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Negative density-dependent emigration of males in an increasing red deer population

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In species with polygynous mating systems, females are regarded as food-limited, while males are limited by access to mates. When local density increases, forage availability declines, while mate access for males may increase due to an increasingly female-biased sex ratio. Density dependence in emigration rates may consequently differ between sexes. Here, we investigate emigration using mark-recovery data from 468 young red deer *Cervus elaphus* marked in Snillfjord, Norway over a 20-year period when the population size has increased sixfold. We demonstrate a strong negative density-dependent emigration rate in males, while female emigration rates were lower and independent of density. Emigrating males leaving the natal range settled in areas with lower density than expected by chance. Dispersing males moved 42 per cent longer at high density in 1997 (37 km) than at low density in 1977 (26 km), possibly caused by increasing saturation of deer in areas surrounding the marking sites. Our study highlights that pattern of density dependence in dispersal rates may differ markedly between sexes in highly polygynous species. Contrasting patterns reported in small-scale studies are suggestive that spatial scale of density variation may affect the pattern of temporal density dependence in emigration rates and distances.

Keywords: dispersal; sex bias; local mate competition; local resource competition; ungulates; large herbivores

1. INTRODUCTION

Sex-biased dispersal is very common in animals and may depend strongly on the mating system (Greenwood 1980; Lawson Handley & Perrin 2007). In species with female-defence polygyny, such as in many ungulates, female fitness is limited mainly by food resources necessary for raising offspring, while males are limited more by access to mates (Clutton-Brock *et al.* 1988). For males, access to mates is determined by fighting ability, which in turn is linked to body size (Clutton-Brock *et al.* 1988). A male-biased dispersal pattern is expected when the local mate competition (LMC; Dobson 1982) in males exceeds local resource competition for food (LRC; Greenwood 1980) in females (Lawson Handley & Perrin 2007). Females in such systems are expected to have much lower dispersal rates than males (Greenwood 1980; Dobson 1982; Pusey 1987; Clobert *et al.* 2001) in contrast to weaker dimorphic species with resource-defence tactics (Gaillard *et al.* 2008).

Despite considerable theoretical interest in the form of the density-dependent dispersal function in population regulation (Stenseth & Lidicker 1992; Sæther *et al.* 1999; Travis *et al.* 1999), empirical evidence of density dependence in vertebrate dispersal is comparably scarce (Lambin *et al.* 2001; Bowler & Benton 2005; Matthysen 2005). In polygynous ungulates, an increase in density may decrease fitness differently for females and males, because density-dependent changes in levels of sexual selection are sex

specific (Clutton-Brock *et al.* 1997). While increasing population density leads to intensified local food competition (affecting females more than males), LMC may decrease due to an increasingly female-biased sex ratio (affecting only males). In red deer *Cervus elaphus*, the increasing bias in female : male ratio is caused by density-dependent reduction in male birth rates (Kruuk *et al.* 1999; Mysterud *et al.* 2000) as well as in male relative to female survival rates at all ages (Clutton-Brock *et al.* 2002). In some harvested populations, this pattern can be even stronger because males experience an increased probability of being shot (Langvatn & Loison 1999), resulting in fewer and younger males per female as density increase.

Causes of dispersal are expected to be scale-dependent, since both costs and benefits are likely to depend on the scale of movements (Bowler & Benton 2005). Proximity of suitable patches was decisive for emigration rates in voles (Andreassen & Ims 2001). Detection of a better area may be facilitated by small-scale variation in density, if this results in spatial variation in patch quality at a scale smaller than exploratory searches. On the north block (12 km^2) of Rum, a small island in the Inner Hebrides in Scotland, positive density-dependent dispersal rates were reported for male red deer (Clutton-Brock *et al.* 2002; Fan *et al.* 2003), while female offspring most often settled close to their mother's home range independent of density (Clutton-Brock *et al.* 1988). The strong small-scale density gradient on Rum allows annual excursions from low-density feeding areas to high-density breeding areas. So far, no study has been conducted in areas where red deer are free to operate on much larger spatial scales, with more gentle spatial density gradients.

