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Survival of chicks and adults explains variation in population growth in a recovering red grouse *Lagopus lagopus scotica* population

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Understanding demographic mechanisms is key to managing animal populations, both in conservation and game management. We examine which life-stages contributed most to population growth in a recovering red grouse *Lagopus lagopus scotica* population following restoration of management aimed at resuming economically viable harvesting. Demographic parameters derived from biannual grouse counts and from radio-tagged individuals were analysed using 'standard demographic accounting'. When parameter estimates were based on counts, a combination of adult summer and winter survival appeared to contribute most to population change. When based on radio-tagged birds, deemed more reliable because of independence between parameters and years, adult summer survival and chick survival contributed most to population change. The contributions of clutch size, nesting success (i.e. the proportion of nests with ≥1 egg hatching) and hatching success (proportion of eggs hatching in successful nests) were negligible. Overall, the survival rate of adults and chicks contributed most to annual population change and reduced the rate of population recovery. Analysis of grouse carcasses found that 82% were associated with signs of predation or scavenging by raptors. Rates of juvenile production exceeded those of adult mortality, allowing modest population growth, but insufficient to resume economically viable harvesting.

Animal populations are managed most efficiently when the underlying contributions of different demographic rates to population growth (λ) are understood (Sibly and Hone 2002, Coulson et al. 2005). Identification of variables limiting λ is key to population recovery, and thus central to both conservation and game management (Caswell et al. 1999, Bro et al. 2000, Sim et al. 2010). There are two complementary approaches to demographic analysis: 'retrospective' analysis identifies demographic rates contributing to observed population changes and expresses the variation in λ as a function of the variation in demographic rates, whilst 'prospective' analysis identifies the demographic rates to which λ is most sensitive (Caswell 2000).

The red grouse *Lagopus lagopus scotica* is a gamebird of economic importance on heather *Calluna vulgaris* moorland in parts of the British uplands (McGilvray 1996, Sotherton et al. 2009). Landowners employ gamekeepers to maximise grouse numbers for sport shooting by managing generalist predators, grouse parasites and heather vegetation (Hudson and Newborn 1995). Declines in numbers of grouse shot in Scotland have been frequently associated with a loss of heather-dominated moorland (Thompson et al. 1995, Robertson et al. 2001), reductions in predator control, and heather burning (Robertson et al. 2017) and, in some cases, increases in protected predators of grouse such as raptors (Thirgood et al. 2000a).

Here, we examined which grouse life stages best explained population change following restoration of management at Langholm Moor in southwest Scotland, managed for grouse (Sotherton et al. 2009) until 1999, with grouse last shot in 1996 (Thirgood et al. 2000a). Declines in numbers of grouse shot at Langholm, from a 10-year average of 2482 ± 343 birds in the 1950s to 1207 ± 272 birds during the 1980s, were associated with the loss of nearly half of the heather-dominated moorland (Thirgood et al. 2000b). However, on remaining areas of dominant heather, predation by increased numbers of hen harriers *Circus cyaneus* and peregrines *Falco peregrinus* between 1991 and 1996 reduced pre-shooting grouse densities by 50% within a single breeding season and rendered shooting economically unviable (Redpath and

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Thirgood 1999, Thirgood et al. 2000b). Between 2000 and 2007, in the absence of active grouse moor management, harrier numbers declined and grouse numbers remained low (Baines and Richardson 2013, Ludwig et al. 2017). In 2008, management recommenced with the aim of increasing grouse numbers sufficiently to resume economically viable driven shooting. In this project, this was defined as shooting 2000 grouse in at least one year within the 10-year project. Apart from the shooting target, the project also aimed at maintaining the hen harrier population and extending and improving the heather habitat.

We quantified demographic rates of grouse from two different monitoring approaches, the first based on biannual counts, the second on intensive monitoring of radio-tagged females. In both cases, we used retrospective analysis to identify the contribution of each demographic rate to annual population change between 2008 and 2016, compared results between approaches, and interpreted them in the light of additional information on life-stage-specific causes of mortality.

Methods

Study area

Our study at Langholm Moor (55°21′9″N, 2°88′5″W) between 2008 and 2016 formed part of a larger project, whose aim was to reduce conflict between raptor conservation and driven grouse shooting (Ludwig et al. 2017). The 42-km^2 study area, dominated by heather moorland, was surrounded by a 73-km^2 'buffer zone' of chiefly acid grassland (i.e. grassland communities on nutrient-poor, acidic soils), with a mix of agriculturally-improved enclosed grassland fields, commercial coniferous forestry and mixed deciduous woodland in the wider area (Land Cover Map 2007, see Morton et al. 2011). Much of this wider buffer area had lost formerly dominant heather cover since 1948 (Thirgood et al. 2000b). Thus, Langholm is an isolated heather moor some 30 km from the nearest other grouse moor and not part of a wider contiguous area managed for grouse. Given that young female grouse disperse on average < 1 km (Warren and Baines 2007) and only 1% of 202 grouse radio-tagged on the study area were subsequently located outside the project boundary, grouse movements to and from Langholm and the nearest grouse moors were probably minimal. Thus, we regarded Langholm's grouse population as effectively closed from a population dynamics perspective, with changes in numbers from consecutive counts over the moor as a whole representing estimates of 'true' survival.

