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Diversionary feeding of red fox in spring increased productivity of forest grouse in southeast Norway

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In Eurasia, forest grouse have been declining throughout most of their geographical ranges. Presumably, poor recruitment due to high predation of nests and chicks is one important causal factor. In a southeastern Norwegian forested landscape (Fjella), we provided diversionary food to predators – directed mainly at the red fox *Vulpes vulpes* – during the nesting and early brood season of capercaillie *Tetrao urogallus* and black grouse *T. tetrix* in three nearby areas. In Eidsberg, where populations were censused during 33 years (1985–2017), food was provided during the last 22 years. In two other areas, a six-year experimental program was conducted (2003–2008) by providing food in one area for three years, then switching feeding to the other area for three years. During May and June, 10 kg of food – mainly moose offal and ungulate carcasses – was deposited at feeding stations once a week. In Eidsberg, black grouse breeding success increased by 43% after feeding was initiated, mainly due to larger brood sizes. In capercaillie, overall breeding success tended to increase, solely due to more females successfully rearing chicks. In the experimental areas, feeding increased breeding success an estimated 57% in black grouse. In capercaillie there was also a tendency for a positive effect, but sample sizes were too small for statistical inference. No increases were detected in adult birds. However, in capercaillie, increased breeding success after feeding led to a significant skew in sex ratio favouring males. A similar tendency in black grouse suggested source–sink dynamics and a net loss of young females during natal dispersal. We conclude that diversionary feeding of foxes in spring and early summer might be a feasible management tool to increase the reproductive output in local grouse populations, but that it needs to be implemented on a larger scale in order to improve breeding numbers.

Keywords: black grouse, boreal forest, capercaillie, predator control, reproduction

In Europe, many populations of forest grouse have been on a declining trend during the last decades (Storch 2007), with poor recruitment of chicks inferred as one important causal factor (Moss et al. 2001, Baines et al. 2004, 2016, Ludwig et al. 2008). A wide range of scavengers and predators are known to depredate eggs of ground nesting birds (Söderström et al. 1998), but there is a general consensus that mammals – especially red fox *Vulpes vulpes* (hereafter fox) and pine marten *Martes martes* – are the most important predators of nests and young chicks of forest grouse in Fennoscandia (Marcström et al. 1988, Kurki et al. 1997, Storaas et al. 1999, Wegge and Kastdalen 2007, Wegge and Rolstad 2011, Jahren 2012).

Forest grouse are highly praised game species. To increase chick production and increase bird numbers for hunting, predator control – aimed mainly at fox, pine marten and corvid birds – has been widely conducted (Reynolds and Tapper 1996, Tapper et al. 1996, Coté and Sutherland 1997, Smith et al. 2010, Fletcher et al. 2013). Marcström et al. (1988), Kauhala et al. (2000) and Summers et al. (2004) all showed that strong reduction of predators increases reproductive performance in grouse. However, only Marcström et al. (1988) reported that increased breeding success had a positive effect on the number of breeding adult birds.

Predator control as a management tool is both labour intensive, costly and to some degree controversial (Reynolds and Tapper 1996). Also, if it results in increased populations of non-target predators, this may counteract the effort. Providing supplemental food is another way to improve species' viability and abundance or to reduce human–wildlife conflicts (Conover 2002). An alternative approach is the use of diversionary feeding. Diversionary feeding is a special form of supplemental feeding, defined as the use of food to divert the activity or behaviour of a target species from certain actions, without the intention of increasing the density of the target population (Kubasiewicz et al. 2016).

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The most common type of diversionary feeding is to offer alternative crops or set up feeding stations to divert herbivores from commercially important field crops, or to keep them away from roads and railways to prevent accidents (Conover 2002, Andreassen et al. 2005). Feeding predators to increase populations of important game or threatened species is a different type of diversionary feeding. This method has been used to reduce nest predation in waterfowl by striped skunk *Mephitis mephitis* in the US (Crabtree and Wolfe 1988, Greenwood et al. 1998), to reduce predation on red grouse *Lagopus l. scotica* from hen harrier *Circus cyaneus* in the UK (Redpath et al. 2001), and to reduce predation on roe deer *Capreolus capreolus* fawns by foxes in Sweden (Nordström et al. 2009). Lindström et al. (1987) tried out diversionary feeding to test if they could prevent generalist predators – with rodents as their main prey – from turning to forest grouse nests and broods as their alternative prey during a small rodent crash-year (a test of the alternative prey hypothesis, Hagen 1952, Lack 1954, Angelstam et al. 1984). Breeding success remained stable where food was provided and decreased in the control areas.

Forest grouse nest in a wide range of habitat (Storaas and Wegge 1987) and tests with trained dogs have shown that nests are difficult to detect by scent (Storaas et al. 1999). From their low predictability and detectability, it has been hypothesized that mammalian predators do not actively search for grouse nests but find them mainly by chance (Storaas et al. 1999). Other studies of nest predation in waterfowl and grasslands birds lend support for this hypothesis (Crabtree and Wolfe 1988, Vickery et al. 1992). By offering a stable supply of food at predictable feeding stations, diversionary feeding presumably should make predators spend less time searching for natural food and thereby reduce encounters with nests. The same general line of reasoning goes for young broods, although finding them is easier due to detection by scent, and a higher predictability (Storaas et al. 1999).

In the mid-1990s, populations of capercaillie and black grouse in our study area (Fjella) in south-eastern Norway had been declining for several years. To stop this trend, and preferably increase the populations, we looked for alternative ways to increase the recruitment of young birds. Inspired by the successful experiment of Lindström et al. (1987), we started a diversionary feeding program in one part of our study area in 1996. The program was later expanded with experimental work in two nearby parts of the same general area.

The main objective of this study was to assess whether diversionary feeding of predators could increase the breeding success of the two sympatric species of forest grouse. Breeding success is here defined as the net production of chicks per adult female, recorded in August before brood-break up. Secondly, we wanted to examine whether a possible increase in breeding success would increase the abundance of adult birds.

Study area

The study was conducted in the greater Fjella area (59°30′N, 11°30′E) encompassing 240 km^2 of contiguous conifer forest in Østfold county of south-eastern Norway (Fig. 1). Surrounded by agricultural landscapes to the north, west and partly east, it is subdivided in three municipalities, Eidsberg, Marker and Rakkestad, hereafter called sub-areas. Bioclimatically, it is located at the border of the southern boreal and boreonemoral zone (Abrahamsen et al. 1977). The landscape is characterized by rugged and undulating hills 150–300 m a.s.l, where low productive forest of Scots pine *Pinus silvestris* dominates. Mixed forest of pine and Norway spruce *Picea abies* and pure spruce forest occur on hillsides and lower valleys. Ericaceous shrubs dominate the field layer on ridges and hillsides, with various species of forbs and graminoids more common at lower elevations. The forested area has been subject to commercial forestry for centuries, however, mostly by means of small-scale, high-grading logging. After 1950, clearcutting became the main harvesting regime, but cutting blocks are typically fairly small (<10 ha). The natural variation in productivity and topography makes the forest a fine-grained mosaic of different tree compositions and forest age.