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We investigated patterns of sex- and density-dependent emigration in an open red deer population in Snillfjord, Norway using mark-recovery data of 468 individuals of both sexes. Over the 20-year period, the population density has increased sixfold at the marking site, and has also affected the geographical distance that dispersers would need to travel in order to reach low-density areas.

2. MATERIAL AND METHODS

(a) *Study area and red deer population*
The study area is Snillfjord municipality in Sør-Trøndelag county at the west coast of Norway. The climate is seasonal (mean January and July temperatures are $-2.2°C$ and $12.9°C$, respectively). During the winter months (December–March), snow cover is normally extensive in high altitude inland areas, but not along the coast. The majority of female red deer migrate seasonally between small winter (coast) and summer (inland) ranges, each area covering only a few square kilometres, but separated by up to 70 km (Albon & Langvatn 1992). The timing of spring migration may vary among years with respect to timing of vegetation green-up (Pettorelli *et al.* 2005). Most individuals move from winter to summer range in April–May and return in September–November, each using from a few days up to three weeks on the migration route. Seasonal migration patterns in males have not been investigated, but preliminary global positioning system (GPS) data on a few males (E. Meisingset, L. E. Loe & A. Mysterud 2006–2009, unpublished data) are indicative of broadly similar timing of seasonal migration as in females. The mating system is defined as temporary harem polygyny (Darling 1937; Clutton-Brock *et al.* 1982). Median calving date is 16 June (Loe *et al.* 2005) and median date of ovulation (and hence mating) is 15 October (Langvatn *et al.* 2004).

(b) *Red deer data*
A total of 773 individuals (355 females and 418 males) were marked as calves (83%) or yearlings (17%) in late winter with coloured and numbered plastic ear tags in the period 1977–1997 at eight different marking sites in Snillfjord (see Albon & Langvatn (1992) for a description of marking method). Altogether 78 calves (31 females and 47 males) died the same winter as they were marked. Since they were together with their mother at that time they were excluded from the analyses (Gaillard *et al.* 2008). Of the remaining individuals, 468 were later recovered dead at a known date (a total recovery rate of 67%), consisting of 180 females (recovery rate: 56%) and 288 males (78%; see figure S1 in the electronic supplementary material for spatial distribution). The higher recovery of males than females was caused by a much higher probability of males being shot by hunters in the annual hunting season from 10 September to 15 November (approx. 50 versus 20% annual probability of being shot in adult males and females, respectively; Langvatn & Loison 1999). Death causes were hunting (95.3%), 'natural' causes, in particular, drowning (1.5%) or killed in traffic (3.0%).

(c) *Potential biases*
A total of 33 per cent of the initially marked animals were not recovered dead. This is a mixture of individuals that are still alive and individuals that are dead but not recovered. We have no information regarding potential spatial variation in the probability of recoveries to be reported.

The impression is that there is great interest in retrieving information on marked animals, regardless of whether they are harvested or found dead. Importantly, a hypothetical bias is not expected to affect the relative difference between sexes in density-dependent dispersal, because any observer is highly unlikely to pay attention to sex or population density when deciding to report a dead marked animal or not. Owing to higher hunting pressure, average age at recovery for males (2.3 years) was lower than for females (5.0 years). This effect is accounted for by including age category of death as a factor in analyses. Also since we report that males dispersed at a higher rate than females, our results are conservative (because females would have had a longer time to disperse). We follow the definition of dispersal being either movement from the natal area (range used by mother prior to weaning) to the breeding area (natal dispersal) or between breeding areas (breeding dispersal) (Clobert *et al.* 2001), and emigration simply as the first step of the dispersal process (Ims & Hjermann 2001; Bowler & Benton 2005), not necessarily as leaving the population. We acknowledge that the nature of our data does not allow for categorization of each single individual as stationary, seasonally migrating, natal disperser or breeding disperser. We used a threshold of 8.7 km to identify dispersers (see below for rationale why we selected this distance), but acknowledge that the estimates of dispersal rates might be biased high due to some individuals returning to wintering grounds after 1 November (the date we chose for plotting predicted emigration rates; selecting a later date was not possible due to limited data later in the year). When discussing male dispersal patterns it is always with the relative difference to females in mind.