In 2008, five gamekeepers began managing the moor for grouse, continuing until spring 2016. They controlled generalist predators such as red fox *Vulpes vulpes* and carrion crow *Corvus corone* over 115 km^2 (i.e. study area and buffer zone). Furthermore, they managed the heather by rotational burning and cutting with a tractor-drawn flail mower within parts of the heather-dominated core frequented by grouse, where they also used an anthelminthic drug to help control an intestinal parasite *Trichostrongylus tenuis* of grouse to increase grouse survival and breeding success (Hudson et al. 1998, Newborn and Foster 2002). Raptors were fully protected in accordance with the law, but to reduce the impact of hen harrier predation on grouse chicks, diversionary food was provided on a daily basis to all harrier broods for up to 60 days after hatching between 2008 and 2015 (Redpath et al. 2001, Ludwig et al. in press). In addition, sheep *Ovis aries* grazing ceased completely from 2011 onwards on 39 km^2 of degraded moorland, predominantly within the study area, to help restore the extent of heather habitat for grouse.

Red grouse counts

Pre- and post-breeding grouse were counted with pointer dogs along line transects in spring (March/early April) and summer (July/early August) respectively (Warren and Baines 2011). Grouse were counted in ten 0.5-km^2 blocks of representative moorland habitat, two in the areas managed by each of the five gamekeepers (Ludwig et al. 2017), and along 18 line transects (mean transect length = 2.0 ± 0.2 km) positioned at 500-m intervals that avoided duplication with the blocks, giving a total transect length of 68.4 km (blocks and transects combined). The perpendicular distance from the transect to the grouse's position was recorded to estimate the 'effective strip width' (ESW), using the program DISTANCE 6.0 (Thomas et al. 2010). We used the conventional distance sampling analysis engine with a half-normal key function and cosine adjustment, and selected models giving the best fit on minimum Akaike's information criterion scores and χ^2 goodness-of-fit tests (Warren and Baines 2011). Mean pre- and post-breeding densities (birds km^{-2}) were then calculated using:

$$Grouse\ density = \frac{Total\ grouse\ counted}{Transect\ length \times (ESW \times 2)}$$

Radio-tagged grouse

From 2008–2015, 202 grouse were dazzled at night in autumn and winter using a lamp and caught in a hand-held net. The birds were sexed by size and wattle intensity and aged by plumage as either immature (1st year after hatching) or adult (Cramp and Simmons 1980), then fitted with necklace-mounted radio-transmitters (Holohil RI-2DM, <2% of body weight) equipped with motion-sensitive mortality sensors. Tagged birds were checked monthly in 2008–2011 and weekly in 2012–2016, with date of death estimated as half-way between when found dead and last seen alive.

We monitored 86 radio-tagged females during the 2009–2016 breeding seasons (61 females in one season, 21 females in two and four females in three consecutive seasons). We monitored nests of tagged females from the onset of incubation (119 first clutches and 14 replacement clutches), with the females flushed only once to record clutch size. The nest-site was visited again only to confirm either the number of eggs hatched (= initial brood size), or that the attempt had failed. Broods hatched by tagged females were located when approximately 50 days old, when chicks were almost full-grown but still distinguishable from adults, and

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all chicks counted using a pointing dog. This time coincided with the start of post-breeding counts, enabling comparisons of breeding success between methods and with other studies.

In 2013–2015, 73 chicks from 35 broods (30 from tagged females) of average age 9 ± 5 SD days (range 1–23) had radio-transmitters glued onto their backs (Holohil LB2X: 0.31g, BD-2N: 0.43 g, life-span three weeks). Chicks were tracked to 20–50 m, two or three times per week, without flushing the brood. If the chick's signal was close to the female's signal, the chick was assumed alive; if it was further away, the chick was located, and the tag/carcass retrieved (i.e. confirmed dead or shed tag). If missing before the expected end of tag-life, the chick was presumed dead as no chicks were located alive away from the female. Chicks from untagged females were approached carefully until either the female was seen nearby (in which case the chick was assumed alive) or the tag/carcass retrieved.

Between 2010 and 2016, 348 chicks (≥5 days old) from tagged females and opportunistically-found broods were caught and inspected around their eyes, comb and base of beak for ecto-parasitic sheep ticks *Ixodes ricinus.* High rates of tick infestation can reduce grouse chick survival, particularly if they are vectors for pathogens such as louping ill virus, a tick-borne flavivirus (Flaviviridae) (Duncan et al. 1978).

Derivation of demographic parameters

From the 2008–2016 counts, we estimated annual rates of 'female summer survival' as:

July adult female density in year t/spring female density in year t

and 'female winter survival' as:

spring female density in year t + 1/July female (adults and juveniles) density in year t

Broods per adult female, *brood size* (from adult females with broods) and *young per adult female* were also estimated from post-breeding counts.

For radio-tagged grouse, we calculated staggered-entry, interval-based Kaplan–Meier survival estimates (Bland and Altman 1998) for summer (April to July) and winter (August to March) using GenStat 17.0 (VSN International 2014). Monthly bird fates (dead, alive or unknown) were assigned, with unknown fates censored. Survival estimates and reproductive parameters were available only for 2009–2015, as no birds were radio-tagged in 2008 and too few remained in 2016 (n = 8) from which to provide sufficiently robust estimates.

To maintain the multiplicativity of parameters required by demographic models, only the female's last clutch in a year was used (red grouse produce only one brood per year but can lay a replacement clutch after a failed first attempt), and nests that failed through loss of the female were censored. *Nesting success* was the proportion of clutches where ≥ one chick hatched (surviving females only), and *hatching success* the proportion of eggs laid that hatched from successful attempts. *Chick survival* was the proportion of chicks hatched that were alive at 50 days. *Broods female*$^{-1}$*, brood size* and *young female*$^{-1}$ were compared with the same estimates from counts.