Potential mammalian predators on grouse are fox, pine marten, badger *Meles meles* and stoat *Mustela erminea*. During the first half of the 1980s, an outbreak of the sarcoptic mange disease *Sarcoptes scabiei* drastically reduced the fox population regionally (Lindström et al. 1994, Smedshaug et al. 1999), from which it later partly recovered (Fig. 6). Among avian predators, raven *Corvus corax* and jay *Garrulus glandarius* are common along with raptors like sparrowhawk *Accipiter nisus* and common buzzard *Buteo buteo*. Goshawk *Accipiter gentilis* breeds regularly, but at rather low density. Black grouse and capercaillie are common but hazel grouse *Bonasa bonasia* is rare and was not included in this study. All three sub-areas are situated approximately at the same distance from farmland with similar predator communities.

To strengthen the statistical analysis, the grouse census data from Eidsberg, the sub-area with the longest series of census data, was compared with a similar long-term census series from the Varaldskogen area (60°10′N, 12°30′E) located 90 km northeast of Fjella. Varaldskogen has slightly lower temperatures and topography is less rugged. Fauna and flora are similar, but grouse densities are slightly lower (Wegge and Rolstad 2011, 2017).

Material and methods

Grouse census

Using well-trained pointing dogs, grouse were censused in August during 1985–2017 in the Eidsberg sub-area (34 km^2) and during 2003–2008 in the Marker (38 km^2) and Rakkestad (32 km^2) sub-areas (Fig. 1). Man-dog teams searched opportunistically for birds within pre-defined, non-overlapping sections of the sub-areas where they recorded species, sex and age (adult or chick) and number of chicks in broods of flushed birds. Numbers of counted birds per 10 h effective census work were used as an index of density. Newly logged clearcuts were avoided. Apart from that, no particular habitat was sought out during the surveys. As both man-dog teams and habitat changed over the 33-year period, census routes did vary, but the same parts within each study area were sampled in successive years. Within the sub-areas, census sections were placed randomly with respect

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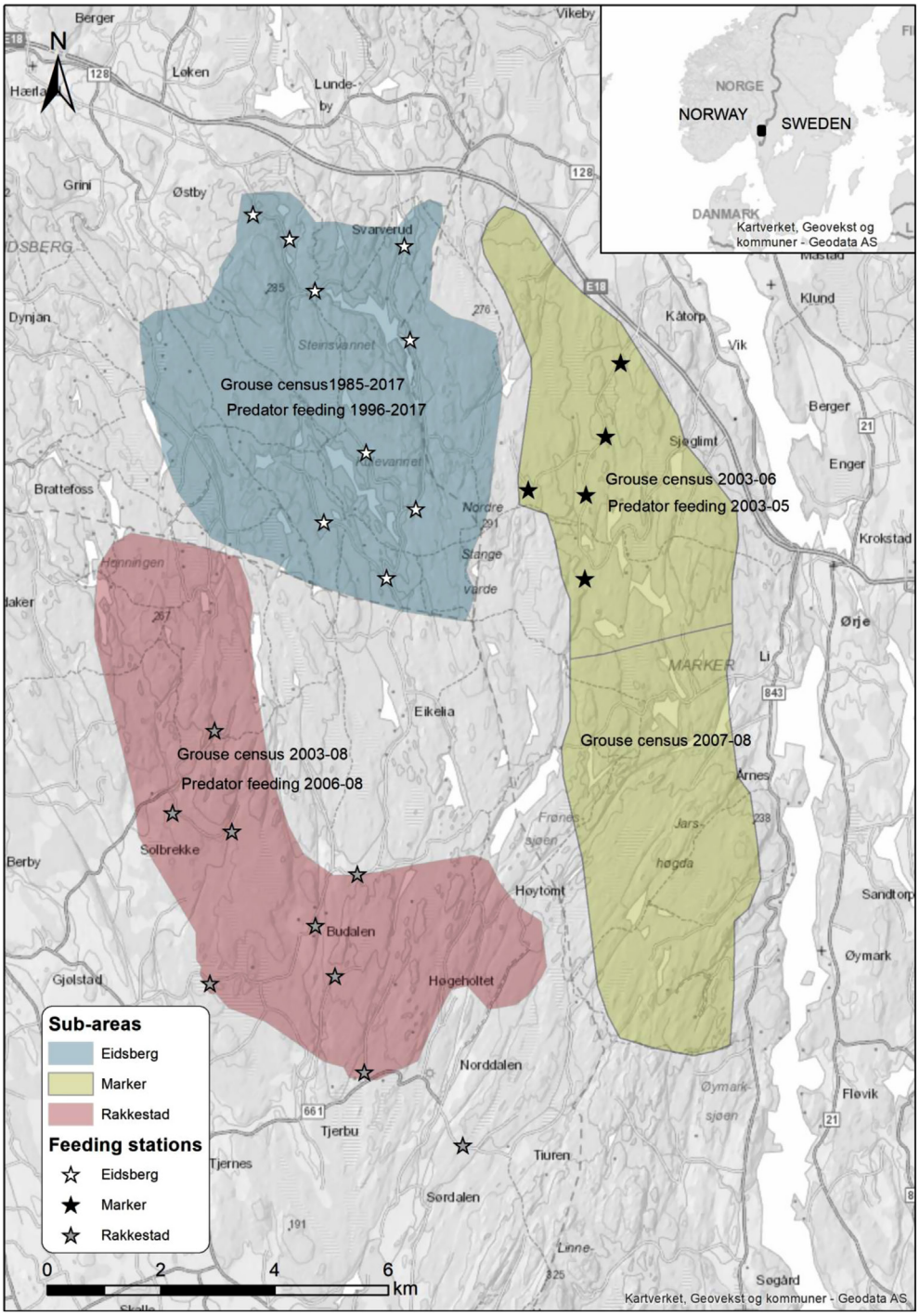


Figure 1. The Fjella study area with the three sub-areas Eidsberg, Marker and Rakkestad. The long-term census of grouse (capercaillie and black grouse) was conducted in the Eidsberg sub-area during 11 years of non-feeding (1985–1995) and 22 years of diversionary feeding of predators (1996–2017). The short-term feeding experiment was conducted in the Marker and Rakkestad sub-areas during 2×3 years in 2003–2008. Feeding stations are shown with stars. In the Marker sub-area, censusing was conducted in the northern part (where the feeding stations were located) in 2003–2006, and in the southern part in 2007–2008.

to the location of feeding stations, except in Marker in 2007 and 2008, when sampling was carried out some distance south of the feeding stations. In all three sub-areas, two–four man–dog equipages conducted on average 78 (SD = 27.6) h of census work each year and recorded on average 32.0 (SD = 19.2) black grouse females and 28.7 (SD = 12.34) capercaillie females annually. Based on total time spent censusing (78 h year^{-1}), estimated walking speed while surveying (2 km h^{-1}) and estimated effective strip width of the man–dog teams (80 m, M. Kjønsberg unpubl. mat. based on Distance sampling with pointing dog), approximately 15% of the sub-areas were thoroughly covered each year. The same general sampling method was applied at Varaldskogen during 1979–2017 (reported in Wegge and Rolstad 2011, 2017).

