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Expanding the range of black grouse *Lyrurus tetrix* in northern England - can wild females be successfully translocated?

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The range of black grouse *Lyrurus tetrix* in northern England was expanded by translocating males beyond the species' currently occupied distribution between 2006 and 2014. Translocation of wild males resulted in the establishment of new leks, attraction of females and successful breeding. To determine whether females could also be translocated to supplement the few present, 24 were moved and released in 2013 and 2014. Following release, 20 females survived to nest in their first spring on average 1.7 km from the release point. Annual survival by females over the first two years following release averaged 0.81 (0.63–0.90, 95% CL), comparable to that of resident birds in the core northern England range. Females exhibited fidelity to their breeding areas, with distance between nest locations in consecutive years averaging 0.2 km. Of the 35 nests monitored, 71% hatched chicks. Brood survival averaged 28% and the proportion of females with broods was 20%. Clutch size, egg volume, nest and brood survival were all comparable with estimates from birds from studies in northern England. Chicks reared per female averaged 0.3 (±0.1 SE), lower than resident birds from four sites in northern England. Post-translocation lek attendance varied between nine and 12 males. When attempting to expand black grouse range into formerly occupied areas, our study demonstrated that wild females translocated into areas where males had previously been released, settled, survived well and exhibited a propensity to breed.

In the UK, black grouse *Lyrurus tetrix* have declined in numbers and range over the past century (Sim et al. 2008, Balmer et al. 2014) and are red-listed as a species of high conservation concern (Eaton et al. 2015). In England, black grouse were once widespread (Gladstone 1924), but are now restricted to the North Pennines, where in 1998, 773 males remained (Warren and Baines 2008). Here, to restore numbers, land managers have been encouraged to conduct a suite of conservation measures, including reductions in grazing by sheep *Ovis aries* to improve moorland breeding habitats (Calladine et al. 2002), establishing patches of scrub woodland to provide food and cover in severe winters (Warren et al. 2013) and refraining from shooting until numbers recover (Warren et al. 2011). Since 1998, numbers increased to 1029 males in 2006 and to 1437 males in 2014 (Warren et al. 2015), but with no signs of range expansion.

Formerly occupied habitats extend to the south of their existing range into the Yorkshire Dales National Park and Nidderdale Area of Outstanding Natural Beauty (AONB). Here connected habitat mosaics were present within the dispersal range of black grouse, but no lekking males were present (Warren et al. 2017). Natural range expansion was considered to be limited by juvenile males which moved only short distances (up to 1 km) in comparison to females which dispersed up to 19 km (mean 9.3 km) (Warren and Baines 2002). We initiated recolonization of parts of this former range by translocating 62 wild males into three sites between 2006 and 2014 to establish new leks and attract wild dispersing females to settle and breed. Released males established leks, with females subsequently seen with released males in the first spring following release at two of the sites, but at the third release area in Nidderdale (Fig. 1), no females were observed (Warren et al. 2017). Here, we considered whether a similar translocation of wild females into Nidderdale to complement previous translocations of males could lead to successful breeding and population growth. We measured 1) settlement patterns, 2) survival rates, 3) breeding parameters, and 4) annual numbers of males attending leks. We compared these metrics with published estimates from elsewhere in the UK and from the donor population in northern England.