Grouse demography

Based on counts, the demographic parameters available were female summer survival (s), female winter survival (w), proportion of females with broods (p), and mean number of (female) chicks per brood (b). Based on radio-tagged birds, the demographic parameters available were female summer survival (s), female winter survival (w), number of (female) eggs per clutch (e), nesting success (n), hatching success (h) and chick survival (c). These can be combined to give a rate of annual survival $a = sw$ and an annual productivity rate $y = pb$ or $y = enhc$. The annual change in female abundance was calculated in two ways using different starting points: end March before reproduction ('pre-breeding'), or end July after reproduction ('post-breeding'), which generated two datasets with different ordering of the annual parameters. The change in annual number of pre-breeding females from year t to t+1 is given by $s_t(1+p_tb_t)w_t$, $s_t(1+e_tn_th_tc_t)w_t$ or $a_t(1+y_t)$ where $a_t = s_tw_t$; that of the annual number of females post-breeding is $w_{t-1}s_t(1+p_tb_t)$, $w_{t-1}s_t(1+e_tn_th_tc_t)$ or $a_t(1+y_t)$ where $a_t = w_{t-1}s_t$. These equations describing the change in abundance of female red grouse from one year to the next make the following assumptions, which are in line with what is known about grouse population dynamics (Hudson 1992, Watson and Moss 2008) and are either verified in the Results or considered in the Discussion: age effects on survival (s, w) and reproductive parameters (p, b, e, n, h, c) are negligible; the sex ratio of eggs and young is 1:1; all young females recruit as breeding adults in the year after hatching and breed annually for as long as they survive; a female that dies in the summer produces no offspring.

We used 'standard demographic accounting' (SDA; Brown et al. 1993, Coulson et al. 2005) to identify the contribution that each grouse demographic parameter made to the overall variation in annual change. SDA analysis takes as its starting point the variance of observed change from year to year in population size. It produces a complete breakdown of that variance in terms of the variances and covariances involving the demographic parameters. From the equations above, the change in numbers from one year to the next N_{t+1}/N_t can always be expressed as the sum of two terms T1 + T2, each term being a product of one or more parameters. Hence, the variance in population change can be described as $\text{var}(N_t/N_{t-1}) = \text{var}(T1) + \text{var}(T2) + 2\,\text{cov}(T1, T2)$. Partitioning each of the constituent variances and covariances into contributions due to variation in and covariation between their constituent factors following Brown and Alexander (1991), and scaling the contributions so that they sum to 100, gives a full percentage decomposition of $\text{var}(N_t/N_{t-1})$. Confidence limits on these were obtained by bootstrapping at the level of the full annual cycle. An alternative approach using 'life table response experiments' (LTRE, Caswell 1989, Horvitz et al. 1997) was applied to the same models and data. It gave essentially identical results, so it is not considered further.

Variation in demographic parameters and tests of assumptions

Differences in summer (April–July) and winter (August–March) survival of radio-tagged grouse between sexes and

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age classes (first-year, adult) were tested using log-rank tests within the time-point Kaplan–Meier procedure in GenStat 17.0 (VSN International 2014). We then compared the summer and winter survival estimates derived from radio-tagged birds with those from counts in the same year in a general linear model (GLM) with normal distribution, weighted by the reciprocal of each estimate's variance, and year and method as factors. To analyse trends over time we replaced the categorical year factor by year as a continuous variable; we tested its interaction with method (i.e. count and radio-tag) to check for differences in trend between methods.

Breeding success of first-year and adult radio-tagged females was compared at the level of the individual female in a GLM with year, age and their interaction as factors. For chick survival and broods female^{-1} we used a binomial distribution with logit link (binomial totals were number of chicks hatched per female, and 1, respectively), and for brood size a Poisson distribution and logarithmic link. When considering differences in breeding success derived from radio-tagged birds and counts (based on annual means), we used broods female^{-1} (binomial distribution, logit link function, females in July as binomial totals and females with broods as response variable), brood size (Poisson distribution, logarithmic link function, chicks as a response variable with ln(females) as offset) and young female^{-1} (log-transformed, normal distribution) in turn as response variable within GLMs, with year and method as factors. To test for changes in breeding success over time, we replaced the categorical year factor by year as continuous variable and tested its interaction with method.

Survival of radio-tagged chicks was compared between years using a log-rank test (time-point Kaplan–Meier procedure). In the absence of a year effect, we combined years and calculated daily Kaplan–Meier survival estimates (interval-based) for up to 30 days after hatching.

Apparent causes of mortality and nest failure

Carcasses (bones, flesh or primary feathers present) were collected from four sources: 1) radio-tagged birds, 2) birds found ad-hoc during fieldwork by research staff, 3) birds found by gamekeepers, and 4) those from monthly searches of up to nine of the grouse count blocks between October and February during four winters, following Thirgood et al. (1998). Also following Thirgood et al. (1998), carcasses showing signs of consumption by a predator based on field signs were assumed to have been predated unless found next to fences or roads. However, as some predators may also scavenge carcasses, it is difficult to determine whether a grouse was killed or merely scavenged, so we refer to 'mammal signs' and 'raptor signs' to recognise this uncertainty. Carcasses were grouped into five categories based on field signs: 1) signs of a raptor (plucked feathers, sometimes accompanied by a feather trail, notched sternum, faecal splash or pellets), 2) signs of a mammal (bitten feathers, sometimes accompanied by crunched bones or scats, or buried with puncture wounds), 3) unknown predator (evidence of both raptor and mammalian presence), 4) collision (found next to fences or roads), and 5) unknown (including carcasses that were too old to allow cause of death to be identified). To test whether the proportion of carcasses with raptor signs varied between sources and seasons, we used a binomial GLM (number of carcasses assigned to raptors as response variable, sum of carcasses showing signs of predation as binomial total) with source, season and year as factors.

