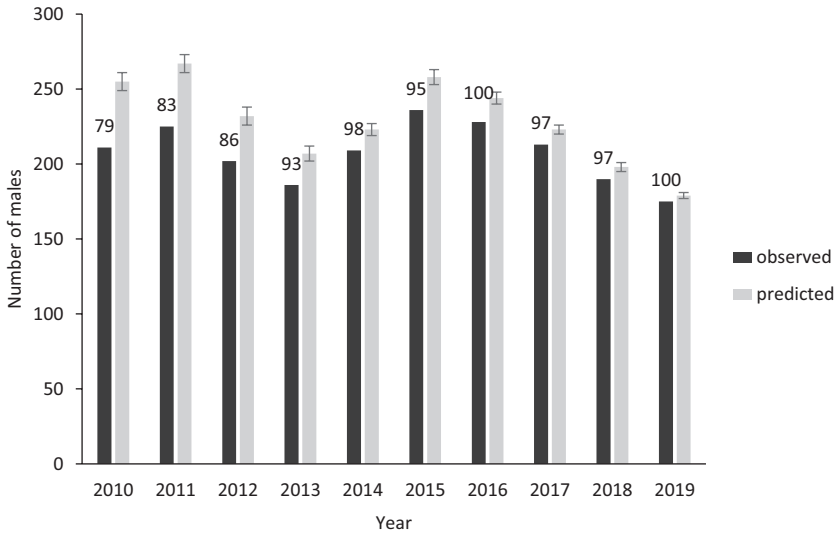

Figure 2. (a) Annual numbers of male capercaillie observed at leks (numbers of leks sampled given) and numbers of males predicted (± SE) from a Poisson regression model with lek and year as factors to allow interpolation of missing data values for unvisited leks amongst a total of 110 leks.

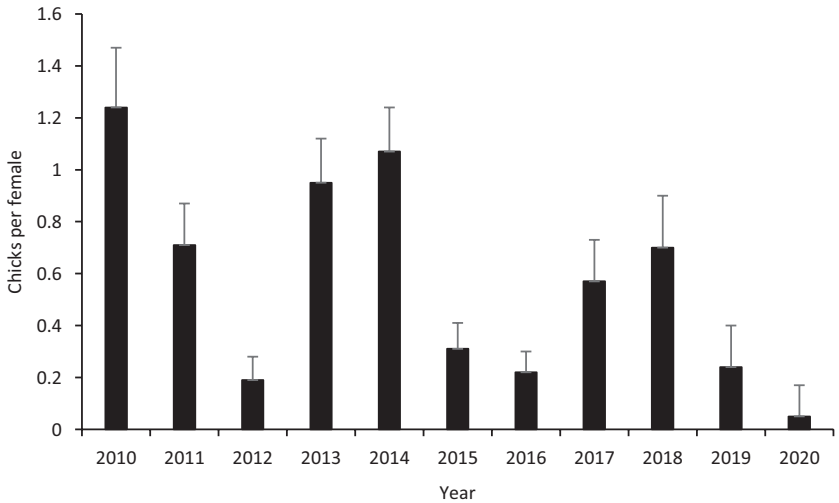

Figure 2. (b) Annual breeding success of capercaillie measured at up to five forests in Badenoch and Strathspey. Values are back-transformed means and standard errors.

years. In early years, lower mortality without fences resulted in a modelled population size higher than in the scenario with fences, so there was a bigger difference between early and late years (670 in 2011 versus 339 in 2020) for the no fence scenario than for the one with fences (580 versus 304), equating to annual decline rates of 4.8% (1.3 SE) ($t_8 = -3.60$, $p = 0.007$) without fences (Table 5a) and 4.6% (1.2 SE) ($t_8 = -3.77$, $p = 0.005$) when using mortality rates that included fence mortality (Table 5b). Comparison of the predicted number of males based on actual counts at leks versus the male population size modelled using survival rates that included fence mortality gave a correlation coefficient of 0.815 ($p = 0.007$). The slope of the first principal axis was 1.02 (95% CL: 0.51–2.06), not significantly different from a 1:1 relationship. With no fence mortality, the correlation coefficient was 0.804 ($p = 0.009$), and the slope of the principal axis was 0.80 (95% CL: 0.36–1.58).