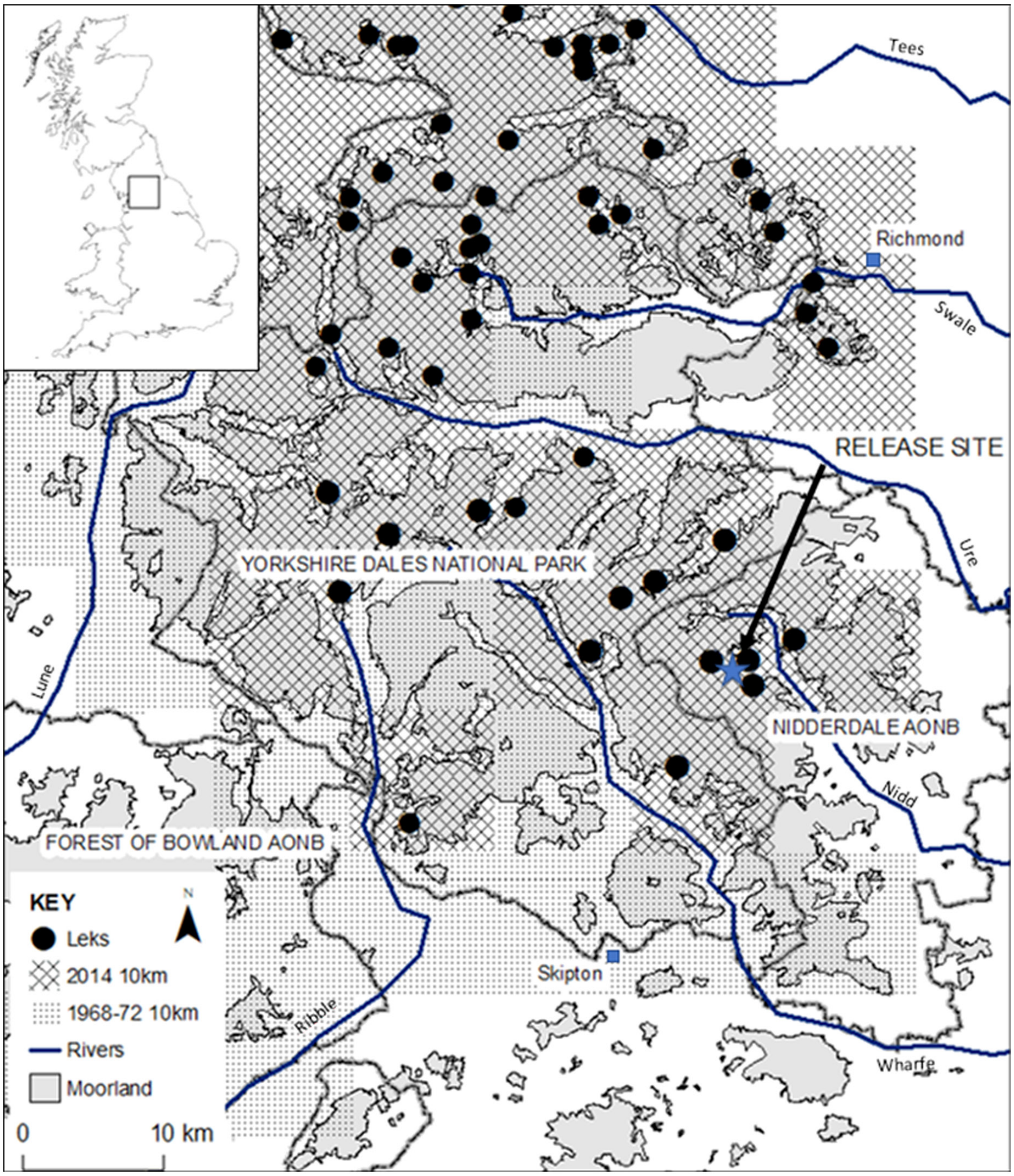

Figure 1. Location of the release site in Upper Nidderdale in relation to black grouseleks and occupied 10 km grid squares in spring 2014 and formerly occupied areasin 1968–1972.

Methods

Study area

The study was undertaken in Upper Nidderdale in North Yorkshire. The Nidderdale valley is drained by the River Nidd, with the upper slopes dominated (39%) by unenclosed heather and cotton grass *Eriophorum vaginatum* moorland managed for red grouse *Lagopus lagopus scotica* shooting (Hudson and Newborn 1995). Grass moorland dominated the lower moorland slopes (25%) which adjoined large unimproved rough grazing fields, typically enclosed by drystone walls (20%). These were characterised by a mix of grasses (mat grass *Nardus stricta*, wavy hair-grass *Deschampsis flexusosa*, sheep's fescue *Festuca ovina*, Yorkshire fog *Holcus lanatus*, common bent *Agrostis capillaris*), sedges *Carex* spp. and rushes (heath rush *Juncus squarrosus*, soft rush *Juncus effusus*, sharp-flowered rush *Juncus acutiflorus* and jointed rush *Juncus articulatus*), grazed by hill sheep with some beef cattle *Bos taurus*. In the valley bottom, more intensively farmed improved pastures and meadows dominated (15%). Native woodland cover was sparse (>1%) and restricted to stream sides along the valley slopes and floor.

