Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates

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Abstract. Understanding the drivers of seasonal migration among large herbivores is crucial for management and conservation. The forage maturation hypothesis predicts migration even at low population density, due to the benefits of increased access to newly emergent, high quality forage. We provide the first study comparing migration tendency of the two most widely distributed deer species in Europe, roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). The study was conducted in an area with a low population density of both species. We found that 94% of the GPS-collared red deer, but only 27% of the roe deer, migrated. This supports the forage maturation hypothesis in red deer only. Our study thus provides evidence of multiple causation of migration in ungulates, and is consistent with the hypothesis that the forage maturation hypothesis might be a more important driver for migration in grazers compared to browsers.

Key words: competition avoidance; deer; diet type; feeding type; forage maturation; ungulates.

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INTRODUCTION

Large herbivore migrations are globally considered threatened by human development (Berger 2004, Sawyer et al. 2009). In order to conserve this phenomena there is an urgent need to better understand the primary drivers of migration, and studies of partially migratory populations are considered especially enlightening (Chapman et al. 2011). The most common pattern of migration of large herbivores at northern latitudes involves a cycle of movements from low elevation winter areas to high elevation summer areas (Brazda 1953, Mysterud 1999). While the movement in fall to low elevation is mainly related to more snow accumulating at high elevation (Cagnacci et al. 2011), there are multiple hypotheses that predict the subsequent uphill migration in spring (Mysterud et al. 2011). Surprisingly, there have been no comparative studies of migration in sympatric deer at northern latitudes that can provide insight into the generality of drivers of migration. We here compare migration tendency of the two most widely distributed deer species in Europe, roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*).

The forage maturation hypothesis (FMH) states that ruminants should follow the phenological development during the growing season

to increase access to the optimal forage in terms of balancing quality and quantity (Fryxell et al. 1988, Albon and Langvatn 1992, Hebblewhite et al. 2008). Since temperature is lower and snow depth deeper at high elevation, uphill migration can yield benefits in terms of increased access to newly emergent, high quality forage over the growing season (Hebblewhite et al. 2008, Bischof et al. 2012). The FMH has so far mainly been applied to grazers. For browsers (or concentrate selectors; sensu Hofmann 1989) such as white-tailed deer (Nelson 1995) and roe deer (Mysterud 1999), it has been proposed that the range expansion in spring is related to high population density and thus forage competition within the winter range, termed the competition avoidance hypothesis (further developed in Mysterud et al. 2011).

An interesting comparison would therefore be in a low density population of species differing in diet type. Only the FMH predicts a high level of migration even at low population density, while the competition avoidance hypothesis predicts mainly stationary animals at low elevation in low density populations. Consistent with the suggestion that species might differ in migration propensity even in sympatry (Mysterud et al. 2011, Mysterud 2012), we found a much higher proportion of migrating red deer than roe deer in a low density population, suggesting FMH as a driver of migration only in red deer.

MATERIAL AND METHODS

Study area

The study area is located in south Norway (Fig. 1). Most of the animals were marked in the Hallingdal valley in Buskerud County close to mountain habitats, with some red deer being marked in the municipality Modum, in Buskerud County and some roe deer in Lardal, Vestfold County and Siljan, Telemark County (Table 1). The area is forested with a domination of Norway spruce (*Pices abies*) on richer soils and Scots pine (*Pinus sylvestris*) on poorer soils, with birch (*Betula* spp.) dominating at higher elevation (>1000 m). The area is dominated by steep elevation gradients from valleys and up to mountains above 1000 m above sea level. The area is marginally suitable for roe deer, due to long winters, deep snow and predation by

Eurasian lynx (*Lynx lynx*). Red deer colonized the area from the west within the last few decades, and remains at low population density partly due to harvesting. Densities of both species are therefore low (red deer: 0.08 felled/km^2; roe deer: 0.11 felled/km^2).

Roe deer GPS data

The roe deer data derive from 19 females (6 juv.; 13 aged ≥2 yrs) marked in winters 2009–2011 and with data covering the expected spring and fall migration periods, from March/April to November/December. Animals were caught in box traps at winter feeding sites and fitted with GPS-collars (Televilt/Followit, Sweden and Vectronic, Germany).

Red deer GPS data

The red deer data derive from 17 adult (≥2 yrs) females marked in winters 2009 and 2010 (Mysterud et al. 2011, Bischof et al. 2012). Animals were darted and immobilized at established winter feeding sites and equipped with GPS-collars (Televilt/Followit, Sweden). All marking procedures were approved by the Norwegian Animal Research Authority.

Screening of GPS data

The GPS data was screened automatically for errors using a standard procedure based on animal movement theory (Bjørneraas et al. 2010). To determine whether an animal was stationary, migratory, dispersing or non-typical, we used first an automated approach using net-square-displacement (Bunnefeld et al. 2011), together with additional criteria described in Bischof et al. (2012). Then, a visual assignment procedure allowed us to determine if the fitted curves were appropriate, since the automated procedure lead to some apparent spurious classifications for red deer (Bischof et al. 2012). For roe deer, the Bunnefeld et al. (2011) and visual inspection classifications were consistent in all cases.