Nest failures were assigned to three causes: 1) female death, classified as above, 2) clutch predation, and 3) clutch desertion. Temperature loggers (Thermocron iButton DS1921G) that recorded nest temperature every 15 min were placed in 52 nests, allowing us to determine the timing of nest failure, identified by a sudden drop to ambient temperature. However, we cannot exclude that some nests may have been deserted before being predated. Forty nests were also equipped with concealed nest cameras to identify predators.

Results

Trends in grouse density over time

Red grouse pre- and post-breeding densities increased by 9 ± 3% and 8 ± 3% per annum between 2008 and 2014, and then declined by 28 ± 4% and 26 ± 6% per annum between 2014 and 2016 despite the absence of shooting (Fig. 1).

Demographic analysis

Whether from counts (four parameters) or radio-tagged females (six parameters), the sum of the contributions from covariances between three or more parameters was at most 13%; they always included zero within their 95% confidence intervals, so could be considered relatively unimportant.

From the parameters based on counts (Table 1), joint contributions that did not include zero within their 95% confidence limits were *sw* (pre-breeding, 30%) and *pb* (pre-breeding and post-breeding, 9–12%). For the parameters taken individually, the confidence intervals were comparable for the contributions of *s* and *w*, and those of *p* and *b*, so it is not possible to identify which parameter within each pair is more important. The combined contributions of *s*, *w* and *sw* were 38–84% compared with 23–27% for *p*, *b* and *pb*.

For the parameters based on radio-tagged females (Table 2), joint contributions were 25–30% (zero not included within the 95% confidence limits) for *sc* (pre-breeding and

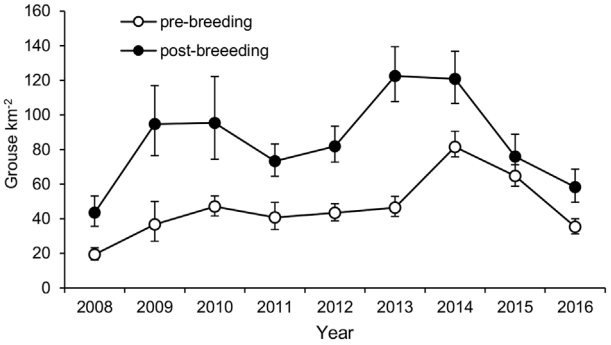


Figure 1. Mean pre- and post-breeding densities (± 95%CI) of red grouse on Langholm Moor 2008–2016, derived from distance sampling.

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Table 1. Contributions (%) to annual change in female red grouse abundance on Langholm Moor (2008–2016) from four demographic parameters summer survival *s*, winter survival *w*, broods female^{-1} *p* and brood size *b*, estimated from counts and analysed by standard demographic accounting. 95% confidence intervals are given in brackets. The starting point for calculating annual change was either before reproduction ('pre-breeding') or after reproduction ('post-breeding'). a) Individual contributions of parameters, b) joint contributions of two parameters and total higher-order covariances (i.e. joint contributions from three or more parameters).

(a)

Change in abundance of	Years	Contribution (%)			
		s	*w*	*p*	*b*
Pre-breeding	8	20.3 (6–82)	33.8 (13–78)	6.8 (2–23)	8.4 (3–22)
Post-breeding	8	15.4 (3–170)	27.8 (11–130)	6.5 (5–28)	6.9 (2–38)

(b)

Change in abundance of	Contribution (%)						
	sw	*sp*	*sb*	*wp*	*wb*	*pb*	Total higher–order covariances
Pre-breeding	30.4 (5-61)	–4.2 (–32–7)	–5.4 (–43–6)	–1.9 (–39–11)	5.8 (–22–20)	11.9 (4–38)	–5.8 (–29–12)
Post-breeding	–5.5 (–173–14)	–2.6 (–68–8)	–4.8 (–87–11)	23.6 (–2–56)	10.6 (–13–46)	9.3 (2–50)	12.7 (–52–27)

post-breeding), and 7–9% for *nc*. The former boosted the effective contributions of *s* and *c*, which were already the two parameters that stood out as important based on their individual contributions, 9-10% for *s*, 30–31% for *c*. The 95% confidence limits for *s* and *c* overlapped only slightly (pre-breeding) or not at all (post-breeding), indicating that *c* contributed most to explaining the variation in population growth rate; together *s*, *c* and *sc* explained on average 68% of it. Among the remaining parameters, the contributions of *e* and *h* were practically nil, those of *n* around 1% and those of *w* around 6%.

Combining parameters to give one for survival and one for productivity (Table 3) produced results that reflected those of the previous analyses. The contributions from the covariance between *a* and *y* appeared large, and for radio-tagged breeders the 95% confidence limits did not include zero. For parameters derived from counts, the contributions of *a* were roughly two to three times higher than those of *y*, but the wide 95% confidence limits showed so much overlap that the opposite was also possible. Parameters derived from radio-tagged females showed the opposite tendency, with the contribution of *y* over twice as high as that of *a*, though again the amount of overlap in 95% confidence intervals was considerable.