To stimulate range expansion, 10 males were released in autumn/winter of 2011/2012 and 2012/2013 (Table 1) into formerly occupied habitat (Warren et al. 2017) where gamekeepers controlled corvid species, red fox *Vulpes vulpes*, stoat *Mustela erminea* and weasel *Mustela nivalis* (Hudson and Newborn 1995). Following these releases, three single males were observed lekking in both spring 2012 and 2013, but no females were observed (Warren et al. 2017). A further eight males were released in autumn/winter 2013/2014 and nine in 2014/2015 (Warren et al. 2017). In spring 2014, nine males were observed lekking at four lek sites in Upper Nidderdale (Fig. 1).

Table 1. Numbers of translocated males and females released each year into the Nidderdale AONB in northern England, the subsequent numbers of males observed displaying at leks in spring (2011–2017) and annual breeding success of released females in comparison to values from resident birds in northern England (values are means ± SE). Breeding success measures were broods per female (the proportion of females that were accompanied by a brood), brood size (chicks counted in relation to broods observed) and chicks per female (chicks counted in relation to females observed).

				Females with broods		Brood size		Chicks per female	
Year	Males released	Females	Males on leks	Moved	Resident	Moved	Resident	Moved	Resident
2011	8	0	0	NA	NA	NA	NA	NA	NA
2012	2	0	3	NA	NA	NA	NA	NA	NA
2013	8	4	3	NA	NA	NA	NA	NA	NA
2014	9	20	9	0	0.75 (0.06)	NA	3.6 (0.3)	0	2.7 (0.3)
2015	0	0	12	0.17 (0.09)	0.23 (0.05)	2.0 (1.0)	2.5 (0.7)	0.3 (0.2)	0.6 (0.2)
2016	0	0	9	0.27 (0.14)	0.49 (0.07)	1.7 (0.3)	2.5 (0.3)	0.5 (0.2)	1.2 (0.2)
2017	0	0	11	0.25 (0.25)	0.18 (0.06)	1.0 (1.0)	1.9 (0.3)	0.3 (0.3)	0.3 (0.1)

Capture and release

In autumn/winter 2013, four females (one adult, three juveniles) were released with a further 20 females (five adults, 15 juveniles) in 2014. Criteria for donor moors from which females could be removed were 1) the presence of a spring lek with $\geq$ 10 displaying males, and 2) a stable or increasing trend over the past 10 years in numbers of males. Up to two females were taken from each of 13 such sites. These 'donor' sites were on average 67 km (range 52–81 km) from the release site. Females were caught at night-time roosts in late autumn and winter using a high-powered lamp and a hand-held net. They were released within three hours of capture, into areas of tall cover at the release site. All females were released at the same single location in Nidderdale where males had been released. Birds were fitted with 12-g necklace VHF radio-transmitters (maximum lifespan 30 months) with mortality sensors (Holohil Ltd).

Settlement and survival

Female black grouse were located at least fortnightly by triangulation until death or radio failure (determined by intermittent or weak signals at end of expected tag lifespan). Causes of death were assigned to either predation by mammal (red fox or stoat) following criteria described in Thirgood et al. (1998), shot or unknown. An estimate of the bird's condition was made when dead from a subjective score (1–5) of the quantity of pectoral muscle. A condition score of 1 was ascribed to a bird in a very emaciated condition, with very little pectoral muscle and where the sternum was very obvious (Newborn and Foster 2002).

To assess settling patterns following release and subsequent female fidelity to nesting areas, we measured the straight-line distance from the release point to each female's nest location ($n = 20$), the distance between nests in subsequent years ($n = 13$) and the distance from nests to the nearest lek ($n = 35$). These measures excluded any replacement clutches.