(d) *Population density*
As an index for local population density, we used the total number of red deer shot per municipality per year, divided by the area defined as suitable red deer habitat by the management authorities (same area for all years; Mysterud *et al.* 2001). During the study period, the harvest has increased sixfold (figure S2 in the electronic supplementary material; Statistics Norway 2007) indicating a marked population increase. We have recently found a close match between harvest size and the number of deer seen by hunters and population size estimated with cohort analysis (Mysterud *et al.* 2007) This implies that harvest size is an adequate proxy for deer density at the municipality scale (fairly coarse) used in this study. Spatial heterogeneity in resource availability is predicted to affect dispersal (McPeek & Holt 1992; Johst & Brandl 1997). Density may be a poor indicator of resource availability if high density simply reflects higher habitat quality. Body weight of young individuals is a reliable indicator of resource availability in ungulates (Morellet *et al.* 2007). In our study area, there was a negative relationship between body weight in young males and density across municipalities (fig. S3 in the electronic supplementary material). This suggests that in our case, high density was a good proxy for low resource availability. In addition, earlier studies that used number of shot deer as a density index found expected patterns of density dependence in other life-history traits (sex ratio of calves: Mysterud *et al.* 2000; body weights: Mysterud *et al.* 2001; female reproduction: Langvatn *et al.* 2004).

(e) *Statistical analyses*
(i) *Effect of density on emigration*
Defining philopatry versus emigration

Distance from marking site to recovery site had a large peak at zero distance (figure S4 in the electronic supplementary material). This was partly because the most frequently used marking site was also a hot spot for hunting, but also because coordinates of recovery locations were recorded as identical with the coordinates of the marking site for animals shot in the immediate surroundings of this site. We divided the recoveries into two distance categories as recommended by Bennets *et al.* (2001; also done by Gaillard *et al.* 2008). We chose the threshold distance as the median diameter of annual 95 per cent home ranges in seasonally migrating female red deer in another study area at the west coast of Norway (8.7 km; $n=24$; unpublished GPS data). According to this classification, 176 individuals were classified as not emigrating (recovered less than 8.7 km from the marking site; denoted 0) and 292 as emigrants (recovered more than or equal to 8.7 km; denoted 1). This binary response variable was used in analyses of probability of emigration.

Date of recovery

The majority of recovery data consisted of shot deer and was therefore collected in the hunting season where migrating animals could either (i) be in their summer range, (ii) be on their way back, or (iii) already have returned to their winter range (which would be close to the marking site if the animal has not dispersed). It was therefore crucial to incorporate date of recovery and to model it adequately in order to exclude the effect of seasonal migration. We used generalized additive models (GAM; Woods 2006) to flexibly incorporate the relationships between date and distance to marking site (figure S5 in the electronic supplementary material). A cyclic spline function was used because the predicted value is expected to be similar on Julian dates 1 and 365. Splines for each sex were fitted separately to account for potential differences in timing and proportion of seasonal migrants. In addition we fitted a multiplicative $\text{density}_{\text{calf}} \times \text{date}$ term to investigate whether the amplitude of the date-effect changed with density. The latter would be significant if the probability to migrate seasonally was density dependent. This term is important for disentangling the otherwise confounding density-dependent effects of seasonal migration and permanent emigration.

Age at recovery

Age at recovery (death) was modelled as a three-level factor (yearlings, 2-year olds and 3-years and older).

