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Original article

The effects of population density on the breeding performance of mountain hare *Lepus timidus*

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Feedback between population density and demographic parameters often plays a determining role in population dynamics, and it is particularly important in managing exploited or harvested populations. The mountain hare *Lepus timidus* is a traditional game species, which is hunted in Scotland for sport and population control. However, information about how population parameters respond to changes in population density is lacking. To assess how reproduction and juvenile recruitment change in response to population density, we sampled 189 hares (88 females and 101 males) from 10 independent private hunting estates. We found a significant negative correlation between population density and the proportion of juveniles recruited into the breeding population, along with a significant interaction between population density and sex, which revealed that the proportion of juvenile females recruited decreases more rapidly with population density compared to the proportion of male juveniles. However, we found no evidence of density-dependent fecundity. Our results suggest density-dependent compensation in this species, acting on recruitment, not fecundity, with rates of juvenile recruitment differing between the sexes. We conclude that the significant correlation between population density and juvenile recruitment may provide harvested populations with the potential for compensatory juvenile recruitment, although harvesting rates need to be accurately estimated to avoid the risk of overharvesting.

Key words: compensation, fecundity, harvesting, juvenile recruitment, Lepus timidus, mountain hare

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The role and relative importance of the interaction between population density and basic demographic parameters (i.e. births, deaths, immigration and emigration) are fundamental questions in ecology. Despite the historic and ongoing debate over the mechanisms of population regulation and population limitation (Sinclair 1989), density dependence (i.e. the feedback between population density and

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demographic rates) remains a central principle in population ecology and management. Under density dependence, reducing population density by harvesting may lead to increased *per capita* survival or reproduction, resulting in an increased population growth rate (Boyce et al. 1999). If harvesting occurs at, or below, the same rate as population growth, sustainable harvesting can be achieved (Caughley & Gunn 1995, Sutherland 2001).

In terrestrial vertebrate populations, population density has been demonstrated to affect survival (e.g. Angerbjörn 1986), dispersal (see Matthysen 2005 for review) and reproduction (Both 1998, Coulson et al. 2000, Soutullo et al. 2006). Negative density-dependent reproduction has been detected in birds (Both 1998, Dhont et al. 1992) and mammals (e.g. Coulson et al. 2000). To understand the effects of population density on reproduction, and implications for population dynamics, it is important to consider both fecundity (i.e. the numbers of live offspring a female gives birth to) and recruitment (i.e. the numbers of young born that subsequently survive to enter the breeding population). The effects of population density on juvenile recruitment can lead to changes in the age structure of populations. Consequently, populations composed of older individuals may have different population growth rates than those composed of younger individuals, influencing the population response to harvesting (Sinclair et al. 2006).

The mountain hare *Lepus timidus* is harvested for sport, subsistence and commerce across its circumpolar distribution. Mountain hares show unstable population dynamics throughout their distribution (Newey et al. 2007a,b, Reynolds et al. 2006), further complicating sustainable management of this species (Lande et al. 2003). Although knowledge of the relationships between population density and female fecundity, juvenile recruitment and population age and sex structure are potentially important in understanding the dynamics of mountain hare populations and their sustainable management, this has yet to be investigated.

Studies of the effects of population density on reproduction and recruitment of the mountain hare are currently limited to two studies in the 1970s and 1980s. By following population density, survival and fecundity of a Scottish mountain hare population over one 10-year cycle, Hewson (1976) found higher rates of reproduction during the low and increasing phases of the cycle, and higher juvenile survival rates during the increase phase of the cycle. Angerbjörn (1986) compared island populations of different population densities and found that although litter size was unaffected by density, juvenile recruitment was higher on islands and in years with lower density populations (Angerbjörn 1986). The aims of our study are to further this knowledge and investigate whether population density affects fecundity and juvenile recruitment in Scottish mountain hare populations. Specifically, we tested the following non-exclusive hypotheses: 1) Litter size will change with increasing population density; litter size may be expected to decrease due to higher resource competition at high-density sites; 2) Prenatal mortality will change with increasing population density; mortality may be expected to increase due to the effects of higher resource competition at high-density sites; and 3) The proportion of juveniles in the population will change with increasing population density; the proportion of juveniles may be expected to decrease due to lower recruitment of juveniles into higher density breeding population due to increased resource competition.