Assessment of reproduction

During the breeding season females were tracked weekly between 1 May and 10 August to locate nests and follow broods. Egg dimensions (length (L) and breadth (B)) were measured using callipers, only if the female was not present at the nest. Egg volume (V) was calculated using the equation ($V = 0.51 \times L \times B^2$) following Hoyt (1979). Successful nests were those where at least one egg hatched. Failed nests were either predated or deserted. Nest predators were identified by field signs (Green et al. 1987) with nests considered deserted if all eggs remained present but were no longer incubated. Hatch date was estimated by taking the mid-point between the date when last observed incubating and that when discovered hatched.

To assess the availability of chick prey within brood habitats, sawfly larvae (Tenthredinidae, Symphyta), the main chick prey item (Baines et al. 2017), were sampled with sweep nets within brood ranges at the release site. Sampling consisted of 10 rounds of 25 sweeps taken from the mid-point between the broods actual and previous location. Sampling was undertaken from late June to early July, coinciding with peak chick intake of invertebrates (Starling-Westerberg 2001, Baines et al. 2017). Similar samples of typical brood habitat were taken at one of the 'donor' moors in northern England in the same years. In August, approximately eight weeks after hatching, all females that hatched chicks were flushed and their vicinity searched using English pointing dogs to find and count chicks. Breeding productivity was compared with that from four North Pennine moors counted in the same years where defined areas of moorland were searched using pointing dogs to locate females and their broods in late July and August.

To monitor male juvenile recruitment into lekking groups we counted males attending leks in Nidderdale annually prior to and following translocation (2011–2017). Surveys were undertaken between dawn and 07:00 once in April and then again in May. Surveyors visited all past lek sites and searched all habitats where all known radio-tagged males were located. The open landscape of the study area and good road network meant that most leks and single displaying birds could be detected from vantage points such as roads and tracks using telescopes. Total numbers of males were calculated as the sum across leks of the maximum of the two counts from each lek.

Statistical analyses

Statistical analyses were carried out in Genstat 17 (<www.vsni.co.uk>). Dispersal from release to breeding site was analysed by considering distance from release point to first-nest (log-transformed to normalise) in relation to age at release (juvenile or adult) using ANOVA. To identify factors influencing fidelity to breeding areas at the release site, we considered two dependent variables, 1) distance between nests (log transformed), and 2) distances from nests to leks (log transformed), using two separate general linear mixed models (GLMM). We included age, juveniles were considered to become adults in the September of the year following capture (Baines and Richardson 2007) and nest success the previous year (1 = success, 0 = failure) as fixed effects, and individual as a random effect. We used a random-effect model as from the 20 females providing breeding data, seven provided data for one year, eight for two and five for three years. Thus, 65% of females had repeat data and 47% (18 out of 38) of bird years were not independent of female.

Survival of females was estimated by calculating the duration from release to either death (mid-point between last location alive and body recovered), loss of radio signal or date last alive (for those birds still alive). Birds in the latter two categories were considered to be censored in a Kaplan–Meier survival analysis (Kalbfleisch and Prentice 1980). Post-release survival during the first year (365 days) was calculated for juveniles and adults separately, and for adults only in their second year, with any difference tested using Wilcoxon (Breslow) tests.

Differences in clutch size, egg volume and hatch date between age and year were tested using separate GLMMs, with individual included as a random effect. Analyses of clutch size, egg volume, nest survival and hatch date were restricted to first clutches only. Differences in nest survival between age and year were analysed using a mixed logistic regression (MLR, binomial error distribution and logit link). The number of exposure days for each nest (Mayfield 1975) were calculated using the equation $s = t + y - 1$, where t = number of nest exposure days, and y = success (1) or failure (0) (Aebischer 1999). Exposure days were entered as the dependent variable in the MLR, with the total number of nest exposure days as the number of binomial trials. Year and age were fixed effects and individual a random effect.