The emigration model

We tested our predictions by fitting a GAM with a logistic link and binomial error distribution (Woods 2006). The response variable was emigration (1 or 0). The following predictor variables were fitted as linear terms: age at recovery; sex; North Atlantic Oscillation$_{\text{utero}}$ (NAO$_{\text{utero}}$); $\text{density}_{\text{calf}}$; and $\text{sex} \times \text{density}_{\text{calf}}$. The remaining three predictor variables were fitted as cyclic splines: intercept for Julian date for males; intercept for Julian date for females; and multiplicative effect of Julian $\text{date} \times \text{density}_{\text{calf}}$ for females. Based on exploratory analyses, the multiplicative effect of Julian $\text{date} \times \text{density}_{\text{calf}}$ for males was not included because it did not appear important in simpler models and because inclusion of this term overparametrized the
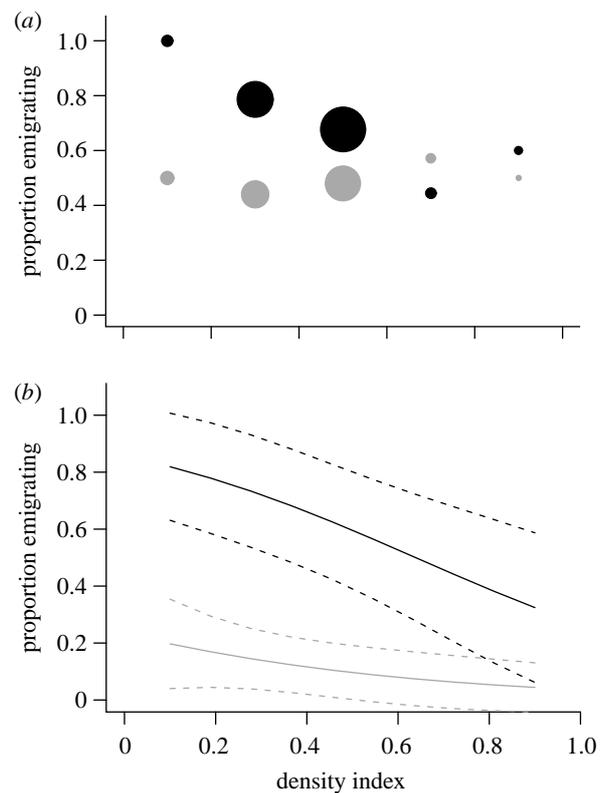
Figure 1. Probability of emigrating (defined as recovery greater than or equal to 8.7 km from the marking site) as a function of population density at marking site in male and female red deer. Figure (*a*) shows raw data where points (black circles, males; grey circles, females) are the proportion of emigrants in five density classes (more than 0.2, 0.21–0.4, 0.41–0.6, 0.61–0.8 and more than 0.8 deer harvested per km^2). The area of the circles is proportional to the amount of data in each category. Figure (*b*) shows predicted values and 95% confidence limits of the proportion emigrating with increasing density accounting for other factors (see the model in §2; black lines, males; grey lines, females). The date for the prediction was set to 1 November, when most seasonal migrants will have returned to their winter site and within the time period where we have most data.

final model. All GAM's were run using the library mgcv in R (R Development Core Team 2008).