Extinction probabilities

We evaluated extinction probabilities first using as starting point 133 adult and 15 yearling males obtained from the modelled output for 2020 (average of results with and without fences). Using the model parameters in Table 1, when survival included fence mortality, the probability of population extinction after 25 years was 23%, after 50 years 95% and after 100 years 100%. Without fence mortality, the extinction probabilities were 0, 3 and 40% respectively. We repeated the evaluation process with new initial conditions of 237 adult and 27 yearling males generated by projecting forward from the winter 2015/2016 national survey (average of projections with and without fences). From this higher starting point, the probabilities of population extinction after 25, 50 and 100 years were 10, 91 and 100% respectively, while without fence mortality they were 0, 0.1 and 25%.

Discussion

Modelled population size of capercaillie almost halved over the period 2011–2020 from 580 (95% CL: 462–698) birds in spring 2011 to 304 (95% CL: 239–369) in spring 2020 confirming perceived declines. This broadly agrees with a separate Bayesian modelling exercise by Niven (2021), who reconstructed the Strathspey capercaillie population from 2002 to 2020. Although the reconstruction indicated stability between the national surveys of 2009/2010 and 2015/2016, numbers then declined by 4.5% per annum from 2015 to 2020, followed by a predicted steeper decline of 10.5% per annum to 2030. Niven (2021) estimated a probability of extirpation of 32% for 2030, more severe than our own estimate of 23% extinction probability after 25 years with fence mortality.

Our population estimates from lek counts, augmented to adjust for an extra four months of mortality incurred between the national surveys and the lek counts, were only approximately half those from the two national surveys broadly occurring within the same period. Whilst the 2015/2016 national survey estimated 1114 birds (95% CL: 805–1505) (Wilkinson et al. 2018), our combined estimate for that winter (averaged across scenarios) was 522. Similarly, the previous national survey in 2009/2010 estimated 1285 birds (95% CL: 822–1882) (Ewing et al. 2012) compared to our adjusted estimate (averaged across scenarios) of 705 birds in January 2011. The apparent discrepancies between our lek-based population estimates and those from the transect-based national surveys are consistent with similar underestimates from lek-based surveys relative to capture–recapture models involving genetic sampling (Jacob et al. 2010, Mollet et al. 2015). Aleix-Mata et al. (2019) suggest that male-based lek surveys of capercaillie underestimate numbers by 50%, a similar value to that reported in this study and previously in Scotland by Watson and Moss (2008). This suggests that the

Table 4. Annual estimates of capercaillie breeding success (chicks per female in August predicted from a generalised linear model involving forest and year as categorical variables. Values are back-transformed means and standard errors). Also presented are the proportion of poults and adults that are male from observations during brood counts.

		Breeding success		Poult sex ratios		Adult sex ratios	
Year	Forests surveyed	Mean	SE	Proportion of male chicks	Number of sexed chicks	Proportion of adult males	Number of sexed adults
2010	5	1.24	0.23	0.67	3	0.47	76
2011	5	0.71	0.16	0.29	17	0.51	69
2012	5	0.19	0.09	0.60	5	0.56	99
2013	5	0.95	0.17	0.47	51	0.45	154
2014	5	1.07	0.17	0.42	48	0.37	123
2015	5	0.31	0.10	0.32	25	0.54	171
2016	5	0.22	0.08	0.27	15	0.52	167
2017	5	0.57	0.16	0.39	56	0.49	127
2018	2	0.70	0.20	0.52	21	0.48	67
2019	1	0.24	0.16	0.17	6	0.49	57
2020	2	0.05	0.12	–	0	0.52	33
Mean (SE)				0.41 (0.02)		0.49 (0.02)	

Table 5. Modelled capercaillie population size in Scotland in the following spring (May in year t+1) broken down into age and sex using predicted numbers of males attending leks in the previous spring, sex ratios of adults and ratios of chicks to females in August (year t) and estimated survival rates from Moss et al. (2000); models were run using survival rates that (a) included fence mortality and (b) assumed no fence mortality. Values in parentheses are SEs and 95% confidence limits obtained through randomisation.