Differences in brood survival (1 = chicks present at eight weeks, 0 = brood lost) and the proportion of females with broods in August (coded 1 or 0) (including replacements) were considered in relation to age and year using separate MLRs with individual as random effect. Differences in the number of chicks reared per female in relation to year and age (fixed effects) were examined using mixed Poisson regression (logarithmic link), with individual as a random effect. Differences in the mean annual abundances of sawfly larvae between the release area and a site in northern England were compared using a Mann–Whitney U test.

To consider differences in breeding productivity estimates between moved and resident birds, we compared estimates of breeding success, 1) overall breeding success expressed by chicks per female and 2) brood size (chicks counted in relation to broods observed) using Poisson regression. Chicks counted in August was the response variable, with either the natural logarithm of the number of females (breeding success) or numbers of broods (brood size) specified as offsets, with moved or resident (coded 1 or 0) and year and the two-way interaction included as explanatory factors. Broods per female (the proportion of females that were accompanied by a brood) was modelled using logistic regression, categorising females as successful if they had one or more chicks and unsuccessful if they had no chicks.

Results

Settlement and survival

Twenty females survived and nested in their first spring on average 1.7 km (± 0.3 SE, range 0.6–6.9 km, n = 20) from the release site, and distances were similar between age ($F_{1,18} = 0.41$, $p = 0.531$) (Table 2). Distances between subsequent nests were similar between age ($\chi^2_1 = 1.12$, $p = 0.404$) or outcome the previous year ($\chi^2_1 = 1.76$, $p = 0.285$) and were an average of 0.2 km (± 0.1 SE, range 0.0–1.2 km, n = 15) from the nest in the previous year. The distance between nests and the nearest lek were similar between age ($\chi^2_1 = 0.38$, $p = 0.544$) and were an average of 0.5 km (± 0.1 SE, range 0.0–3.5 km, n = 35) from leks.

No birds were found dead within two weeks of translocation, suggesting no immediate impact on survival. Two females went missing within 10 and 55 days post release respectively and were not relocated despite a widespread search. The female which disappeared within 10 days after release was excluded from further analyses. Fifteen females were followed for an average 735 days ± 61 SE (range 367–1040 days) until radios failed. Seven birds died: one

Table 2. Breeding parameters from released black grouse females in Upper Nidderdale (2014–2017). Values are means (± SE) and range.

	Juveniles			Adults		
	n	Mean (± SE)	Range	n	Mean (± SE)	Range
Distance (km) from release site to first nest	14	1.8 (0.3)	(0.8–3.8)	6	1.4 (0.7)	(0.6–6.9)
Distance (km) from nests to nearest lek	14	0.5 (0.2)	(0.0–3.5)	21	0.6 (0.1)	(0.2–1.6)
Distance (km) to subsequent nest	9	0.2 (0.1)	0.0–1.2	6	0.2 (0.2)	(0.0–0.9)
Clutch size (eggs)	14	7.3 (0.5)	(5–10)	21	8.5 (0.4)	(5–11)
Egg volume (ml)	12	33.6 (0.6)	(30.2–36.2)	10	35.7(0.9)	(30.4–41.4)
Mayfield estimate	14	0.59 (0.0012)		21	0.71 (0.0006)	
Hatch date	8	16 June (3.0)	(6 June – 3 July)	17	15 June (1.0)	(6 June – 18 June)
Brood survival	8	0.25 (0.16)	(0.00–1.00)	17	0.29 (0.11)	(0.00–1.00)
Females with broods	13	0.15 (0.10)	(0–1)	22	0.23 (0.09)	(0–1)
Brood size	2	2.5 (1.5)	(1–4)	5	1.4 (0.2)	(1–2)
Chicks per females in August	13	0.4 (0.3)	(0–-4)	22	0.3 (0.1)	(0–2)

was predated by a red fox, one by a stoat, one was shot and two died during incubation. The cause of death of two birds could not be determined. Mean annual survival of 23 females over the first two years following release was 0.81 (0.63–0.90, 95% CL, n = 23).