In summer, both seasonal migrants and permanent emigrants were away from the winter-marking sites. We therefore plotted predicted values for emigration for a date after the return of the seasonal migrants (figure 1*b*), choosing 1 November which is towards the end of the time interval where we had many recoveries (hunting season). The reason for the seemingly 'discrepancy' between the proportion of emigrants in the raw data (figure 1*a*) and predicted values (figure 1*b*) is precisely due to this. Both permanent and seasonal emigrants were included in the raw data proportions (figure 1*a*), while the contribution from the seasonal migrants was removed in the predicted values (figure 1*b*) by predicting for a date after arrival at the winter marking site (when only permanent emigrants were shot away from marking site). We argue that the reported density-dependent patterns and differences between sexes were most likely caused by sex- and density-dependent natal dispersal in males. When subsetting only individuals marked as calf and recovered before breeding age (less than 3 years; figure S6 in the electronic supplementary material) exactly the same pattern occurred as when using all data (figure 1). This is in line with results from Rum, where the
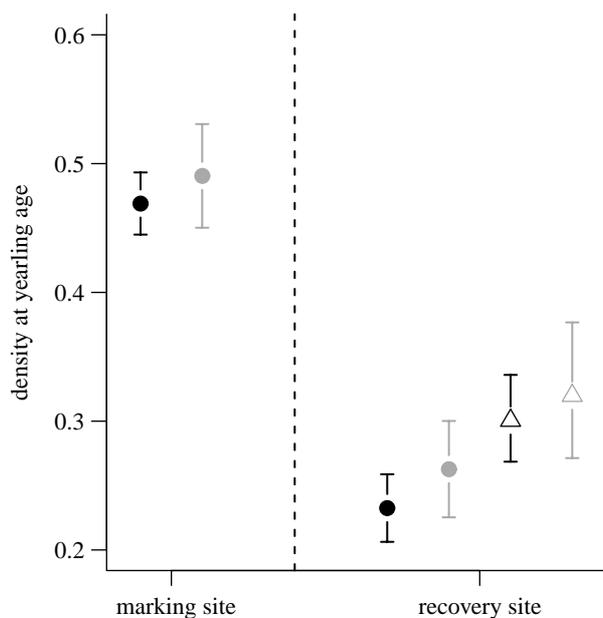
Figure 2. Dispersal in relation to the density gradient in emigrating Norwegian red deer. Mean observed density values at marking site (left in the plot) and at true recovery sites (to the right in the plot) are presented with filled circles (black, males and grey, females). In addition, we present mean density at random recovery locations with triangles (black, males and grey, females; see §2). Error bars are ± 1 s.e for observed density values and 95% bootstrap CI for density values at randomly selected sites.

probability of dispersal in male red deer was very low from calves to the age of 1 year, approximately 15 per cent from 1 to 2 years, 20 per cent from 2 to 3 years and very low above 3 years of age (Fan *et al.* 2003).

(ii) *Settlement 'up' or 'down' the density gradient*

Because marking took place in areas with high deer density, individuals that dispersed in a random direction were expected to end up in areas with lower deer densities. We therefore compared density at actual recovery sites with density at paired, randomly selected sites, constrained on true dispersal distances for individuals classified as emigrants (recovered more than or equal to 8.7 km from the marking site). We maintained the actual transition distance for each individual, but selected a random number (α) from 0 to 359 to simulate a new and random direction for dispersal. From the coordinates of the marking site (X_{mark}, Y_{mark}), the angle (α) and transition distance (d) we calculated the simulated coordinates of death using basic trigonometry ($X_{rand} = \sin(\alpha) \times d + X_{mark}$; $Y_{rand} = \cos(\alpha) \times d + Y_{mark}$). The process was repeated for coordinates ending up in the sea. We ran 1000 iterations of this procedure and present median values together with 2.5 and 97.5 percentiles as confidence limits for density at random recovery sites (figure 2).

3. RESULTS

Emigration rate was overall higher in males than in females (figure 1; table 1). Males were also recovered further from the marking site (median: 21 km; range: 0–147 km) than females (median: 6 km; range: 0–151 km), confirming that males are the dispersing sex in red deer. Density at birth negatively affected the probability of emigrating, but only for males (figure 1; table 1). However, emigrating

males settled in areas with lower density than expected by chance (figure 2). Emigrating males also dispersed 42 per cent longer when born in the high-density phase (37 km in 1997) compared with the low-density phase (26 km in 1977) of the study period (table S1 in the electronic supplementary material). In the same time period, there has been an increasing saturation of red deer in the area surrounding the marking sites (figure S7 in the electronic supplementary material). Two-year old individuals had the highest probability of being recovered away from the marking site, suggestive of a peak in exploratory behaviour at this age (table 1). Emigration probability decreased marginally with the NAO_{utero} (table 1). The strong effect of Julian date confirms the pattern of seasonal migration in this red deer population (table 1, figure S5 in the electronic supplementary material).