Factors affecting adult survival

Grouse survival did not differ between sexes or age classes (tagged birds), thus supporting our model assumptions, or between estimation methods (tagged birds versus counts) and averaged 75 ± 3% (SE) during summer and 59 ± 3% during winter (Fig. 2). The mean monthly survival rate of 94 ± 0.4% did not differ between seasons. During the study, summer survival declined by 4 ± 1% per annum ($F_{1,13}=9.01$, $p=0.010$) irrespective of the method, whilst winter survival showed no change.

Of the 202 radio-tagged grouse, 65% were confirmed dead, 15% went missing before the expected end of their tag-life, for 5% the tag was found without a carcass or signs of predation, 12% were lost for other reasons (11% tag-life expired, 1% tag removed by observer) and 3% were alive

Table 2. Contributions (%) to annual change in female red grouse abundance on Langholm Moor (2008–2016) from six demographic parameters summer survival *s*, winter survival *w*, clutch size *e*, nesting success *n*, hatching success *h*, chick survival *c*, obtained from radio-tagged females and analysed by 'standard demographic accounting'. 95% confidence intervals are given in brackets. The starting point for calculating annual change was either before reproduction ('pre-breeding') or after reproduction ('post-breeding'). a) Individual contributions of parameters, b) joint contributions of two parameters and total higher-order covariances (i.e. joint contributions from three or more parameters).

(a)

Change in abundance of	Years	Contribution (%)					
		s	*w*	*e*	*n*	*h*	*c*
Pre-breeding	7	8.9 (3–17)	5.6 (0–23)	0.3 (0–1)	1.3 (0– 4)	0.2 (0–0)	30.0 (12–59)
Post-breeding	6	9.6 (4–17)	6.2 (0–38)	0.3 (0–3)	1.3 (0–11)	0.2 (0–1)	31.3 (18–77)

(b)

Change in abundance of	Contribution (%)							
	sw	*se*	*sn*	*sh*	*sc*	*we*	*wn*	*wh*
Pre-breeding	2.9 (–4–14)	1.6 (0–4)	3.0 (–1–6)	–1.3 (–3–1)	25.1 (10–45)	1.2 (0–7)	2.4 (–1–10)	0.8 (–1–3)
Post-breeding	2.5 (–31–12)	1.5 (–1–9)	3.3 (–3–14)	–1.3 (–4–2)	30.2 (4–41)	–0.8 (–19–1)	–2.3 (–22–0)	–0.7 (–2–4)

Change in abundance of	Contribution (%)							
	wc	*en*	*eh*	*ec*	*nh*	*nc*	*hc*	Total higher–order covariances
Pre-breeding	0.2 (–29–12)	0.4 (0–2)	–0.3 (–1–0)	1.0 (–4–5)	0.1 (–1–1)	7 (0–13)	–1.2 (–6–2)	10.6 (–12–24)
Post-breeding	6.6 (–19–26)	0.4 (–1–6)	–0.2 (–1–0)	0.6 (–8–9)	0.2 (–1–3)	9.1 (1–36)	–1.2 (–7–5)	3.1 (–23–14)

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Table 3. Contributions (%) to annual change in female red grouse abundance on Langholm Moor (2008–2016) from two combined demographic parameters survival *a* (*sw*) and reproduction *y* (either *pb* or *enhc*). Datasets obtained from counts and from radio-tagged (RT) females, analysed by 'standard demographic accounting'. 95% confidence intervals are given in brackets. The starting point for calculating annual change was either before reproduction ('pre-breeding') or after reproduction ('post-breeding').

Change in abundance of	Years	Contribution (%)		
		a	*y*	*ay*
Pre-breeding (counts)	8	87.6 (39–227)	28.1 (9–100)	–15.7 (–183–35)
Post-breeding (counts)	8	38.9 (14–106)	22.3 (9–108)	38.8 (–77–52)
Pre-breeding (RT)	7	17.9 (9–49)	39.1 (22–61)	43 (17–55)
Post-breeding (RT)	6	18.9 (4–37)	42.6 (23–142)	38.4 (–57–54)

when monitoring ended in July 2016. Predation attributed to raptors was the main apparent cause of female mortality during the incubation period (10 raptor, 2 fox, 1 unknown predator) and occurred mostly during incubation breaks. Of the 35 radio-tagged females that died during summer, 74% did not hatch chicks and 14% had lost their brood by the time of their death, in line with our model assumption, while 11% may still have had chicks.

Of 1442 carcasses found, 93% showed signs of predation or scavenging of a predated bird (82% raptor, 8% mammal, 3% unknown predator), 3% of collisions and for 4% the cause of death was unknown. The proportion of carcasses with raptor signs varied between sources (Fig. 3; $F_{3,40} = 19.48$, $p < 0.001$), with gamekeepers attributing 97% of carcasses to raptors, compared to 79% by researchers, but did not differ between seasons or years. The species of raptor responsible for signs at carcasses could not be identified from the field evidence. However, on two occasions raptors were seen to strike grouse (peregrine and goshawk *Accipiter gentilis* each once) and raptors were flushed from freshly killed grouse on 15 occasions: peregrine and buzzard *Buteo buteo* (each 5), goshawk (3), and hen harrier and sparrowhawk *Accipiter nisus* (each 1). Mammal signs at carcasses were mostly attributed to fox (80%) with only 2% by stoat *Mustela erminea* or weasel *M. nivalis*, while 18% were not specified.