Methods

Study species and sites

Our study was carried out on 10 independently managed private hunting estates managed for red grouse *Lagopus lagopus scoticus* shooting (labelled A-J in Table 1) across the Central Scottish Highlands. All sites were between 340 and 740 m a.s.l. with between 60 and 380 m of altitude change within each site. The distances between individual sites varied between 3.5 and 28 km. The mountain hares used in our study were legally killed as part of routine estate management or sporting activities during January-April 2009. In Scotland, mountain hares begin mating in late January/early February, with leverets being born from March onwards, and they do not breed in the year of their birth (Flux 1970, Hewson 1976). Therefore, hares used in our study were either breeding for the first time (juvenile) or had survived at least one previous breeding season (adult). With post-partum mating and a 50-day gestation, female mountain hares typically produce up to three litters a year, although four is theoretically possible (Hewson 1976). Mountain hares are traditionally harvested from December to April; therefore, measures of fecundity used for our study only apply to the first litter. Samples collected from two study sites (sites E and F), where hares were shot in January or early February, are omitted from the fecundity analysis

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Table 1. Site code (A-J; to allow anonymity of individual hunting estates), the time period when distance sampling was carried out, population density estimates (in hares ha^{-1}; with upper (UCL) and lower (LCL) confidence limits given in brackets), date when hares were harvested and the total number of females (sample size of each site for the fecundity analysis, sites E and F not included in fecundity analysis due to sample collection occurring prior to breeding) and total number of hares of both sexes (sample size of each site for the age structure analysis, sites E and F are included in this analysis).

Site code	Period of distance sampling data collection	Population density estimate (UCL, LCL)	Date of sample collection	Number of females	Total number of hares
A	10/02/2009-11/02/2009	0.57 (0.42, 0.79)	01/04/2009	10	29
B	13/02/2009-20/02/2009	0.29 (0.11, 0.75)	23/03/2009	10	19
C	17/02/2009-19/02/2009	0.07 (0.04, 0.11)	24/03/2009	9	20
D	24/02/2009-25/02/2009	0.10 (0.05, 0.21)	26/03/2009	16	27
E	06/01/2009-07/01/2009	0.06 (0.03, 0.10)	08/01/2009	na	23
F	14/01/2009-20/01/2009	0.10 (0.02, 0.49)	02/02/2009	na	16
G	21/02/2009-28/02/2009	0.02 (0.01, 0.05)	05/03/2009	8	15
H	26/02/2009-01/03/2009	0.03 (0.01, 0.07)	05/04/2009	16	27
I	03/03/2009-04/03/2009	0.11 (0.03, 0.35)	09/03/2009	17	37
J	05/03/2009-06/03/2009	0	24/03/2009	7	20

due to sample collection occurring prior to, or very early in, the breeding season. However, all individuals, including those from sites E and F, are included in the juvenile recruitment analysis.

Population density estimates

Population assessment of small, nocturnal and cryptic species, like mountain hares, is difficult (Newey et al. 2011). Distance sampling (Buckland et al. 2001, Thomas et al. 2010) has been shown to be effective at estimating mountain hares in the Scottish uplands (Newey et al. 2003), and in our study, we used this method to estimate population density at each site between January and March 2009 prior to any hunting. Exact dates of data collection for each site are given in Table 1. We placed 4-12 parallel transect lines spaced 500 m apart over each study area. Each transect line was between 0.5 and 4.5 km long, depending on the size and shape of the area. Transects were orientated parallel to the altitude gradient in order to take account of associated changes in vegetation or hare density with altitude, reducing between-transect variation within sites. Transect lines were traversed on foot by a single observer. Adjacent transect lines were not sampled on the same day to minimise repeated counting of hares flushed from one transect line to the next. Hares are generally crepuscular, with increased activity at dusk and dawn (Angerbjörn & Flux 1995). Therefore, to reduce bias in detection probability caused by diurnal changes in activity, we only carried out surveys between 08:30 and 15:00 (i.e. >1 hour after sunrise and <1 hour before sunset) when hares are generally inactive. When hares were sighted, the time and the distance (estimated using a laser range finder; Bushnell YardagePro, Bushnell, Denver Co, USA) and bearing to the hare (measured with a sighting compass) were recorded. The sighting angle and distance were used to estimate the perpendicular distances used in Distance analysis. Data were analysed using DISTANCE 5.0 (Thomas et al. 2010).