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Predator feeding

Diversionary food was distributed at nine stations within the Eidsberg sub-area (2.7 stations per 10 km^2) in the period 1996–2017, at five stations in Marker (2.8 stations per 10 km^2, in the northern part) in 2003–2005, and at eight stations in Rakkestad (2.5 stations per 10 km^2) in 2006–2008 (Fig. 1). For easy access, stations were located along forest roads. Furthermore, location of feeding stations was a compromise between the vicinity to predator hotspots (e.g. known fox dens), and distance to public places (forest trails, cabins) to avoid odour nuisance. Because of these considerations, feeding stations were not perfectly spread out within the study areas. Approximately 10 kg of meat was provided to each station once a week. The food consisted mainly of moose offal from the hunting season, roe deer and moose carcasses from traffic deaths, sheep carcasses from a local farm and some fish (caught in local lakes). Altogether, approximately 80 kg of food was deposited at each station per year. To minimize the risk of a numerical response in the local fox population, e.g. an increase in number of fox territories or increased litter sizes, we kept the period of feeding as short as possible; 1 May–30 June. The feeding period coincided with the time of grouse incubation and the first three–four weeks after hatching, when broods are most vulnerable to predation (Wegge and Kastdalen 2007).

As the nutritional needs of a fox-vixen with cubs are largely unknown (Nordström et al. 2009), we decided to place a 'large amount' of meat at each station so that an over-abundance of food was supplied for the local foxes. All the meat was normally removed quickly, and we suspected that the visiting foxes cached some of the food.

To assess which predator consumed the food, we monitored eight stations in the Eidsberg sub-area with camera-traps (Uovision UV 565, IR black led flash). During 12 monitoring sessions of an average of 28.5 days in 2013–2017, foxes were most frequently photographed (9 of the 12 sessions, Table 1), together with jay (4 of 12 sessions). Since we had indications that foxes avoided the camera-surveyed feeding stations, we reduced camera-monitoring to a minimum. From the small sample of camera-trapping and the observation that large bones and meat all disappeared from the feeding stations, we feel confident that foxes removed most of the food from the stations.

Experimental design

After some years, the feeding program in Eidsberg appeared to have had a positive effect on the reproductive output of the two species of grouse. Thus, we decided to expand the study to include an experimental setup involving the two other sub-areas – Marker and Rakkestad – within the greater Fjella area (Fig. 1). During the first three-year period (2003–2005), predators were supplied with food in Marker, leaving Rakkestad as a control area. During the next three years (2006–2008) we switched areas, and predators were supplied with food only in Rakkestad. Unfortunately, a controversy with a local landowner forced us to monitor grouse further south in Marker during the last two non-feeding years (2007–2008) (Fig. 1). The area to the south was similar to the northern part in all major aspects (size, habitat composition, topography and anthropogenic influence). This happened when Marker served as a control area, thereby reducing the risk of bias in the experiment. Type and amount of food given in the two experimental areas was the same as in Eidsberg.

Fox abundance, small rodents and temperature

Due to longer periods with little snow, the abundance of foxes could not be reliably assessed from snow tracking indices. Monitoring by means of sampling scats on forest roads (Baines et al. 2013) was also not feasible due to capacity constraints. Instead, we present hunting statistics from the adjacent farmland 3–5 km north of the study area (1998–2016). For the regional trend in the fox population we present hunting statistics at the county level (Østfold).

Fluctuating populations of small rodents may influence diversionary feeding by decreasing possible effects in peak years and strengthen the effects in small rodent crash years. Therefore, we sampled small rodents by snap trapping in August–September during 1993–2007 and 2014–2017 (300 trap-nights per year).

In a recent study at Varaldskogen, Wegge and Rolstad (2017) showed that breeding success of both capercaillie and black grouse was enhanced during warmer springs and summers. Hence, a warming temperature trend is likely to have affected the breeding success also in our study area, thus necessitating an assessment of this factor in addition to diversionary feeding. Climate data were downloaded from Rygge meteorological station, 45 km southwest of the study area (The Norwegian Meteorological Institute, <www.met.no>). We used the average daily minimum temperature during April, May and June, as this correlated best with breeding success in both species (Supplementary material Appendix 1 Table A1).

Statistical analyses

We modelled the Eidsberg census data using generalized least square regression with annual values of breeding success (chicks per female), brood frequency (proportion of females with broods), and average brood size (number of chicks in broods) as response variables. Chicks per female and brood size were log-transformed, and we used a quadratic term to normalize brood frequency. We used a Gaussian (identity) variance structure since the first- and second-year autocorrelations were negligible (acf <0.2). We tested for possible

Table 1. Frequency of visiting scavengers during 12 monitoring sessions and 343 monitoring days in the period 2013–2017 in the Eidsberg sub-area (Fig. 1).

	Fox	Badger	Unknown mammal	Raven	Common buzzard	Jay	Hooded crow
No. (%) of days with visits (n = 343)	31 (9.1%)	7 (2.0%)	1 (0.3%)	5 (1.5%)	12 (3.5%)	20 (5.8%)	6 (1.8%)
No. (%) of sessions with visits (n = 12)	9 (75.0%)	1 (8.3%)	1 (8.3%)	2 (16.6%)	1 (8.3%)	4 (33.3%)	2 (16.6%)

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effects of diversionary feeding using years with feeding and no feeding as a bivariate explanatory variable; this way, the regression coefficient (slope) represents the effect size, i.e. the relative difference (ratio or percentage) of feeding versus non-feeding years. To control for higher temperatures in the feeding period, we included average minimum April–June temperature as a covariable in a multiple regression model and present the residuals to represent the partial difference between feeding and no-feeding years when temperature was accounted for.