Year	Males (leks May)	Females (May)	Chicks (Aug)	Adults (May t+1)	First years (May t+1)	Population size (May t+1)	Males (t+1)
(a) Using survival rates that include fence mortality							
2010	255 (6)	295 (15)	341 (66)				
2011	267 (6)	307 (15)	205 (49)	392 (35)	188 (45)	580 (60)	259 (25)
2012	232 (6)	267 (14)	55 (26)	407 (35)	113 (31)	520 (49)	235 (21)
2013	207 (5)	238 (12)	212 (40)	356 (31)	30 (15)	386 (36)	178 (16)
2014	223 (4)	256 (12)	254 (42)	316 (27)	117 (27)	433 (42)	195 (18)
2015	258 (5)	296 (14)	87 (30)	341 (29)	139 (30)	480 (45)	216 (19)
2016	244 (4)	280 (13)	62 (24)	395 (33)	48 (18)	443 (39)	204 (17)
2017	223 (3)	256 (11)	140 (42)	371 (32)	34 (14)	405 (37)	187 (16)
2018	198 (3)	227 (10)	151 (44)	341 (28)	77 (25)	418 (39)	190 (17)
2019	179 (2)	206 (9)	56 (39)	303 (24)	83 (27)	386 (38)	175 (16)
2020				273 (24)	31 (22)	304 (33)	139 (14)
(b) Using survival rates that assume no fence mortality							
2010	255 (6)	294 (15)	347 (68)				
2011	267 (6)	307 (15)	208 (48)	429 (18)	241 (56)	670 (62)	299 (25)
2012	232 (6)	268 (13)	55 (26)	447 (18)	145 (37)	592 (43)	268 (18)
2013	207 (5)	238 (12)	215 (42)	391 (15)	38 (19)	429 (25)	197 (10)
2014	223 (4)	257 (12)	261 (45)	347 (14)	148 (34)	495 (39)	223 (16)
2015	258 (5)	296 (14)	93 (32)	374 (13)	182 (38)	556 (43)	248 (17)
2016	244 (4)	280 (13)	62 (23)	432 (16)	65 (24)	497 (30)	227 (12)
2017	223 (3)	255 (12)	143 (44)	408 (15)	43 (17)	451 (24)	208 (9)
2018	198 (3)	228 (10)	157 (45)	373 (13)	99 (33)	472 (37)	214 (14)
2019	179 (2)	206 (10)	57 (42)	332 (12)	109 (33)	441 (36)	199 (15)
2020				300 (11)	39 (29)	339 (31)	155 (13)

quality of data from counts at leks, especially when comprised of one visit only, are affected by differences in detection probabilities between sites and survey visits (Abrahams 2019). This is likely to be attributable to a combination of both lek attendance by males and their position on the lek being age dependent, with not all males attending leks (Hjorth 1970).

This study assumed that by 2019 all leks had been discovered and were being surveyed annually. Whilst this assumption may not be true, the number of newly found leks had peaked by 2014 and the subsequent discrepancy between observed and predicted males was minimal. We also assumed that leks found mid-way through the study period had been there at the start of the study period, which may have inflated the population estimate at the start of the period and the subsequent severity of the decline. Colonisation–extinction dynamics also include the possibility that some lekking groups may have gone extinct before they were detected, especially during the earlier years of the decade, thereby reducing any back-calculated population estimate. These elements may account for the discrepancy between our population estimates based on counts of males at leks, which are then extrapolated to females and juveniles, and those from the transect-based national survey.