Due to a low number of hare sightings at some sites, we pooled distance data from all sites to generate a global detection function, with estate density estimated by post-stratification. The greatest 5% of perpendicular distances in the data were truncated to remove outliers and increase precision (Buckland et al. 2001). We identified the best fit detection function by comparing the distribution of perpendicular distances with a range of candidate models. Model fit was first visually assessed by examining histograms and q-q plots, where special attention was paid to the crucial model fit close to the transect line. The best fit model was selected on the basis of the lowest AIC score, χ^2 goodness-of-fit-tests and results of the Kolmogorov-Smirnov test for normality for the distribution of perpendicular distances. Details of the models tested in distance sampling analysis can be found in Appendix I.

Tissue sample collection

Tissue samples were collected within 48 hours of the hares being killed. Body mass and length of the hind foot (from the talocrural joint to the tip of the longest toe, excluding the claw) were recorded. Both jaw mandibles were extracted and the right kidney and associated kidney fat (fat that came away with the kidney) were removed and frozen within 12 hours of collection and stored at -20°C until processing.

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Animals were sexed by internal examination and for each female, the uterus was removed and examined. Foetuses, if present, were counted and body length (crown to rump) recorded. Both ovaries were also removed and placed immediately in 4% formalin for 24 hours, before being transferred and stored in 70% alcohol.

Body condition and skeletal size

The kidney and kidney fat were weighed separately and used to calculate an index of body condition as the mass of kidney fat divided by mass of kidney (Finger et al. 1981). Hind foot length was used as a measure of skeletal size (Iason 1990).

Fecundity estimates

A total of 93 females were killed across the eight sites (A-D, G-J) used in the fecundity analysis. The majority of post-implantation loss of litters occurs before half-term, when foetuses are 1-2 cm in length (Flux 1970). With the exception of three foetuses, from different study sites, all foetuses were > 3 cm in length. Therefore, we assume that females were past midterm and that further embryo loss would have been minimal, allowing us to assume that the number of foetuses accurately represents litter size. For 50 females drawn from five sites (two high density, i.e. A and B and three low density, i.e. G, H and J), both ovaries were sectioned laterally and the four halves embedded into wax blocks. Each block was then serially cross-sectioned at 5 μm thickness. For each block, the 5th, 10th and 15th sections were mounted onto a microscope slide and stained with hematoxylin and eosin (H&E; VWR International, Pennsylvania, USA and TAAB Laboratories Equipment Ltd, Berks, UK) to give a total of 12 sections/ovary. This enabled mature Graafian follicles and *corpora lutea* (CL), the structure that forms after follicles have shed ova, to be counted. For sites C, D and I, both ovaries were cross-sectioned by hand every 1 mm and CL counted under a 10x stereomicroscope. Cross-sectioning by hand does not allow follicle health to be assessed. However, the large size of CL during gestation (7-11 mm in diameter (Angerbjörn & Flux 1995, A. Knipe, S. Ramsay, S. Thirgood & S. Newey, unpubl. data) means that the CL can be counted as reliably in hand-sectioned ovaries as the stained ovary sections. Therefore, the CL counts of the different methods are comparable. CL counts can be used to give an estimate of the number of ovulations (Iason 1990, Newey et al. 2010) and, when numbers of foetuses are subtracted, prenatal mortality (Iason 1990).

Age determination

We estimated the age of shot hares by counting adhesion lines in the lower mandible. These lines are formed by differing bone density produced by seasonal changes in growth, giving rise to annual 'rings' in the periosteal zone of the jawbone (Frylestam & Schantz 1977, Henderson & Bowen 1979, Iason 1988). Jawbones were sectioned using a circular saw and polished with a fine grade emery paper to create a smooth bone surface allowing the adhesion lines to be counted using a 10x stereomicroscope. This method enables individuals to be aged to the year and then assigned as juvenile (≤ 1 year) or adult (> 1 year old).

Statistical analysis

The effect of population density, body condition (kidney fat index), skeletal size (hind foot length), previous breeding experience (juvenile or adult) and hunting method (shot or snared) on litter size and prenatal mortality of the first litter were assessed using a Generalised Linear Mixed Model (GLMM) with Poisson errors and log-link function. To account for uncontrollable differences between sites, we include site in the model as a random effect. As all females included in the fecundity analysis were killed within a month of each other (see Table 1), and the date was not thought to confound reproductive status of females between sites, the date was not included in the model. The effect of population density, method of hunting and sex on the proportion of juvenile animals in the killed sample were assessed using a GLMM with binomial errors and logit-link function with site included in the model as a random effect. We first specified the full model including all terms and second order interactions, and then sequentially removed terms through a process of stepwise deletion of the least significant term, determined by the t value closest to zero. Candidate models were compared, and the best fit model chosen, using Log-Likelihood Ratio Tests (LRT). To account for uncertainty in the population density estimates, models were rerun and weighted by the reciprocal of the square root of the confidence interval. This resulted in no change to the overall results and so the simpler, non-weighted models are

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Table 2. χ^2 values, degrees of freedom (df), and P-values of the Log Ratio Test (LRT), and order of deletion of each explanatory variable, from the full GLMM investigating the effects of population density on litter size and prenatal mortality of the first litter across eight independent sites.