Although partial residuals can be a useful diagnostic tool in multiple regression, they may fail to indicate proper relationships when explanatory variables are highly correlated. As this was the case in our model with feeding and temperature, we supplemented the statistical inference of the temperature-corrected Eidsberg series with a comparative study involving an independent census series of grouse from Varaldskogen to serve as a control area (offset in the model) with no diversionary predator feeding (Wegge and Rolstad 2017). Varaldskogen experiences the same year-to-year variation in temperature regime as Eidsberg, although the average temperature is slightly lower. Small rodents and insect larvae, which are influential covariables, also fluctuate in the same general manner (Supplementary material Appendix 1 Table A2), although the year-to-year amplitude of the rodent fluctuations has been higher at Varaldskogen (Wegge and Rolstad 2018). For each successive year, we calculated the relative difference (ratio) between Eidsberg and Varaldskogen. Based on the annual log-ratio indices as independent sampling units, we tested for relative difference (ratio of ratios) between feeding and no-feeding years at Eidsberg using the same generalized least square regression models. The influence of small rodent cycles was tested by correlating the relative difference in breeding parameters between Eidsberg and Varaldskogen with the small rodent trapping index during the predator feeding period at Eidsberg (1996–2017).

In the Marker–Rakkestad experiment, we also used annual average values as independent sampling units. Small annual samples (especially in capercaillie) restricted the possibility for statistical inference, so we combined the two three-year periods (when feeding area was switched), pooled the six years, and checked for differences using simple t-tests on the annual log-ratio values between feeding and non-feeding averages. Similar to the analysis of the Eidsberg series, log-transforming the response variable ensured that we got the relative difference (ratio) between feeding and no-feeding periods.

We wanted to see if possible higher breeding success was followed by increasing numbers of breeding birds in subsequent years. Potential trends ($\beta \neq 0$) in adult male and female grouse were tested by regressing number of adult birds against running number of years, including the year prior to when feeding was started. Similarly, we tested if the sex-ratio changed by regressing the log-ratio of adult males versus females against year after feeding.

Calculations were done using R (<www.r-project.org>), S+ (TIBCO Software Inc.) and Statview (SAS) software. We considered differences at $p < 0.05$ statistically significant and $0.05 < p < 0.10$ as marginally significant or tendencies.

Results

Eidsberg: temperature controlled

Both capercaillie and black grouse had higher breeding success in the period when predators were supplied with food (1996–2017) than in the previous period (1985–1995) (Fig. 2a–b, Supplementary material Appendix 1 Table A3). Expectedly spring and early summer temperature was also higher in the years with feeding (Fig. 2c) implying that breeding success correlated with temperatures in both species (Supplementary material Appendix 1 Table A1).

After controlling for increasing temperature, brood frequency improved by 23% in capercaillie after diversionary feeding was initiated ($p = 0.047$), but brood size was unaffected (Fig. 3b–c). Although overall breeding success increased by 45%, this was only marginally significant ($p = 0.089$) due to large year-to-year variation (Fig. 3a). After controlling for temperature in black grouse, overall breeding success was significantly higher (43%) in feeding years ($p = 0.037$). Opposite to capercaillie, feeding resulted in 32% increase in brood size ($p = 0.012$), but not in higher brood frequency (Fig. 3d–f).

At Eidsberg, the breeding success of capercaillie correlated positively with the small rodent index ($p = 0.003$). Correlation was marginally significant in black grouse ($p = 0.070$). However, no relationships were found between the small rodent index and the effect of diversionary feeding

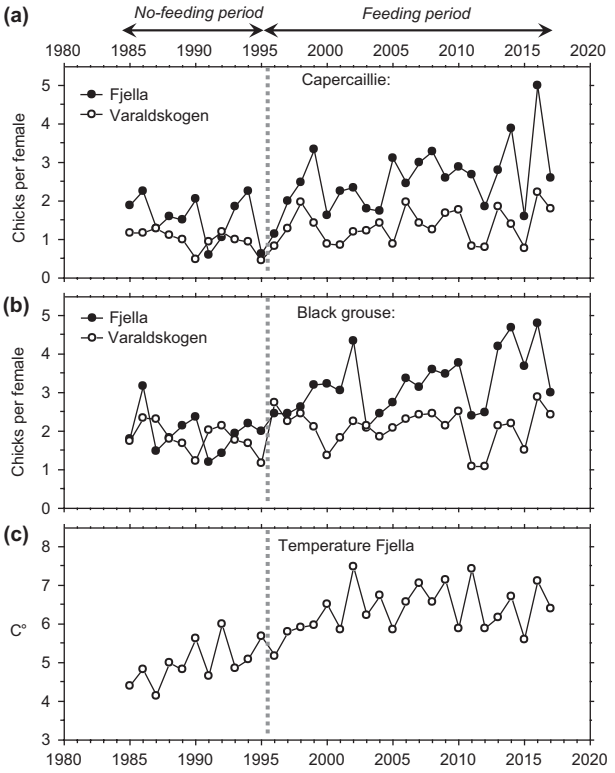


Figure 2. Breeding success (chicks per female) of capercaillie (a) and black grouse (b) in the Eidsberg sub-area (●) and the Varaldskogen control area (○) during periods of no-feeding (1985–1995) and feeding (1996–2017) in Eidsberg, shown together with (c) average minimum daily temperatures during April, May and June in Eidsberg.

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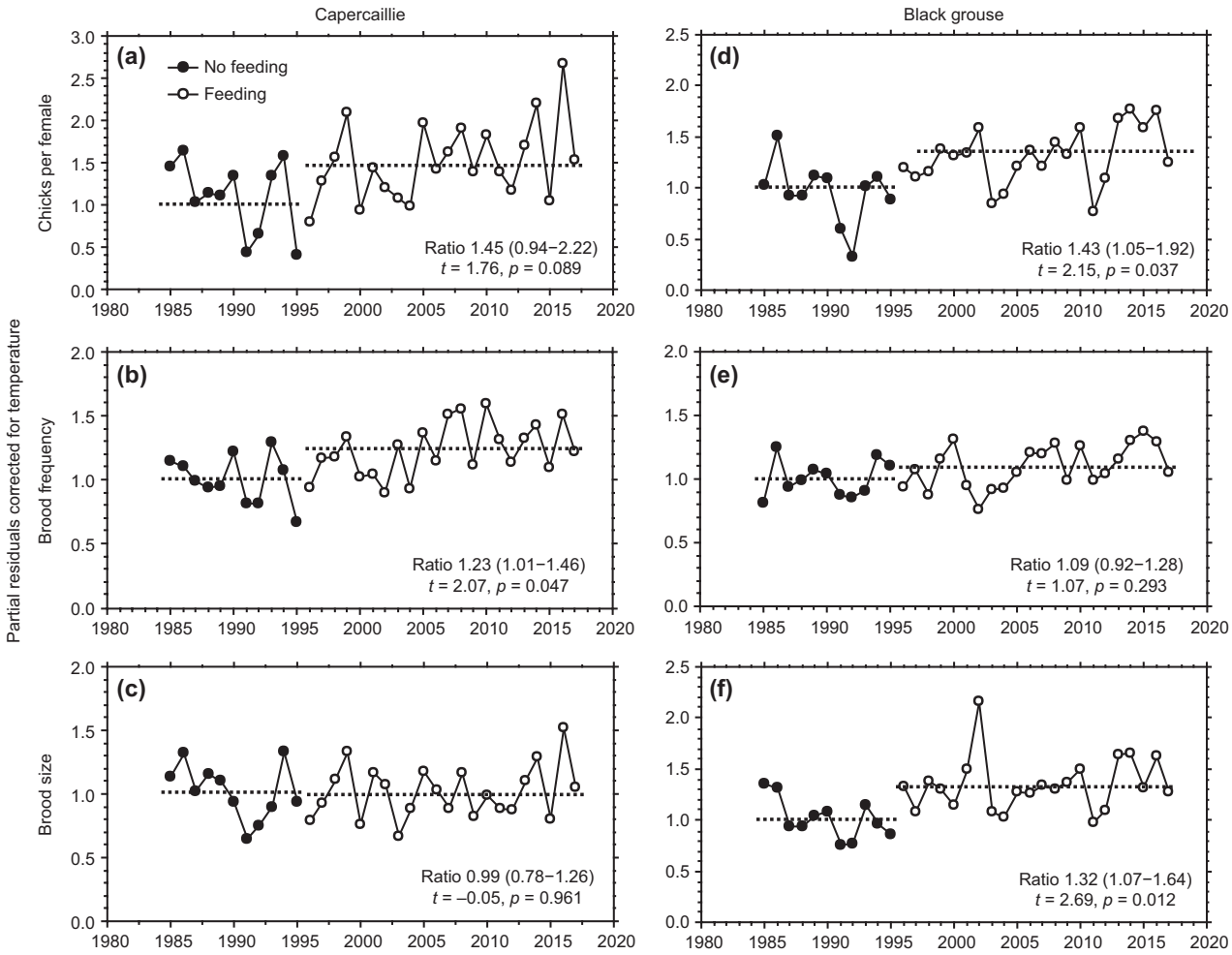