Statistical analysis

We used Fishers exact test for count data to analyse whether the likelihood of migration differed depending on species, which are adequate with small sample in some cells (i.e., only one stationary red deer). Figures were plotted
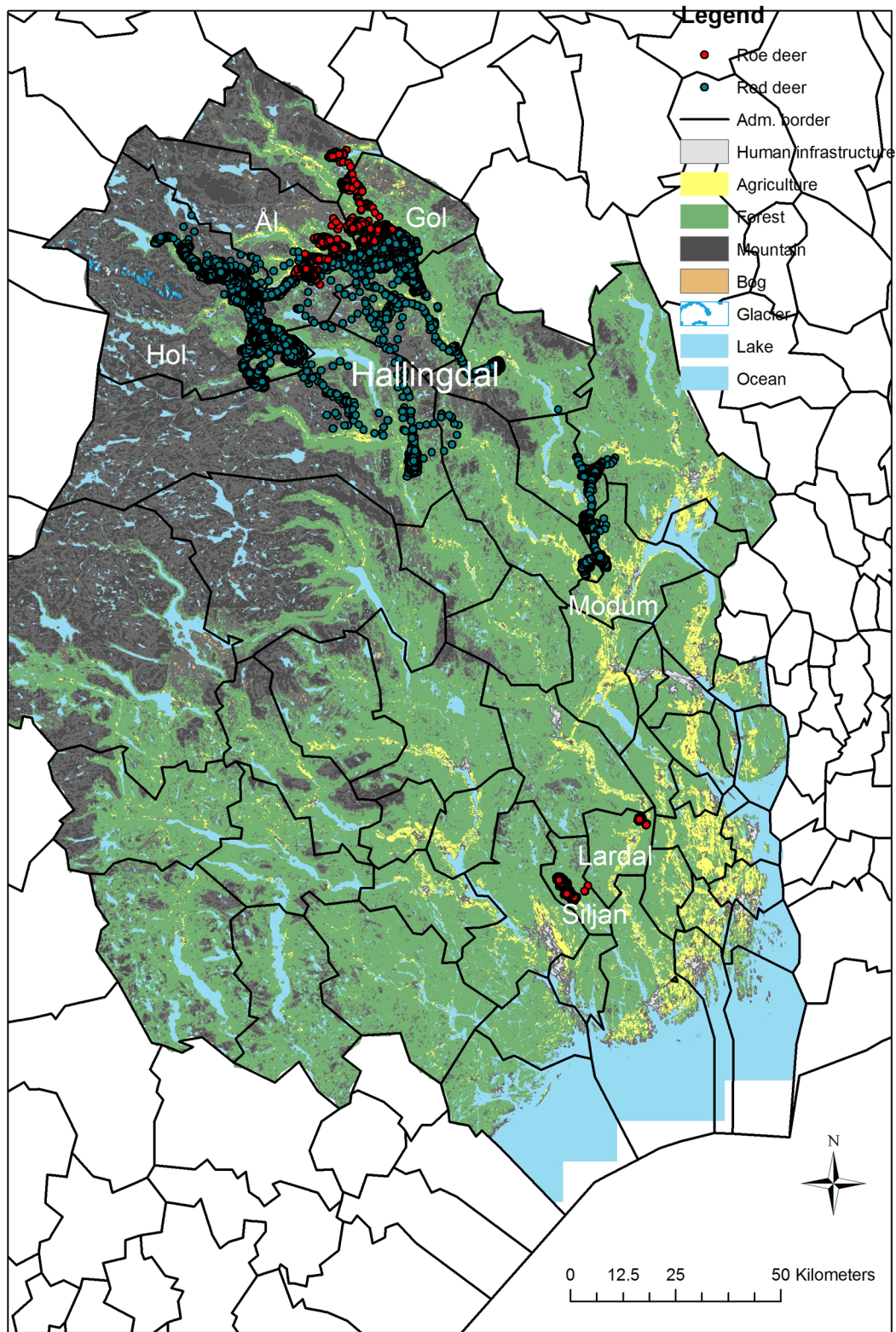
Fig. 1. Map showing the location of red deer and roe deer in the study area in south-east Norway.

Table 1. An overview of the municipalities and years of GPS-marked female roe deer and red deer in south east Norway.