	Litter size				Prenatal mortality			
Explanatory variable	χ^2	df	P	Order	χ^2	df	P	Order
Skeletal size	0.36	1	0.55	1	$5x10^{-5}$	1	0.90	1
Method	0.59	1	0.44	2	0.68	1	0.41	4
Density	1.80	1	0.18	3	1.08	1	0.30	5
Body condition	2.34	1	0.13	4	1.97	1	0.16	3
Previous breeding experience	3.63	1	0.06	5	0.35	1	0.55	2

presented here. We performed analyses using the lme4 package (Bates & Maechler 2010) for R version 2.12.0 software (R Development Core Team 2010).

Results

Population density estimates

Model selection suggested that the half-normal cosine model fitted the distribution of perpendicular distances best, indicated by both the visually good fit of the half-normal cosine model to the histogram of perpendicular distances (Appendix II), and by the lowest AIC score and highest P-values of the Kolmogorov-Smirnov and χ^2 tests (see Appendix I).

Overall mean population density was estimated at 0.13 hares ha^{-1}, with post-stratification of data used to give estimates of population density for each site. Estimated population density varied from 0 to 0.57 hares ha^{-1} (see Table 1).

Fecundity

The mean litter size (± SE) across the eight sites used in the fecundity analysis was 1.35 (± 0.08), the mean number of ova shed (± SE) was 1.94 (± 0.09) and the mean prenatal mortality (± SE) was 0.59 (± 0.09) ova/female. Overall, 29.3% of ova shed did not result in a developed foetus. Out of the total of 93 females, five (5.4%) showed signs of neither pregnancy nor ovulation. These five individuals came from different sites and were of different ages. None of the second order interactions significantly increased the log-likelihood ratio (LRT) compared to the full additive model (LRT, $P > 0.2$ in all cases). Population density, previous breeding experience, skeletal size, body condition and hunting method had no signif-

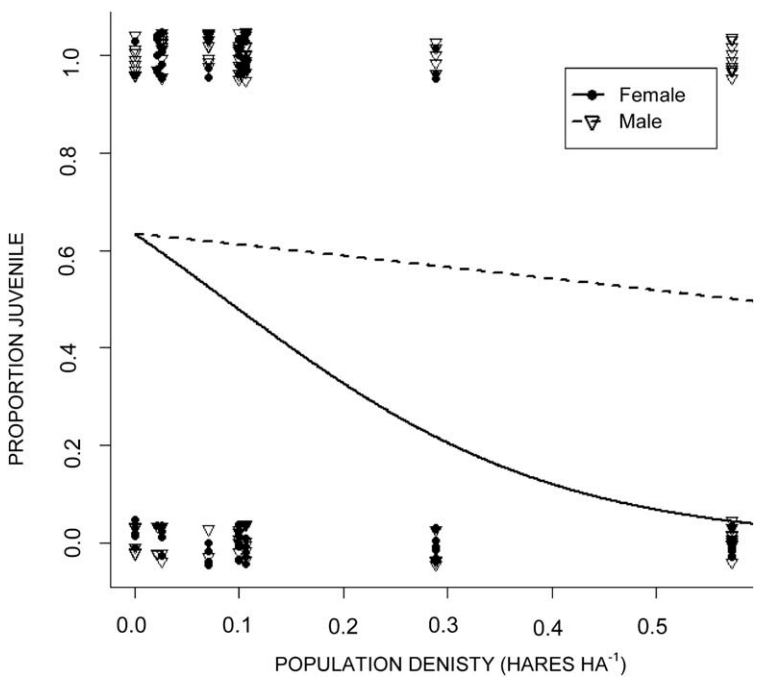


Figure 1. The proportion of female juveniles (—) declines more steeply with increasing population density than the proportion of juvenile males (- - -). Observed data are also shown for both females (•) and males (∇) with each point representing an individual hare at the respective population density estimate of the population from which it originated; individuals are represented as whole numbers, either adult (0) or juvenile (1), individual points are jittered around 0 and 1 to aid interpretation.