4. DISCUSSION

Multiple, ultimate and proximate mechanisms can act simultaneously on the propensity to disperse (Ims & Hjermann 2001; Bowler & Benton 2005). The high level of dispersal in males in our study may be due to LRC (for food) 'pulling' males to low-density areas and/or LMC 'pushing' young males to leave the natal range. The reduction in male emigration rates from 80 to 40 per cent, i.e. negative density dependence, suggests changes in the relative strength of these ultimate factors as density increased over time. Further, emigrating males increased dispersal distances when density increased, i.e. positive density dependence, and settled in lower density areas.

Empirical evidence of density-dependent dispersal in vertebrates is not only fairly scarce, but also difficult to compare because variation in density occur at different temporal and spatial scales (reviews in Clobert *et al.* 2001; Bowler & Benton 2005; Matthysen 2005). Density dependence in dispersal does not always occur. It was reported in only 16 out of 29 bird studies (Matthysen 2005) and was absent in some studies of small (Rodgers 1990; Hanski *et al.* 1991) and medium-sized mammals (Boutin *et al.* 1985; Holekamp 1986), in large herbivores (Gaillard *et al.* 2008) and in large carnivores (Gese & Mech 1991; Zedrosser *et al.* 2007). A positive relationship between dispersal and density has been reported in birds (13 out of the 16 studies showing density dependence; Matthysen 2005), in lizards (Lena *et al.* 1998), in small rodents (Barash 1973) and in ungulates (Clutton-Brock *et al.* 2002; Fan *et al.* 2003; Catchpole *et al.* 2004). However, despite the overall conclusion of Matthysen (2005), dispersal is also frequently negatively density dependent, as reported for birds (Delestrade *et al.* 1996; Wiklund 1996), small mammals (Lambin *et al.* 2001; Ims & Andreassen 2005) and bears (*Ursus arctos*) (Swenson *et al.* 1998; Støen *et al.* 2006). For small mammals, the frequency of aggressive encounters with other conspecifics outside the natal patch increase with density, the so-called social fence hypothesis (Hestbeck 1982). In these species, heavy individuals more often disperse because they have the best fighting abilities. In species where direct aggressive encounters outside the breeding season are rare, such as in red deer, large-scale movement is unlikely to be inhibited by conspecifics (Ims & Hjermann 2001). Consistent with such a view, body weight is not a predictor of dispersal in

Table 1. Parameter estimates of the model predicting emigration of red deer in Snillfjord, Norway. (The response variable is emigration (1) or philopatry (0), i.e. recovery farther away or closer than 8.7 km from the marking site. The model was fitted with a GAM with a binomial link function. All predictor variables were fitted as linear parameters except date and the multiplicative term date×density (females only), which were fitted with cyclic spline function separately for each sex. For the effect of sex, males were the contrast. For the age effect, adults (3 years and older) were the contrast. R^2(adj) = 0.26; deviance explained = 23.8%; n = 468.)

parametric coefficients	estimate	s.e.	lower 95% CI	upper 95% CI
intercept	2.544	0.559	1.449	3.639
sex (females–males)	−3.272	0.759	−4.760	−1.783
density as calf	−2.804	1.113	−4.986	−0.622
age dead (yearling–adult)	−0.239	0.294	−0.816	0.338
age dead (2-year–adult)	0.711	0.290	0.143	1.280
NAO in utero	−0.168	0.065	−0.295	−0.042
sex (females–males) × density as calf	4.573	1.666	1.309	7.838

approximate significance of smooth terms	edf	est. rank	χ^2	p-value
intercept Julian date at death for males	5.421	8	47.21	<0.001
intercept Julian date at death for females	0.000280	1	1.22	0.269
multiplicative term (Julian date of death × density) for females	2.103	5	30.70	<0.001

red deer (Fan *et al.* 2003). Our study represents, to our knowledge, the first strong evidence of a negative relationship between emigration rate and temporal density variation in ungulates, and provides further evidence that dispersal patterns often are sex specific as frequently reported in the mammal literature.