Location	Red deer					Roe deer				
	2008	2009	2010	2011	Sum	2008	2009	2010	2011	Sum
Ål	0	1	0	0	1	0	1	0	0	1
Gol	0	6	0	0	6	5	4	4	0	13
Hol	0	7	1	0	8	0	0	0	0	0
Modum	0	0	2	0	2	0	0	0	0	0
Lardal	0	0	0	0	0	0	0	0	2	2
Siljan	0	0	0	0	0	0	0	0	3	3
Sum	0	14	3	0	17	5	5	4	5	19

with the Clopper-Pearson exact 95% confidence intervals using the function exactci in the R package PropCIs (Scherer 2010). Analyses were done in R vs. 2.15.0 (R Development Core Team 2012).

RESULTS

All except one of the 17 female red deer were migratory (94.1%). Among the female roe deer, 4 were dispersers, 4 were migratory, while 11 were stationary. The dispersers were juveniles (2) or 2 year olds (2). Excluding dispersers, this yielded 26.7% migrating roe deer, which is markedly lower than in red deer (Fisher's exact test; $P < 0.001$). This result was robust when restricting data only to the main study site north in Hallingdal ($P = 0.003$) or when excluding two juvenile roe deer ($P < 0.001$). With only 4 migrating roe deer, we were unable to test for more detailed differences in migration pattern (Table 2). There was a clear tendency for red deer to migrate longer and somewhat earlier in fall, while timing of spring migration was similar.

DISCUSSION

By comparing roe deer and red deer, we provide the first evidence that migration is unlikely to be driven by similar mechanisms across different species of ruminants at northern latitudes, or that migration is hindered by other constraints in some species such as roe deer in our case. On sympatric ranges in low density populations of both species, red deer had a much higher proportion of migrants than roe deer (Fig. 2). At low population density, only the forage maturation hypothesis (FMH) predicts migration, and we can therefore support this hypothesis for red deer, but reject it as an equally strong driver for roe deer relative to other potential constraints.

The FMH is a general framework to explain large scale movements of ungulates on several continents, but has mainly been developed and tested on grazers (wildebeest *Connochaetes taurinus*; Holdo et al. 2009; Thomson's gazelles *Gazella thomsoni*; Fryxell et al. 2004) or mixed feeders (such as elk/red deer *Cervus elaphus*; Albon and Langvatn 1992, Hebblewhite et al. 2008) that mainly forage on grasses during the growing season. It has been argued, but never tested, that ruminants belonging to different diet types may show contrasting migration patterns (Mysterud et al. 2011, Mysterud 2012). In fact, it is unclear whether forage maturation of browse species shows equally marked phenological development along an altitudinal gradient.

Table 2. Descriptive statistics (average, min-max) of roe deer and red deer female migration in low density populations in Norway.

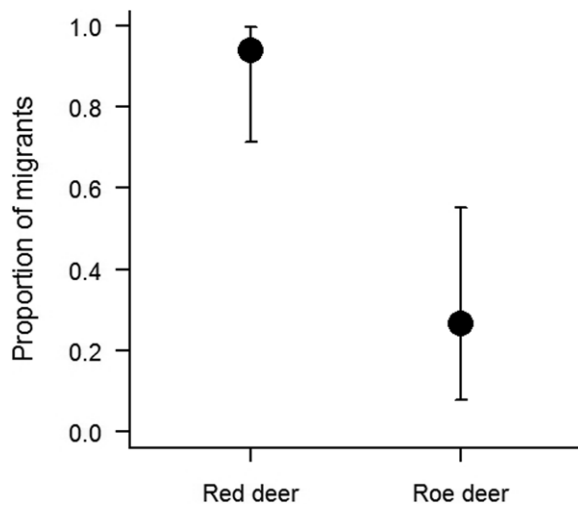| Species	n	Proportion (%)	Distance (km)	Timing of migration		Altitude (m)	
				Spring	Fall	March	July
Roe deer	15	26.7	13.1 (2.7–21.4)	12 May (17 Apr–24 May)	17 Oct (15 Sep–5 Dec)	351 (274–424)	664 (350–842)
Red deer	17	94.1	26.4 (5.4–68.9)	8 May (15 Apr–3 Jun)	21 Sept (27 Aug–16 Oct)	473 (259–648)	823 (339–1064)

Fig. 2. Proportion (with 95% confidence intervals) of migratory roe deer and red deer in a low density population in south-east Norway.

There were very few migratory roe deer in this low density population. In an area further south-east with a higher winter density of roe deer of about 3–5 deer per 100 ha, 70% of female roe deer migrated (Mysterud 1999). These observations are consistent with the competition avoidance hypothesis. The competition avoidance hypothesis only predicts much migration if there is access to potential summer ranges with low population density. In flat landscapes with weaker environmental gradients with much higher densities of roe deer, migration is again less common (Cagnacci et al. 2011).

Our study highlights the utility of comparative studies to shed light on drivers of migration. Evidence is consistent with the suggestion that browsing and grazing ungulates might differ in reasons for why they migrate, and we urge for doing further comparative work including several species allowing us to pinpoint whether differencing in migration is mainly due to diet type or other factors that might differ between groups of ungulates.

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