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icant effect on litter size or prenatal mortality of the first litter period, and in both cases, the null model (no explanatory variables) was the best fit model (Table 2).

Juvenile recruitment

The proportion of juveniles out of the total numbers of harvested hares examined significantly decreased with increasing population density (Estimate = -6.36, SE = 2.23, z = -2.85, df = 5, P = 0.004). Further, there was a significant interaction between population density and sex (Estimate = 5.40, SE = 2.45, z = 2.21, df = 5, P = 0.03), with model selection supported by the LRT ($\chi^2_1 = 6.55$, df = 1, P = 0.01; Fig. 1). The slope describing the relationship between the proportion of male juveniles and population density is less steep than the slope for the proportion of female juveniles with population density. This result indicates that the effect of increasing population density on the proportion of juveniles differs between the sexes (see Fig. 1). There was no significant effect of hunting method on the proportion of juveniles (Estimate = -0.78, SE = 0.51, z = -1.5, P = 0.13), with deletion from the model supported by the LRT ($\chi^2_1 = 2.31$, df = 1, P = 0.13).

Discussion

Density-dependent mechanisms are a pre-requisite for compensatory population dynamics and, therefore, knowledge of density-dependent processes is key in achieving sustainable harvesting of wild populations (Sutherland 2001). We investigated the effect of population density on fecundity and recruitment in 10 mountain hare populations. We found a negative correlation between the proportion of juveniles in the shot sample and population density indicating density-dependent juvenile recruitment, but we found no support for density-dependent female fecundity.

Population density

We estimated population density to be < 0.1 hares ha^{-1} for eight out of the 10 sites sampled, with very little variation between them. The remaining two estates had much larger density estimates of 0.29 and 0.55 hares ha^{-1}.

At site J, the estimated population density was zero hares ha^{-1} as no hares were detected during distance sampling. Although hares are present at site J, as confirmed by the availability of killed hares, the estates management policy is to maintain very low hare numbers and density is extremely low. An estimate of population density at site J, derived by dividing the number of hares killed by the area of the estate, gives an estimate of 0.003 hares ha^{-1}, which could be considered negligible for the purposes of our study.

As found by Newey et al. (2003), confidence intervals were larger at higher hare densities although the highest densities recorded in our study were much lower than the highest densities reported in Newey et al. (2003). The reasons (i.e. counting saturation and disturbance to individuals from observer or other hares) for the large confidence intervals in Newey et al. (2003) did not appear to be of similar significance in the field in our study. Weather, habitat type and time of year all affect the distance from which hares will flush when disrupted (Flux 1970). It is possible that differences in habitat type or management, such as the extent of heather burning, could lead to differences in detection probability between the two studies.

Female fecundity

As reported in previous studies (Hewson 1976, Angerbjörn 1986), we too found no evidence for density-dependent female fecundity in either litter size or prenatal mortality. It is possible that this result is due to our focus on the first litter. In mountain hares, the number of leverets produced in the first and second litters in any one year negatively affect the number in the third litter of the year (Iason 1990). This relationship between litter sizes of different litter groups makes it difficult to infer, from information on first litter size alone, how population density affects annual fecundity. While focusing on the first litter restricts our ability to assess the effects of population density on annual female fecundity, it provides an extremely useful indicator of the effects of population density on female fecundity. Leverets born earlier in the year show higher post-weaning survival, have longer growth period, and hence, grow into larger adults (Iason 1989). Since larger adult females are able to attempt breeding earlier and have lower prenatal mortality rates (Iason 1990), early born leverets will in turn go on to have higher reproductive success. In terms of life history, early breeding is beneficial. However, early attempts at reproduction are associated with a high risk of failure; periods of inclement weather at this time may lead to increased losses, particularly as gestation is in progress before any spring growth of vegetation (Iason 1990). Therefore, it could be expected that any negative effect of

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population density (via increased resource competition or increased dominance interactions) would be most apparent in the first litter period.

Juvenile recruitment

The proportion of juveniles found in the sample of killed hares was significantly higher at lower density sites, a result which is largely consistent with previous studies (Hewson 1976, Angerbjörn 1986). In his study of mountain hare populations on three Swedish islands, Angerbjörn (1986) found higher juvenile recruitment on islands and in years when population density was low, but did not find any corresponding increase in litter size. In his 13-year study of one mountain hare population in the Scottish Highlands, Hewson (1976) did not find any clear association between recruitment and population density as there was considerable annual variation in survival, production of leverets and recruitment. Rather, Hewson (1976) found that demographic parameters tended to be associated with a phase of population growth with low juvenile recruitment during the low phase, when population density was very low, and greatest juvenile recruitment during the increase phase as population density increased. Both these early studies support the results of our study despite differences in methodologies and some concerns over the provenance of the island populations used in Angerbjörn's (1986) study (Newey et al. 2007a).