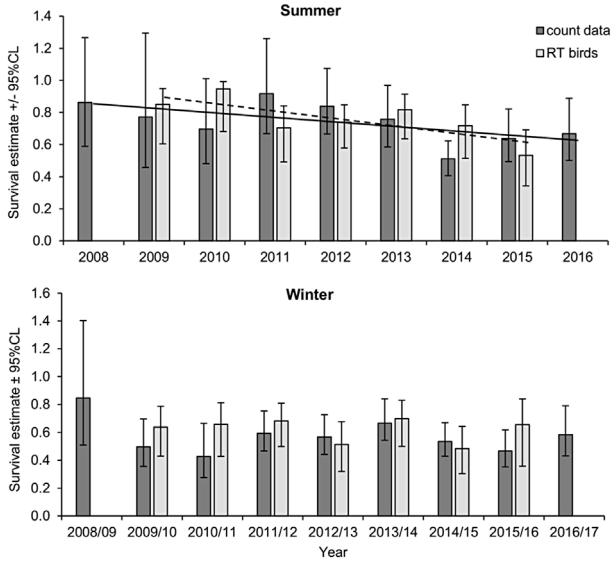


Figure 2. Kaplan–Meier survival estimates (± 95% CI) for red grouse on Langholm Moor 2008–2016 in summer (April–July) and winter (August–March) derived from counts and radio-tagged (RT) birds. Trend lines are presented for significant relationships (summer; RT birds: $y = -0.046x + 94.0$, counts: $y = -0.028x + 58.1$).

Factors affecting reproduction

Nesting success (i.e. the proportion of nests with ≥1 egg hatching) of surviving radio-tagged females was generally high (mean 2009–2015: 0.9 ± 0.04; Table 4) and did not vary between years ($F_{7,88} = 0.93$, $p = 0.49$). Similarly, hatching success (i.e. the proportion of eggs hatching in successful nests) did not vary between years ($F_{7,73} = 0.84$, $p = 0.56$) and averaged 0.88 ± 0.02 (Table 4). However, clutch sizes varied between years (Table 4; $F_{7,100} = 25.51$, $p = 0.002$). Replacement clutches (7.3 eggs) were smaller than first clutches (9.3 eggs), which affected mean clutch size mainly in 2012 and 2016 when the proportion of replacement clutches was 27% and 50% (0–17% in other years). Reasons for nesting failure (n = 37 failed attempts) were clutch predation (49%), death of the female (32%), clutch desertion (14%) and unknown (5%).

In line with the model assumptions, all radio-tagged females bred in each year they were alive, and no reproductive

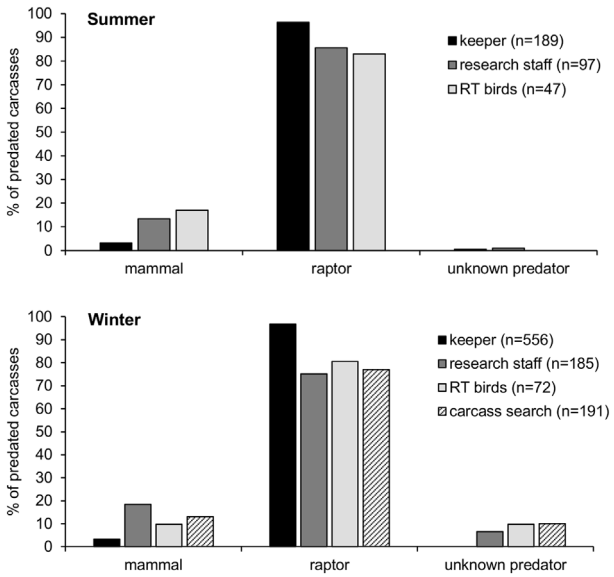


Figure 3. Frequency of red grouse carcasses associated with signs of mammal, raptor and unknown predators from examination of carcasses found between 2008 and 2016 on Langholm Moor by chance (keeper or research staff), during radio-tracking (RT), and during systematic carcass searches (conducted by research staff in winter only) during summer (April–July) and winter (August–March).

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Table 4. Annual mean reproductive measures of red grouse on Langholm Moor (2008–2016) from both radio-tagged females and post-breeding counts. Sample sizes are given in brackets. Parameters of radio-tagged females in 2016 (in italics) were not included in the calculation of the overall mean or analyses of between-year variation (year as categorical variable, see footnotes [a–c]).