Assessment of reproduction

Seven females were monitored for one breeding year, eight for two, and five for three consecutive years. From a possible 38 first clutches, 35 were located, together with three replacement clutches following failure of the first clutch. All three replacement clutches failed to hatch. First clutch size was similar in relation to age ($\chi^2_1 = 3.87$, $p = 0.060$) or year ($\chi^2_3 = 4.82$, $p = 0.226$) and averaged 8 eggs (± 0.3 SE) (juveniles = 7.3 eggs ± 0.6 SE, adults = 8.5 ± 0.4 SE) (Table 2). Egg volume did not differ between age ($\chi^2_1 = 1.47$, $p = 0.241$) or year ($\chi^2_3 = 0.32$, $p = 0.855$) and averaged 34.5 ml (0.5 SE). Hatch date did not differ in relation to age ($\chi^2_1 = 1.53$, $p = 0.231$) or year ($\chi^2_3 = 0.89$, $p = 0.466$) and was on average 16 June (± 1.3 SE). Nest survival averaged 0.66 and was similar between ages ($\chi^2_1 = 0.77$, $p = 0.386$) and years ($\chi^2_3 = 4.79$, $p = 0.211$). Ten of 35 clutches failed; five were predated (two by corvids, two by stoat and one by a badger *Meles meles*), three were deserted (two of which were infertile) and two failed following the females dying during incubation (both in the first year following release). Of the successfully hatched clutches an average of 7.2 eggs (± 0.4 SE) hatched, representing 91% egg hatchability, with 2% of eggs infertile.

Brood survival was similar in relation to age ($\chi^2_1 = 0.27$, $p = 0.610$) and year ($\chi^2_3 = 0.20$, $p = 0.892$), with seven females rearing broods (28%) from 25 hatched nests. Females lost their broods by a median 16 days after hatching (range 3–34 days). When surveyed in August, the proportion of females with broods was similar in relation to age ($\chi^2_1 = 0.01$, $p = 0.906$) and year ($\chi^2_3 = 0.41$, $p = 0.938$). Across all years, seven of 35 females (20%) had broods at six weeks of age. Breeding success (chicks per female) was similar in relation to age ($\chi^2_1 = 0.58$, $p = 0.454$) and year ($\chi^2_3 = 1.83$, $p = 0.616$) and averaged 0.34 (±0.1 SE) chicks per female.

Annual estimates of sawfly abundance did not differ between the release area (0.8 larvae ± 0.4 SE) and a site in northern England (1.3 larvae ± 0.8 SE) (U= 2.5, $p = 0.506$).

Overall breeding success differed between moved and resident birds ($F_{1,14} = 13.54$, $p < 0.001$) and between years ($F_{3,14} = 44.56$, $p < 0.001$) (Table 1). There was no significant moved × year interaction ($F_{3,11} = 1.76$, $p = 0.152$). Moved females reared on average 0.3 chicks per female compared to 1.2 by resident birds on donor moors (Table 1). Mean brood size differed between years ($F_{3,12} = 4.00$, $p = 0.007$) but not between moved and resident birds ($F_{1,12} = 1.45$, $p = 0.228$). There was no significant moved × year interaction ($F_{2,10} = 0.09$, $p = 0.916$). The proportion of females with broods differed between years ($\chi^2_3 = 40.33$, $p < 0.001$) but not between moved and resident birds ($\chi^2_1 = 3.00$, $p = 0.083$). There was no significant moved × year interaction ($\chi^2_3 = 1.41$, $p = 0.702$). Numbers of males attending leks following the cessation of releases in 2014 remained roughly stable, with 12 males observed in 2015, nine in 2016 and 11 in 2017 (Table 1).

Discussion

Following releases, females settled to nest on average 1.7 km from the release point and only 0.5 km from the nearest lek. The latter being comparable with resident birds elsewhere in northern England which nested an average 0.6 km (0.1–2.5 km) from leks (Warren et al. 2012). This lack of dispersal was surprising as three-quarters of released birds being juveniles, which typically disperse 8–9 km (Warren and Baines 2002, Caizergues and Ellison 2002). The compact settlement pattern exhibited by females contrasted with that of translocated males in the same area, which moved on average 3.6 km from the release point to establish leks (Warren et al. 2017). However, females were released into areas where males were already present, and if they had been released into areas with no males present, they may have moved further. In this scenario, we found females settled well where males were already present.