Figure 3. Comparison of breeding success (chicks per female), brood frequency (broods per female) and brood size (chicks per brood) of capercaillie (a–c) and black grouse (d–f) in the Eidsberg sub-area during the early period of no feeding (●: 1985–1995) and the latter period of diversionary feeding (○: 1996–2017) after temperature was corrected for in a multiple regression analysis. Differences are shown as average relative change (hatched lines) from the no-feeding to the feeding period where the partial residuals are set to 1 in the no-feeding period. Confidence intervals of the ratios (feeding/no feeding values) and significance tests are shown in lower right corners.

on breeding performance of black grouse or capercaillie (Supplementary material Appendix 1 Table A6).

When checking if the increased breeding success after feeding resulted in higher numbers of breeding adults within the Eidsberg sub-area, we recorded a weak increase in adult males and a weak decrease in adult females. None of these were statistically significant, although capercaillie males tended to increase ($p = 0.060$, Fig. 4). Due to these opposite trends, the sex ratio changed in favour of males after feeding was initiated, significantly so in capercaillie (male/female log-ratio: $\beta = 0.085$, $t > 2.97$, $p = 0.007$), and marginally significant in black grouse (male/female log-ratio: $\beta = 0.033$, $t > 2.01$, $p = 0.058$).

Eidsberg: Varaldskogen comparison

Overall, the patterns resulting from using the Varaldskogen census series as an offset to Eidsberg supported the results from the temperature-controlled analysis of the Eidsberg series. When the Varaldskogen series was controlled for, breeding success of black grouse increased an average 44% after feeding was initiated at Eidsberg ($p = 0.005$), mostly due to increased brood size (31%, Fig. 2b, 5d–f, Supplementary material Appendix 1 Table A4). In capercaillie, positive effects of diversionary feeding were less pronounced with effect sizes of 26 and 19% for overall breeding success and brood frequency, respectively, none of which were statistically significant due to rather large year-to-year variation (Fig. 2a, 5a–b). Similar to the temperature-controlled analysis, there was no effect of feeding on capercaillie brood size (Fig. 5c).

Experimental areas Marker–Rakkestad

In the two experimental sub-areas (Marker and Rakkestad), there were too few broods to allow for statistical comparisons of the separate three-year periods. When samples were combined over all six years, (i.e. pooling the data where diversionary food was provided versus data from the control areas), black grouse experienced higher breeding success (57%, $p = 0.043$) in years when diversionary food was provided (Table 2, Supplementary material Appendix 1 Table A4). This was mainly due to higher brood frequency (33%, $p = 0.001$), as opposed to the results from the Eidsberg

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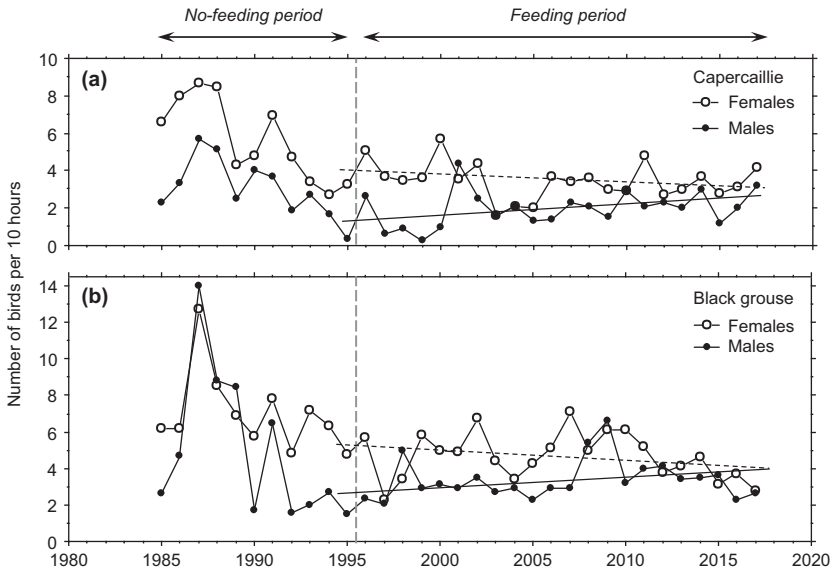


Figure 4. Indices of density (birds per 10 h of censusing) of female (○) and male (●) capercaillie (a) and black grouse (b) in the Eidsberg sub-area during the no-feeding (1985–1995) and feeding periods (1996–2017). Hatched lines are regression slopes for female capercaillie ($\beta = -0.29$, $t = -0.95$, $p = 0.35$) and female black grouse ($\beta = -0.33$, $t = -0.83$, $p = 0.42$) during the feeding period, including the year 1995 prior to feeding. Solid lines are regression slopes for male capercaillie ($\beta = 0.57$, $t = 1.99$, $p = 0.060$) and male black grouse ($\beta = 0.44$, $t = 1.23$, $p = 0.23$).

sub-area where higher brood size was the main contributor. In capercaillie there were too few broods to calculate reliable mean values for statistical inferences, but when both species were pooled, breeding success was 43% higher when food was provided ($p = 0.014$, Table 2), mainly due to increased brood frequency (44%), as there was little evidence for increased brood size (Supplementary material Appendix 1 Table A4).