As female fecundity is unaffected by population density in our study, the higher proportion of juveniles at low density would therefore appear to be the result of increased juvenile survival or immigration, rather than increased numbers of offspring born/female. This suggests that higher juvenile recruitment, rather than greater female fecundity, increases the proportion of juveniles at low population density. A significant interaction between sex and population density shows that the proportion of juveniles declined with population density at a higher rate in females than in males. This could be indicative of different survival rates between the sexes, with lower juvenile survival in females at high density than in males. There is an indication that female mountain hares may tend to be slightly larger and heavier than males (Flux 1970; our study: mean mass ± sd for female = 2.91 kg (± 0.46) and male = 2.58 kg (± 0.33)), although this trend is statistically non-significant. Life-history theory predicts that on the basis of sexual dimorphism in body size, mortality should be higher in the larger sex due to a faster growth rate and higher nutritional demands (Clutton-Brock et al. 1985). However, any trend for greater mean mass or size in female mountain hares would appear to be due to a longer growth period rather than higher growth rate (Iason 1989), and previous studies have not identified female-biased survival (Iason 1989) making this hypothesis unlikely.

Female-biased density-dependent dispersal at high population densities may also lead to fewer juvenile females being observed in the high-density breeding populations when our samples were collected. Density-dependent dispersal has been documented in many species; however, in polygamous species, such as mountain hares, dispersal is usually male-biased (see Matthysen 2005 for a review). Although a study on natal dispersal of mountain hare in Sweden found no evidence for sex-biased dispersal (Dahl & Willebrand 2005), in brown hare *Lepus europaeus*, it was found that males dispersed more frequently, but females on average moved longer distances. However, this sex difference was not affected by population density (Bray et al. 2007), which runs contrary to the idea of female-biased dispersal leading to low proportions of juvenile females at high density.

In red deer *Cervus elaphus*, population density affects the sex ratio of offspring produced (Kruuk et al. 1999). Under nutritional stress, *in utero* mortality of male calves is higher than of female calves. At high population density, competition for resources is greater and so the production is biased towards females, which have a greater probability of survival and reproduction and so increases lifetime fitness of the mother (Kruuk et al. 1999). In mountain hares, prenatal mortality is higher in the first litter when conditions, such as weather, are harsher (Iason 1989). Therefore, it is likely that prenatal mortality will be affected by nutrition. However, there is no evidence of a link between population density and nutritional stress at present, and we found no evidence that prenatal mortality increases with increased population density. Further, it is unknown whether *in utero* mortality differs between the sexes.

In high-density red grouse populations, more young were shot than were expected from pre-shooting grouse counts demonstrating an unintentional harvest bias towards juveniles (Bunnefeld et al. 2009). Unintentional hunting bias in mountain hares could result in more juvenile males being shot at high densities, although this has yet to be tested. A comparison of individuals captured by live traps and individuals flushed into long-nets found heterogeneity in capture probability between capture methods (Bisi et al. 2011).

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However, this study found that adults were more likely caught than juveniles, and females more than males (Bisi et al. 2011), a trend also reported by Flux (1970), countering the notion of male and/or juvenile bias in shooting for mountain hares.

Microclimate and other environmental conditions, such as habitat and vegetation quality and quantity, are likely to differ between sites, years and between successive litters. While it is possible that these uncontrolled, indeed uncontrollable, variables could lead to differences in carrying capacity between the different sites, confounding the effects of population density on vital rates, including fecundity and juvenile recruitment, this was accounted for as far as possible in the GLMM by including site as a random variable. Nevertheless, results of our study should be interpreted in light of this potential limitation.

In conclusion, we found evidence for negative density-dependent juvenile recruitment. Therefore, compensatory juvenile recruitment may be an important factor in the resilience and persistence of harvested mountain hare populations in Scotland. Further research into the effects of population density on nutritional stress, survival rates and dispersal are required to better understand the implications of density-dependent juvenile recruitment for the management of harvested populations. Furthermore, if the number of individuals harvested exceeds the upper limits of compensatory population growth, overexploitation and population decline could occur (Caughley & Gunn 1995). Therefore, for management of harvested populations to be sustainable, the level of harvest should be quantified.