In the absence of more recent data, survival rates of both adults and juveniles used in these analyses were measured from 67 birds radio-tagged in 1989–1995 (Moss et al. 2000). Then, higher mortality rates were expected following collisions with deer fences, especially amongst juveniles (Baines and Summers 1997). Subsequent fence marking, which reduced collision rates of capercaillie by almost two-thirds (Baines and Andrew 2003), together with fence removal, are likely to have increased survival rates relative to the original study involving fence mortality. Nevertheless, those survival rates produced modelled outcomes that frequently straddled the predicted number of males, suggesting that they remain realistic for recent years. By modelling population size with and without fence mortality, we estimated a population size 16% higher in the absence of fences and one with an extinction probability massively reduced from 95% after 50 years with fences to only 3% without fences. This confirms that fence mortality is clearly unsustainable and fence removal must form a priority action, consistent with the recommendation by Moss (2001) that extinction could be avoided were forest fences removed.

Capercaillie productivity declined in Badenoch and Strathspey during the last decade and is now clearly lower than in the period 1991–2009 (Baines et al. 2016), as noted also by Niven (2021), who concurred with Baines et al. (2016) that pine marten *Martes martes* indices and weather were negative correlates of reproductive success. In four of the last six years (or six of the last eight years if including data from 2021 and 2022 (Baines unpubl.)), breeding success has been markedly lower than that of 0.6 chicks per female in August required to maintain the population stable in the absence of fence deaths (Moss et al. 2000). Thus, lowered breeding success in Badenoch and Strathspey is strongly associated with the national capercaillie decline. Despite this,

measuring this critical demographic stage has been abruptly reduced from five forests in 2017 to two in 2018 and one forest in 2019. Furthermore, all recent brood counts have been confined to Badenoch and Strathspey and have occurred in similarly structured old pine forests, with virtually no data obtained from other Scottish regions or forest types in the last decade. These restrictions may have reduced the robustness of productivity estimates, especially when extrapolating to an annual national estimate of productivity.

Both the six-yearly national transect-based surveys and the annual lek counts show close agreement regarding the heightened importance of Badenoch and Strathspey for Scottish capercaillie. The last national survey in 2015/2016 calculated that 83% of remaining birds occurred in this region (Wilkinson et al. 2018), whilst lek counts gave corresponding figures of 85% of males in the same year and 83% in 2019. Previous analyses had indicated a decline in numbers and lower breeding success in more peripheral regions including Donside and Deeside, Morayshire and Ross-shire, Perthshire and Trossachs (Ewing et al. 2012, Baines et al. 2016, Wilkinson et al. 2018), but that numbers were relative stable in Badenoch and Strathspey, where breeding success was also higher. However, annual numbers of males attending leks and breeding success have since both declined in Badenoch and Strathspey over the last five and 10 years respectively.

Improvements in lek-counting methods should include repeat counts at leks to allow estimation of male detection probabilities and counting attending females to inform on sex ratios and any advancement in the breeding season (Coppes et al. 2021). Current observer-based counts at leks could be augmented with bio-acoustic recording to overcome problems associated with the limited availability of experienced observers, associated observer biases and to minimise disturbance (Abrahams and Denny 2018, Abrahams 2019). Improved lek monitoring should be integrated with restored brood counts, not only in the main forests of Badenoch and Strathspey, but also in other Scottish regions. These would provide more robust estimates of annual productivity, and give adult and poult sex ratios, allowing predictive modelling of future population trends and providing insights into possible causal mechanisms underpinning this limiting demographic stage. Genetic material should also be collected as part of population monitoring (Rosner et al. 2014), especially given the likelihood that estimates based on lekking males will underestimate population size (Jacob et al. 2010). This integrated monitoring programme could enhance spatial analyses of capercaillie population responses to conservation managements implemented at forest, regional and national levels.

The trends described here confirm the high importance of Badenoch and Strathspey for capercaillie conservation in Scotland. It is evident that further priority management actions, over and above those already conducted, will be required. A review of capercaillie conservation management was recently conducted by NatureScot (2022). It concluded that steps to reduce predation risk, human disturbance and collisions with fences were urgently required to reduce the increasing likelihood of a second extinction.

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David Baines: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **N. J. Aebischer**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fj6q573zt (Baines and Aebischer 2023).

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