The main results from the three different analyses are summarized in Table 3. We found rather consistent evidence that diversionary feeding improved the breeding success both in capercaillie and black grouse. If anything, the observed effect sizes appeared slightly stronger in black grouse. Notably, brood size in capercaillie seemed to be unaffected by the feeding program.

The fox population

Because of the outbreak of sarcoptic mange disease, the regional number of harvested foxes in Østfold county decreased markedly from the late 1970s to the late 1980s, after which there was a moderate increase that later stabilized at a level well below the 1970s (Fig. 6). To indicate possible regional trends in densities of foxes during our study, we compared the hunting yield during the no-feeding and feeding periods. The average yearly harvest of foxes in Østfold was 22% higher in the feeding (1996–2017) than the no-feeding period 1985–1995 (1380 versus 1130, $t = 2.53$, $df = 30$, $p = 0.017$). Locally, in the farmland 3–5 km north of the Eidsberg sub-area, 20–60 foxes were shot annually during 1998–2016. Except for a high number shot in the 2010–2011 season, there was no apparent trend in the numbers harvested during the feeding period ($R^2 = 0.016$, Fig. 6). Thus, the county statistics from Østfold indicates that the regional density of foxes was somewhat lower in the no-feeding period compared to the feeding period (because of the sarcoptic mange), whereas the local statistics suggests that fox numbers in and around the Eidsberg sub-area were rather constant during the feeding period.

Discussion

Breeding success of capercaillie and black grouse increased by 26–57% in the different comparisons, and the analyses strongly suggest that this was due to diversionary feeding of predators – presumably mainly foxes – in spring and early summer. In several ways, feeding appeared to have affected the breeding parameters in the two species differently. First, effects were more consistently positive in black grouse than in capercaillie. Secondly, in black grouse both brood size and brood frequency contributed to the overall increase in breeding success, whereas in capercaillie only brood frequency was affected.

Extensive movements of broods have been documented in several species of grouse (Robel 1969, Godfrey 1975, Wegge et al. 1982, Wegge et al. 2007, Erikstad 1985). Since the sub-areas in our study were relatively small (32–38 km^2), movements after hatching may have diluted the positive, local effects of feeding: Some large broods may have moved out of the feeding areas, whereas smaller broods may have moved in. At Varaldskogen, radio-marked broods of black grouse and capercaillie moved an average of 2.7 and 3.6 km from June to August, respectively ($n = 4$ and 10 broods, Finne et al. unpubl.). Longer brood movements in capercaillie may have been a contributing reason to why we did not record any effect of diversionary feeding on brood size in this species.

Another reason why diversionary feeding seemed to have affected brood size in black grouse but not in capercaillie

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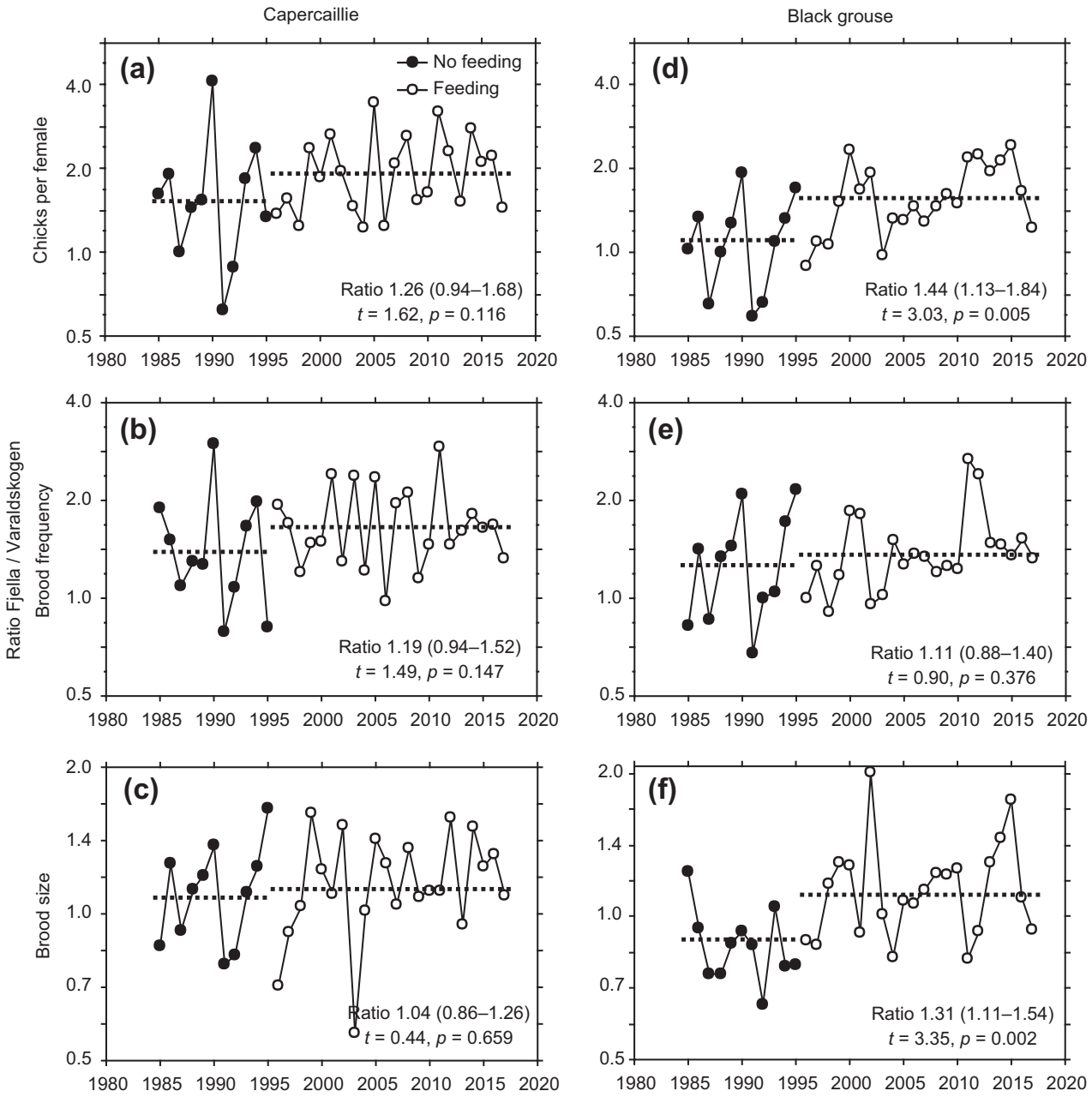


Figure 5. Comparison of breeding success (chicks per females), brood frequency (broods per female) and brood size (chicks per brood) of capercaillie (a–c) and black grouse (d–f) in the Eidsberg sub-area relative to the Varaldskogen control area, shown as annual ratios on log-scale at the y-axis. Hatched lines denote mean ratios during no-feeding (●: 1985–1995) and feeding (○: 1996–2017) periods at Eidsberg. Mean ratios between periods of feeding and no-feeding (ratio of hatched lines) are presented with confidence intervals and significance tests.

may be different vulnerability to predation from common buzzard. Although rarely recorded in camera monitoring sessions, the buzzard was frequently sighted at or near the feeding stations. Reif et al. (2001) found small sized grouse chicks to comprise a substantial part of the diet of this raptor, especially in years with few rodents. They also reported that the larger capercaillie chicks quickly grow out of the buzzard's prey size 'window', whereas black grouse chicks remain an optimal prey for a longer period in summer (Reif et al. 2004). Hence, diverting the common buzzard should have a greater effect on survival of black grouse chicks.