	2008	2009	2010	2011	2012	2013	2014	2015	2016	Mean
Radio-tagged females										
Clutch size		9.5 (15)	9.1 (10)	9.1 (15)	9.1 (21)	10.1 (18)	8.7 (17)	8.5 (15)	*7.5 (4)*	9.2 ± 0.2
Nesting success		0.92 (13)	1.00 (11)	0.85 (13)	0.68 (22)	1.00 (17)	0.92 (13)	0.91 (11)	*0.75 (4)*	0.90 ± 0.04
Hatching success		0.86 (12)	0.88 (9)	0.93 (11)	0.82 (14)	0.85 (17)	0.88 (12)	0.94 (10)	*0.96 (3)*	0.88 ± 0.02
Chick survival		0.50 (12)	0.54 (7)	0.13 (6)	0.25 (13)	0.38 (15)	0.42 (9)	0.04 (7)	*0.20 (1)*	0.32 ± 0.07
Broods female^{-1}, [a]		0.85 (13)	1.00 (7)	0.38 (8)	0.37 (19)	0.87 (15)	0.60 (10)	0.25 (8)	*0.67 (3)*	0.62 ± 0.11
Brood size [b]		4.5 (11)	4.7 (7)	2.3 (3)	3.4 (7)	3.8 (13)	4.7 (6)	1.0 (2)	*2.0 (1)*	3.5 ± 0.5
Young female^{-1}, [c]		3.8 (13)	4.7 (7)	0.9 (8)	1.3 (19)	3.3 (15)	2.8 (10)	0.3 (8)	*1.3 (3)*	2.4 ± 0.6
Post-breeding counts										
Broods female^{-1}, [a]	0.71 (51)	0.91 (80)	0.80 (98)	0.57 (130)	0.64 (143)	0.81 (115)	0.76 (123)	0.54 (134)	0.59 (85)	0.72 ± 0.05
Brood size [b]	4.4 (36)	5.0 (73)	4.8 (78)	3.6 (74)	3.8 (91)	5.6 (93)	5.0 (93)	2.9 (72)	4.9 (50)	4.5 ± 0.3
Young female^{-1}, [c]	3.1 (51)	4.6 (80)	3.9 (98)	2.1 (130)	2.4 (143)	4.5 (115)	3.8 (123)	1.6 (134)	2.9 (85)	3.2 ± 0.4

[a] year: $F_{8,6}=6.11$, $p=0.020$, method: $F_{1,6}=3.33$, $p=0.118$.
[b] year: $F_{8,6}=12.53$, $p=0.003$, method: $F_{1,6}=6.89$, $p=0.039$.
[c] year: $F_{8,6}=3.67$, $p=0.065$, method: $F_{1,6}=5.19$, $p=0.063$.

parameter differed between age classes ($p > 0.19$ in all tests). However, tagged females reared 25% fewer chicks than females recorded on counts (Table 4). All three measures of breeding success obtained from tagged birds and counts varied significantly between years (Table 4), but none changed linearly over time ($p \geq 0.10$ in all tests).

Chick survival from 69 radio-tagged females from hatching until 50 days old averaged 32% (Table 4). Survival of radio-tagged chicks (2013–2015) to 10 days old was 87% (95%CL: 71–94), to 20 days 62% (47–75), and to 30 days 30% (14–48). Of 73 tagged chicks, 10% showed signs of predation (six attributed to raptor and one to stoat or weasel), 23% were lost and presumed dead, 49% shed their tags, and 18% of chicks outlived their tag-life. In addition, 25 carcasses of untagged grouse chicks were found between June and early July: 68% of deaths were attributed to raptors, 8% to mammals (one badger and one stoat or weasel), 12% had died of other causes (no signs of predation), 4% through collisions (road) and in 8% the cause of death was unknown.

Tick burden on grouse chicks was low with 76% of chicks having no ticks (n = 348), the remainder had a geometric mean of 1.6 ticks chick^{-1} (95%CI 1.5–1.8, range 1–9).

Discussion

When grouse moor management recommenced at Langholm, the recovery rate of post-breeding red grouse densities (8 ± 3% per annum) was low compared to the 139 ±20% observed in the initial two to three years of predator control during an experimental study (Fletcher et al. 2013). We used retrospective analysis to identify the life-stages accounting for this limited population recovery. The survival of adults and chicks contributed most to annual population changes, while the contributions of clutch size, hatching success and nesting success were negligible. Based on counts, a combination of adult summer and winter survival appeared most important, whereas with radio-tagged birds it was a combination of adult summer survival and chick survival.

Many studies rely on counts to measure demographic parameters (Potts 1986, Menu et al. 2002, Mougeot et al. 2003, Coulson et al. 2005), while others rely on radio-telemetry (Bro et al. 2000, Baines and Richardson 2007, Dahlgren et al. 2016). The biases in either approach are often difficult to evaluate, and the two are rarely compared to assess how they may differ. Based on such a comparison in this study, the ability to separate the different components of breeding success when using radio-tagged birds, in combination with the smaller confidence limits in comparison with parameters derived from counts, suggest that the results based on radio-tagged birds may be both more detailed and more reliable. However, radio-tagged females had lower breeding success than females recorded on counts. Thirgood et al. (1995) found no effect of radio-tags on adult survival, clutch size or hatching success, suggesting that any potential impact may be at the chick stage, possibly via disturbance associated with regular monitoring of broods. Alternatively, we may be more likely to detect females with broods than single females during transect counts (Brittas and Karlbom 1990, Hörnell-Willebrand et al. 2006), thereby overestimating breeding success from counts.

Raptor signs were associated with most adult grouse carcasses (82%) not only in this study, but also in an earlier study at Langholm (Thirgood et al. 1998, 2000a). Raptors were also associated with 35% of nesting failures, helping to explain the significant contribution of female summer survival to variation in population changes. Adult grouse survival in summer decreased over the study, being lowest between 2014 and 2016. This period was associated with more potential predators of grouse: a 5-fold increase in hen harriers and a 3-fold increase in the fox index, together with the withdrawal of medicated grit (Ludwig et al. 2017). It may be easier to find grouse carcasses associated with raptor signs than with mammal signs owing to the more obvious presence of plucked feathers (Thirgood et al. 1998). However, the proportion of carcasses with raptor signs did not differ between those found by research staff and those found by retrieval of dead radio-tagged grouse, and the latter are located irrespective of the associated field signs. Nevertheless, 15% of radio-tagged birds disappeared without a carcass being found. This could be explained by tag failure, movements or depredated birds either being carried away from the study area or taken underground by a mammalian predator,

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thus potentially underestimating predation by mammals, especially red fox.