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References

Angerbjörn, A. 1986: Reproduction of mountain hares *(Lepus timidus)* in relation to density and physical condition. - Journal of Zoology (London) 208: 559-568.

Angerbjörn, A. & Flux, J.E.C. 1995: *Lepus timidus*. - Mammalian Species 495: 1-11.

Bates, D. & Maechler, M. 2010: lme4: Linear mixed-effects models using S4 classes. lme 4 Package. - http://cran.r-project.org/web/packages/lme4/index.html (Last accessed on 12 February 2013).

Bisi, F., Newey, S., Nodari, M., Wauters, L.A., Thirgood, S., Harrison, A. & Martinoli, A. 2011: The strong and the hungry: Bias in capture methods for mountain hares *Lepus timidus*. - Wildlife Biology 17(3): 311-316.

Both, C. 1998: Density dependence of clutch size: habitat heterogeneity or individual adjustment? - Journal of Animal Ecology 67: 659-666.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. 1999: Seasonal compensation of predation and harvesting. - Oikos 87: 419-426.

Bray, Y., Devillard, S., Marboutin, E., Mauvy, B. & Peroux, R. 2007: Natal dispersal of European hare in France. - Journal of Zoology (London) 273: 426-434.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001: Introduction to Distance Sampling. - Oxford University Press, New York, New York, USA, pp. 15-17.

Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E.J. 2009: Factors affecting unintentional harvesting selectivity in a monomorphic species. - Journal of Animal Ecology 78: 485-492.

Caughley, G. & Gunn, A. 1995: Conservation Biology in Theory and Practice. - Blackwell Scientific, Oxford, UK, pp. 341-377.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. 1985: Parental investment and sex differences in juvenile mortality in birds and mammals. - Nature 313: 131-133.

Coulson, T., Milner-Gulland, E.J. & Clutton-Brock, T.H. 2000: The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. - Proceedings of the Royal Society B-Biological Sciences 267: 1771-1779.

Dahl, F. & Willebrand, T. 2005: Natal dispersal, adult home ranges and site fidelity of mountain hares *Lepus timidus* in the boreal forest of Sweden. - Wildlife Biology 11(4): 309-317.

Dhont, A.A., Kempenaers, B. & Adiaensen, F. 1992: Density-dependent clutch size caused by habitat heterogeneity. - Journal of Animal Ecology 61: 643-648.

Finger, S.E., Brisbin, I.L., Smith, M.H. & Urnston, D.F. 1981: Kidney fat as a predictor of body condition in white-tailed deer. - Journal of Wildlife Management 45: 964-968.

Flux, J.E.C. 1970: Life history of mountain hare (*Lepus timidus scoticus*) in north-east Scotland. - Journal of Zoology (London) 161: 75-123.

Frylestam, B. & von Schantz, T., 1977: Age determination of European hares based on periosteal growth lines. - Mammal Review 7: 151-154.

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Henderson, B.A. & Bowen, H.M. 1979: A short note: estimating the age of the European rabbit *Oryctolagus cuniculus*, by counting the adhesion lines in the periosteal zone of the lower mandible. - Journal of Applied Ecology 16: 393-396.

Hewson, R. 1976: Population study of mountain hares (*Lepus timidus*) in north-east Scotland from 1956-1969. - Journal of Animal Ecology 45: 395-414.

Iason, G.R. 1988: Age-determination of mountain hares (*Lepus timidus*) - A rapid method and when to use it. - Journal of Applied Ecology 25: 389-395.

Iason, G.R. 1989: Growth and mortality in mountain hares - the effect of sex and date of birth. - Oecologia 81: 540-546.

Iason, G.R. 1990: The effects of size, age and a cost of early breeding on reproduction in female mountain hares. - Holarctic Ecology 13: 81-89.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. 1999: Population density affects sex ratio variation in red deer. - Nature 399: 459-461.

Lande, R., Engen, S. & Saether, B-E. 2003: Stochastic population dynamics in ecology and conservation. - Oxford University Press Inc., New York, New York, USA, pp. 121-138.

Matthysen, E. 2005: Density-dependent dispersal in birds and mammals. - Ecography 28: 403-416.

Newey, S., Bell, M., Enthoven, S. & Thirgood, S. 2003: Can distance sampling and dung plots be used to assess the density of mountain hares *Lepus timidus*? - Wildlife Biology 9(3): 185-192.

Newey, S., Allison, P., Thirgood, S., Smith, A.A. & Graham, I.M. 2010: Population and individual level effects of over-winter supplementary feeding mountain hares. - Journal of Zoology (London) 282: 214-220.