We interpret the increased proportion of capercaillie females with broods in feeding areas as mainly a result of reduced nest predation. During incubation, female capercaillie flushes at longer distances than black grouse, and nests of capercaillie are therefore easier to detect by foxes than nests of black grouse (Storaas et al. 1999). This is also a likely explanation for why nest loss in this species is considerably higher than in black grouse (Storaas and Wegge 1987, Wegge and Storaas 1990). Probably, foxes do not actively search for grouse nests but find them mainly by chance (Crabtree and Wolfe 1988, Vickery et al. 1992, Storaas et al. 1999). Since diversionary feeding presumably reduces the time that foxes search for natural food, it is likely that it influenced the survival of capercaillie nests more than the nests of black grouse.

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Table 2. Breeding success (chicks per female), brood frequency (broods per female) and brood size (chicks per brood) of capercaillie and black grouse in the feeding experiment of Marker and Rakkestad sub-areas. In 2003–2005 feeding was conducted at Marker sub-area with Rakkestad serving as control and in 2006–2008 feeding was switched to Rakkestad with Marker as control. Means are based on annual average values and comparisons are based on the mean annual ratios of feeding and control areas. Significance tests are based on log-ratios and significant values at $p < 0.05$ are highlighted with bold letters.

				Breeding success			Brood frequency			Brood size		
	Feeding	Control	Year	Feeding	Control	Mean ratio (95% CI)	Feeding	Control	Ratio (95% CI)	Feeding	Control	Ratio (95% CI)
Capercaillie[a]	Marker	Rakkestad	2003–2005	2.42	2.44	0.99	0.83	0.82	1.08	2.83	3.00	0.94
	Rakkestad	Marker	2006–2008	2.27	1.17	1.94	0.94	0.35	1.97	2.40	3.50	0.69
	Pooled average 2003–2008 (n = 5)[b]			2.35	1.81	1.30	0.89	0.59	1.44	2.62	3.20	0.82
Black grouse	Marker	Rakkestad	2003–2005	3.13	1.43	2.18	0.88	0.64	1.39	3.61	2.21	1.63
	Rakkestad	Marker	2006–2008	3.29	2.67	1.23	0.90	0.71	1.28	3.69	3.74	0.99
	Pooled average 2003–2008 (n = 6)			**3.21**	**2.05**	**1.57[c] (1.02–2.72)**	**0.89**	**0.68**	**1.33[d] (1.18–1.49)**	3.65	2.97	1.26[e] (0.85–1.85)
Both species pooled	Marker	Rakkestad	2003–2005	2.81	1.93	1.46	0.86	0.66	1.30	3.33	2.41	1.38
	Rakkestad	Marker	2006–2008	3.03	2.14	1.42	0.91	0.58	1.58	3.35	3.73	0.90
	Pooled average 2003–2008 (n = 6)			**2.92**	**2.04**	**1.43[f] (1.13–1.94)**	**0.88**	**0.62**	**1.44[g] (1.21–1.69)**	3.34	3.07	1.11[h] (0.82–1.50)

One-sample t-tests of log-ratio values ≠ 0 for combined time period (n = 6).
Capercaillie: [a] Too few birds for statistical inference. [b] n = 5, due to lack of broods in 2007.
Black grouse: [c] Breeding success: $\bar{x} = 0.22$, 0.083 SE, t = 2.70, p = 0.043. [d] Brood frequency: $\bar{x} = 0.12$, 0.019 SE, t = 6.41, p = 0.001. [e] Brood size: $\bar{x} = 0.10$, 0.065 SE, t = 1.53, p = 0.187.
Pooled sample: [f] Breeding success: $\bar{x} = 0.17$, 0.046 SE, t = 3.71, p = 0.014. [g] Brood frequency: $\bar{x} = 0.15$, 0.028 SE, t = 5.46, p = 0.003. [h] Brood size: $\bar{x} = 0.05$, 0.051 SE, t = 0.89, p = 0.414.

Small rodents are the preferred, main food of foxes. Therefore, we expected diversionary feeding to be more successful in low rodent years. Somewhat surprisingly, the effects of feeding did not vary with the abundance of small rodents. Only in black grouse was there a tendency for better effect on brood frequency when numbers of small rodents were low. It is well known that small rodent cycles are dampened in southern Scandinavia compared to the northern parts (Erlinge et al. 1983, Hansson and Henttonen 1985, Erlinge 1987). Also, in the south, the fox does not respond to changes in the abundance of small rodents as much as it does further north, neither numerically (Kurki et al. 1997) nor functionally (Angelstam et al. 1984). Presumably, this also applies to our study area in Fjella.

A recent study reports the average home range size of fox vixens at this latitude to be on average 3 km^2, with male ranges being twice as large (Walton et al. 2017). Too short distances between the sub-areas in Fjella may therefore have affected the experiment. Although the distance between Marker and Rakkestad experimental areas was >5 km, some of the feeding stations in the Eidsberg sub-area were situated closer to Marker (Fig. 1). This may have attracted foxes that were resident in Marker when this area served as a control and feeding was going on at Eidsberg. However, this would have lessened the effect of feeding, and therefore, the effect sizes of the experiment should be conservative.

Because of the sarcoptic mange among red foxes, regional hunting statistics showed a marked drop in number of harvested foxes during the 1980s, but the increase in harvest after the mange ceased was surprisingly small. It has been suggested that it may not correctly reflect the full recovery of the population. During the mange, hunting traditions may not have been upheld, resulting in fewer and less skilled hunters (Selås 1998, Smedshaug et al. 1999), implying that the real increase of the fox population may have been higher.

Critiques have been raised that diversionary feeding might induce a long-term increase in the predator populations, thereby nullifying an intended positive effect on game species (Conover 2002, Kubasiewicz et al. 2016). Acknowledging uncertainties in using hunting statistics to indicate trends in fox abundance this cannot be ruled out (as hunting effort and skills are not controlled for). However, the local statistics was based on a rather constant hunting effort and did not show any marked trend during the feeding period. This indicates that the local fox population was rather stable after feeding was initiated, and that diversionary feeding presumably had little or no effect on the density of resident foxes.