Two partly opposing spatial requirements may affect dispersal decisions in male ungulates, which in turn may suggest a key role for spatial scale when interpreting dispersal and density relationships. Particularly at young ages before main reproductive activities, male ungulates are expected to choose areas enabling foraging efficiency to maximize body growth to achieve the size required for successful reproduction in combat with other males (Clutton-Brock *et al.* 1988). This suggests avoidance of high-density areas and a key role for LRC at this life stage. There were marked density effects on growth rates of males in the study area (Yoccoz *et al.* 2002; Mysterud *et al.* 2008), and the assumption for LRC is therefore likely to be met. Emigrating male red deer were indeed recovered in areas with lower density than expected by chance (figure 2), probably reducing LRC as reported for small rodents (Aars & Ims 2000). However, when reaching main breeding age, males should rut in areas with the highest number of available mates after accounting for the number and body size of other males (LMC). With increasing density in red deer populations in Norway, a male-biased harvesting strategy has yielded a higher female : male ratio and lower mean age of males (Milner *et al.* 2006). Young males synchronized their mating effort with older males only at high density suggesting increased access to mates for young males and thus a density-dependent relaxation in the strength of sexual selection (Mysterud *et al.* 2008). It may therefore be beneficial for males to rut in high-density areas. A similar pattern is found in insects, where male emigration rate increased with male-biased sex ratio (Lawrence 1987, 1988).

The decision to disperse may therefore require the integration of information from both LRC and LMC in the natal range versus explored areas. Exploratory movement prior to dispersal is common in mammals (e.g. red squirrels, *Tamiasciurus hudsonicus*: Larsen & Boutin 1994; roe deer, *Capreolus capreolus*: Van Moorter *et al.* 2008), and 2-year old male red deer were recovered further from the marking site than both younger and older individuals (table 1), suggesting a peak in exploratory ranging behaviour in red deer at this stage. Results from experimental tundra vole, *Microtus oeconomus* populations, subjected to detailed manipulation of temporal and spatial density variation, seems particularly relevant to our study (Aars & Ims 2000; Andreassen & Ims 2001; Ims & Andreassen 2005). Interestingly, dispersal rate was highest between the closest subpopulations and it dropped steeply with increasing distance (Andreassen & Ims 2001), suggesting that geographical distance and lack of information of conditions beyond explored areas may play a role. In red squirrels, the degree of exploration was positively related to the quality of the home range where they later established (Larsen & Boutin 1994), and the lizard *Anolis aeneus* obtained more exclusive home ranges when detecting and settling in low-density areas (Stamps & Krishnan 1998). The prediction would thus be that the relationship between temporal density variation and emigration rate would depend on the strength of contrasts in spatial density within exploration range. This is exactly what we see. For red deer born in the 12 km² large north block on Rum where harvest maintains a much lower density outside the study area just a few kilometres away, young males emigrated more frequently as local density rose (Clutton-Brock *et al.* 2002; Fan *et al.* 2003). In Norway, there was an opposite trend. Here, the mean densities within the exploratory range around marking sites increased markedly during the study, and a deer consequently had to travel further from the marking site to reach low densities (figure S7 in the electronic supplementary material). The few Norwegian red deer males that left moved 42 per cent longer in the high-density period during the late 1990s than in the low-density period during the late 1970s. Our study suggests that reduced emigration of males arose due to a decreased probability

of finding new sites with substantially better foraging conditions than the natal site on their exploratory excursions, i.e. a relaxation in the 'pull' from LRC. This was possibly accompanied by a decreased 'push' caused by relaxation in LMC due to improved local access of female mates.

Our study demonstrates that patterns of temporal density dependence in emigration rate and distance may differ between sexes, and suggests that the spatial scale of density variation may affect the pattern of temporal density dependence in emigration rates and distances.

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