Survival of translocated females (0.81) and males (0.77) were similar (Warren et al. 2017) as well as to those from the core northern England range (0.70) and the Scottish Highlands (0.66) (Baines et al. 2007). Adult survival in the UK tended to be higher than estimates from mainland Europe and Scandinavia – Finland (0.53), Sweden (0.54) and the French Alps (0.56–0.84) (Lindén 1981, Angelstam 1984, Caizergues and Ellison 1997). We speculate that such elevated estimates (in our study) and others from the UK (Baines et al. 2007, Warren et al. 2017) may have resulted given the proximity of our work to managed red grouse moors, where gamekeepers reduced potential predators of red grouse to ensure a surplus for shooting.

Breeding success (chicks per female) was poor and lower than that of resident females compared to 'donor' moors in northern England. Breeding productivity of moved females was hampered by the study coinciding with two poor breeding years (2015 and 2017). Based on 29 years of annual monitoring in northern England, these years were ranked the sixth and third poorest on record, with 2016 also below average. Two of these years, 2016 and 2017, coincided with above average rainfall in June when chicks hatched, and 2015 was colder than average (<www.metoffice.co.uk>). The first year of the study should, however, have been an excellent breeding year, with average sawfly abundance (1.4 larvae per sample) compared to a median of 1.5 (range 0.5–2.7) recorded in northern England (Baines et al. 2017), but with a sample size of two females we were limited in our ability to assess breeding success. We cannot discount the possibility that habitat in these areas may have been suboptimal and negatively affected reproductive performance, but we have no means to assess this. Other factors, including potential impacts of radio-tagging and the associated monitoring disturbance need also to be considered. Tagging females may reduce nest success by increasing predation risk or desertion (Götmark 1992), with radio-tagged females breeding less well than unmarked birds (Caizergues and Ellison 1998), however other studies on red grouse found no impacts (Thirgood et al. 1995). Females deserting clutches in this study may have done so because of disturbance when we were locating nests. Two birds died during incubation, which were both found in an emaciated condition which may have been due to insufficient food availability, although parasitic infection or disease would seem more likely candidates as survival rates of other released birds were high. However, results from post-mortem examinations from one bird were inconclusive. Our reduced breeding success estimates could have been a result of methodological differences in counting broods. Using radio telemetry we were able to locate all marked breeding females, whilst counts using pointing dogs may over-estimate reproductive success of un-marked females. Because dogs can miss birds and may be more likely to find broods rather than single females (Sisson et al. 2000). In addition, radio-tagged females in northern England have been observed moving away from breeding habitats if their breeding attempt has failed (Warren and Baines unpubl.). Such movements could bias breeding estimates from counts using pointing dogs in such habitats.

Although breeding productivity was low, other breeding parameters were comparable with resident birds from two earlier black grouse radio-telemetry studies in northern England between 1999 and 2000 (Baines and Richardson 2007, Baines et al. 2007). Females nested and laid average clutches (juv = 7.3 eggs, adult = 8.5 eggs) similar to the North Pennines (juv = 7.3 eggs; adult = 9.1 eggs) (Baines and Richardson 2007). Egg volume was similar between moved (34.5 ml) and resident birds (35.0 ml ±0.2 SE, n = 116). Nest survival (0.66) was comparable with resident birds (0.47) as were hatch dates (16 June) to resident birds (15 June, range 9–18 June) (Baines and Richardson 2007). Brood survival (0.28) although low, was again similar to that observed in the core of the range, which averaged 0.37 between 1999 and 2004 (Baines et al. 2007). Brood survival is affected by many factors, including the availability of sawfly larvae, the main chick prey, the weather at hatching and predation (Baines et al. 2017).

Our study demonstrated that translocated wild females settled, survived well and exhibited a propensity to breed. They produced fertile clutches, but productivity was poor. Our results from this work and the earlier male translocation trial (Warren et al. 2017) have demonstrated that when attempting to expand black grouse range into formerly occupied areas, males can be moved, which have settled and established leks. If wild females have not already settled with the males, then females can also be moved to augment the release.

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