The increase in chick production did not lead to more adult birds in the local population. However, since the two sexes apparently responded differently, the adult sex ratio changed gradually in favour of males (Fig. 4). Thorough studies of predator control, which also aimed at reducing predation and increase post-breeding populations, have been conducted in Sweden and in Finland. Both showed positive effects on breeding success, but different responses to breeding numbers: In the Swedish study, Marcström et al. (1988) reported that numbers of adults increased after predator removal – females more so than males – whereas in the Finnish study (Kauhala et al. 2000), no increase was detected in pooled samples of the two sexes. We think that

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Table 3. Effect sizes in the different tests of diversionary feeding: (time series Eidsberg controlled for temperature, time series Eidsberg compared to Varaldskogen, and experiment in Marker and Rakkestad), shown as relative change (ratio) between 'feeding' and 'no feeding' periods/areas.

	Capercaillie			Black grouse		
	Breeding success	Brood frequency	Brood size	Breeding success	Brood frequency	Brood size
Time series of Eidsberg sub-area controlled for temperature	1.45°	1.23*	0.99	1.43*	1.09	1.32*
Time series of Eidsberg sub-area in comparison with Varaldskogen control area	1.26	1.19	1.04	1.44**	1.11	1.31**
Experiment at Marker and Rakkestad sub-areas	(1.30)ǂ	(1.44)ǂ	(0.82)ǂ	1.57*	1.33***	1.26

ǂ Too few broods for statistical inference in capercaillie.
° $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

the somewhat contrasting results in the three Fennoscandian studies are related to natal dispersal and source–sink dynamics (sensu Pulliam 1988) and to different spatial arrangements and sizes of study areas. In the two species of forest grouse, natal dispersal is typically female biased and long (black grouse: Caizergues and Ellison 2002, Warren and Baines 2002, capercaillie: Koivisto 1963, Moss et al. 2006). In the Swedish study, the study areas (two islands) were quite small (approximately 20 km^2) and isolated by 3–4 km of non-habitat from nearest contiguous forest. Small sizes and isolation may have restricted juvenile dispersal to and from the mainland. In Finland, the study areas were large (48–116 km^2) and surrounded by a matrix of suitable habitat. Here, the numbers of female chicks dispersing from the removal areas were probably not fully replaced by immigrants, thereby reducing or nullifying any increase in the local breeding population. Our study area was located at the periphery of the large Fjella forest complex, with farmland and other unsuitable habitat along much of its border. More female chicks probably dispersed out of the study area than was received from the surroundings, whereas most male chicks remained and were recruited locally.

By acquiring offal from local hunters, and wild animals from vehicle collisions, feeding of predators is a low-cost management procedure. Depending on density of forest roads, the work effort to distribute meat at feeding stations is normally moderate. In the Eidsberg sub-area (34 km^2) one person used approximately 2–3 h once a week to distribute food.

Our study is the first to assess the effect of diversionary feeding on northern forest grouse based on a long-term comprehensive data set supplemented with a short-term experiment. Although the study has some shortcomings, we conclude that diversionary feeding during a short time-span in spring and early summer might be a feasible management tool for increasing chick production in forest grouse. Owing to source–sink dynamics, feeding predators is likely to have little effect on the local population of breeding birds, especially females. On a landscape scale, however, such management may have conservation value by increasing the recruitment of young females to the surrounding forests.

The study was conducted at the southern edge of the boreal bioclimatic zone where cycles and amplitudes of small rodents are less pronounced than further north. Since

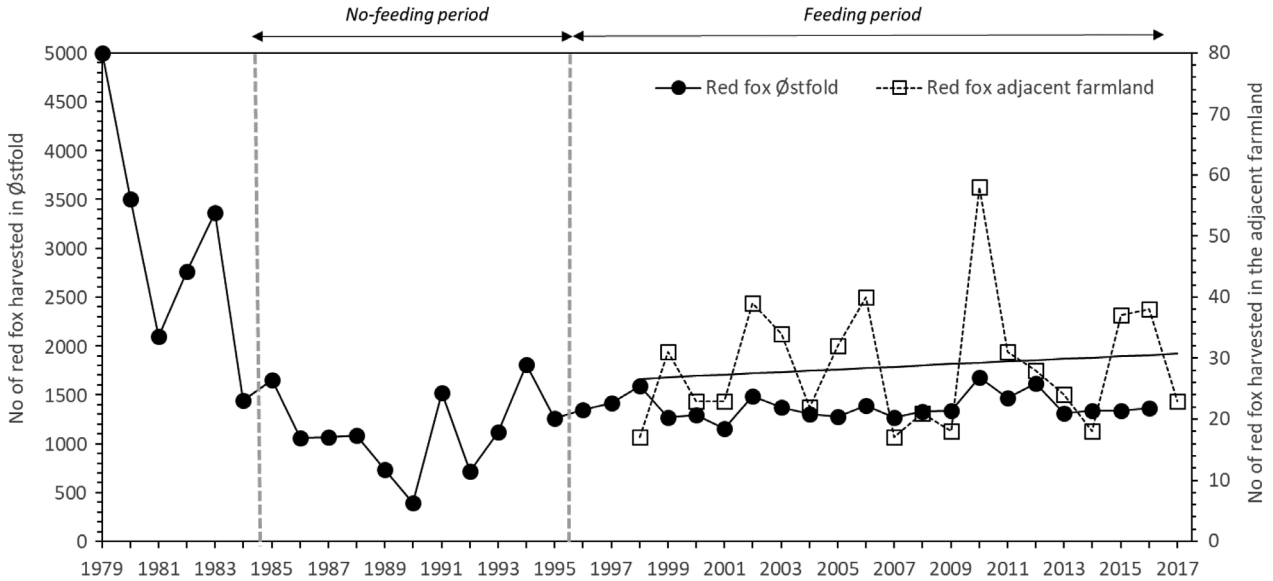


Figure 6. Number of red foxes harvested per hunting season in Østfold county (●) 1978–2017, and number of harvested foxes per year in the adjacent farmland (□) 3–5 km north of the Eidsberg sub-area. Periods of no-feeding and feeding in the Eidsberg sub-area are indicated with arrows on top of the figure. The regression slope is shown for foxes in the adjacent farmland area ($\beta = 0.218$, $t = 0.53$, $p = 0.60$, $R^2 = 0.016$).

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effects of feeding is likely to vary with the predation pressure induced by cyclic rodents, studies of diversionary feeding as a management tool need to be carried out also in boreal forests farther north. Also, diversionary feeding should be tried out at a larger spatial scale in order to minimize dilution effects due to long distance movements of broods and source–sink dynamics of dispersing young females.

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Supplementary material (available online as Appendix wlb-00492 at <www.wildlifebiology.org/appendix/wlb-00492>). Appendix 1.

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