Newey, S., Dahl, F., Willebrand, T. & Thirgood, S. 2007a: Unstable dynamics and population limitation in mountain hares. - Biological Reviews 82: 527-549.

Newey, S., Potts, J., Baines, D., Castillo, U., Duncan, D., Harrison, A., Ramsay, S., Thirgood, S. & Iason, G.R. 2011: Development of a reliable method for estimating mountain hare numbers. - Scottish Natural Heritage Commissioned Report. Report No. 444, 23 pp.

Newey, S., Willebrand, T., Haydon, D.T., Dahl, F., Aebischer, N.J., Smith, A.A. & Thirgood, S. 2007b: Do mountain hare populations cycle? - Oikos 116: 1547-1557.

R Development Core Team 2010: R: A language and environment for statistical computing. - Vienna, Austria: R Foundation for Statistical Computing. Available at: http://www.r-project.org/ (Last accessed on 12 February 2013).

Reynolds, J.C., O'Mahony, D. & Aebischer, N.J. 2006: Implications of 'cyclical' population dynamics for the conservation of Irish hares (*Lepus timidus hibernicus*). - Journal of Zoology (London) 270: 408-413.

Sinclair, A.R.E. 1989: Population regulation in animals. - In: Cherrett, J.M. (Ed.); Ecological Concepts. Blackwell Scientific Publications, Oxford, UK, pp. 197-241.

Sinclair, A.R.E., Fryxell, J.M. & Caughley, G. 2006: Age and stage. - In: Sinclair, A.R.E., Fryxell, J.M. & Caughley, G. (Eds.); Wildlife ecology, conservation and management. Blackwell Science, Oxford, UK, pp. 244-252.

Soutullo, A., Limiñana, R., Urios, V., Surroca, M. & Gill, J.A. 2006: Density-dependent regulation of population size in colonial breeders: Allee and buffer effects in the migratory Montagu's harrier. - Oecologia 149: 543-552.

Sutherland, W.J. 2001: Sustainable explotation: a review of principles and methods. - Wildlife Biology 7(3): 131-140.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. 2010: Distance software: design and analysis of distance sampling surveys for estimating population size. - Journal of Applied Ecology 47: 5-14.

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Appendices

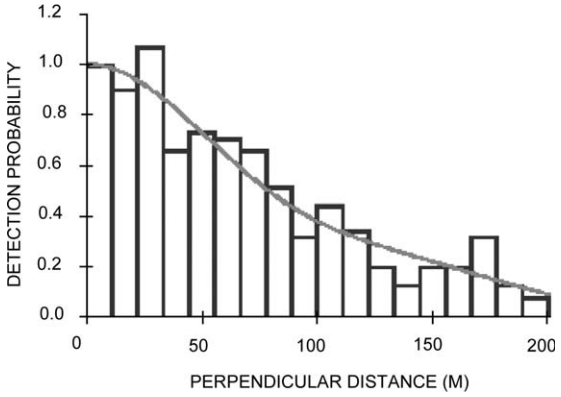
Appendix I

Details of tested models of the distance sampling analysis carried out using a global detection function by pooling data across all sites. The abbreviations are as follows: Key = key term with HN = half-normal and HR = hazard rate; E = expansion term with C = cosine; SP = simple polynomial and HP = hermite polynomial; AIC = Akiake's Information Criteria; ESW = effective strip width; D = density of hares ha^{-1} (global density); LCL = lower 95% confidence limit; UCL = upper 95% confidence limit; CV = coefficient of variation; K-S P = probability (Kolmogorov-Smirnov); and χ^2 P = probability (χ^2).

Key	E	AIC	ESW	D	LCL	UCL	%CV	K-S P	χ^2 P
HN	C	3590.5	95	0.131	0.09	0.180	16	0.956	0.103
HN	SP	3591.1	102	0.121	0.09	0.167	16	0.858	0.090
HN	HP	3593.9	109	0.113	0.07	0.168	20	0.172	0.013
HR	C	3591.1	102	0.121	0.09	0.167	16	0.858	0.090
HR	SP	3591.6	102	0.121	0.09	0.167	16	0.858	0.080
HR	HP	3591.1	102	0.121	0.08	0.181	21	0.858	0.090

Appendix II

The probability of detecting mountain hares decreases with increasing perpendicular distance. The line indicates the detection function as fitted by the half-normal cosine model while the histograms indicate the detection probability of individuals sampled at different perpendicular distances.



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