Whilst we could not differentiate raptor species associated with grouse carcasses, we were aware that the numbers of breeding hen harrier and peregrine were both fewer than in the earlier study (Redpath and Thirgood 1997, Ludwig et al. 2017). Instead, the raptor community was numerically dominated by buzzards, which have a lower proportion of avian prey in their diet (Francksen et al. 2016a, b) and, unlike peregrines and hen harriers, are commonly scavengers as well as predators. Hence, it was possible that some grouse may have been scavenged by raptors rather than predated by them, and further work may help to distinguish field signs which diagnose predation from those which may indicate scavenging of already-dead birds. Furthermore, we cannot exclude that other factors may affect the susceptibility of grouse to predation and thus be the ultimate cause of mortality. However, an earlier study found no effect of habitat on grouse mortality rates (Thirgood et al. 2002). In addition, the likelihood of adult grouse dying from strongylosis, the primary cause of quasi-cyclical fluctuations in grouse numbers (Hudson et al. 1998), was markedly reduced by providing grouse with free-access anthelmintic drugs fixed to grit (medicated grit) to kill the strongyle worm. Accordingly, we observed no diseased grouse during our study period and parasitic worm burdens recorded were substantially below those associated with lethal impacts elsewhere (Supplementary material Appendix 1).

Chick survival at Langholm was low. On average only one-third survived until July, compared to two-thirds in most UK studies (55–71%; Redpath and Thirgood 1997, Park et al. 2001, Baines et al. 2018), but not all (16–30%; Irvine et al. 2014). Chick survival can be influenced by many factors, including weather (Erikstad and Spidsø 1982), invertebrate abundance (Park et al. 2001), female condition (Blomqvist et al. 1997), parental investment (Pedersen and Steen 1985), levels of both ecto- and endoparasite infestation (Duncan et al. 1978, Newborn and Foster 2002) and predation (Steen and Haugvold 2009, Irvine et al. 2014). In this study, predation was the main proximate cause of chick mortality, although we cannot categorically rule out the role of other factors that may have rendered chicks more susceptible to predation. However, average tick burdens on grouse chicks were low compared to other studies (Duncan et al. 1978, Fletcher and Baines 2018), and three-quarters of chicks sampled had no ticks at all. Inclement weather can impact upon chick growth and survival, especially during the first 10 days after hatching (Erikstad 1985, Park et al. 2001), when chicks cannot thermoregulate (Aulie 1976) and need insects (Spidsø 1980). However, we observed relative high chick survival during this period, with most mortality instead occurring when chicks were older, more mobile and when carcasses found suggested they had been predated, often by raptors.

Our results confirmed the model assumptions that age effects on survival and reproductive parameters are negligible and that all females breed annually. However, our assumption that females that die in the summer produce no offspring may not be absolute. If a female dies after hatching, the brood may be reared by the male (Martin and Cooke 1987, Watson and Moss 2008) or adopted by another female (Fingland and Ludwig 2015). We could not test the sex ratio of eggs or young, but other studies on red grouse indicate a balanced sex ratio at fledging (Mougeot et al. 2003).

Retrospective demographic analysis can inform conservation and game management by identifying causes of population dynamics (Watson 1971, Cooch et al. 2001, Sim et al. 2010). In our study, female summer survival and chick survival explained most of the observed variation in population change. Female survival, influenced by predation, also explained most of the variation in λ in declining populations of grey partridges *Perdix perdix* in France (Bro et al. 2000) and in greater sage-grouse *Centrocercus urophasianus* in western North America (Dahlgren et al. 2016).

Recommencing grouse moor management at Langholm increased grouse reproductive success relative to pre-2008 studies (Baines and Richardson 2013, Ludwig et al. 2017), resulting in an initial modest population increase, which was not sustained throughout the study period. Thus, the agreed project target to resume economically viable harvesting (i.e. shooting 2000 grouse in at least one of the 10 years of the project) was not met. Although legal predator control reduced the number of foxes (–80%) and crows (–65%) present in the study area and lowered their impact on grouse (Ludwig et al. 2017), the majority of predation was associated with signs of raptors, which are legally protected species. Managing hen harrier depredation of grouse chicks by diversionary feeding reduced predicted levels of predation, but together with habitat restoration, predator control and medicated grit provision was insufficient to increase grouse numbers to allow driven shooting during the ten-year duration of the project (Ludwig et al. in press). Extending the provisioning of diversionary food to other raptor species may contribute to reducing the overall level of raptor predation, especially during the breeding season. However, for species such as buzzard, whose diet consists of low proportions of grouse year-round (Graham et al. 1995, Francksen et al. 2016a, b) and whose abundance has increased at Langholm since the mid-1990s (Ludwig et al. unpubl.), it would first be helpful to establish whether some of those grouse assumed predated have instead been scavenged.

We conclude that adult survival of grouse, especially in summer, together with low chick survival, were the demographic stages contributing most to variation in annual population change. Several factors may influence these rates, but the evidence available suggested that mortality associated with raptor signs was the most important factor determining adult survival and was closely linked, possibly alongside weather, to low rates of chick survival.

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