

Male red deer (*Cervus elaphus*) dispersal during the breeding season

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Abstract Breeding dispersal can be of significant ecological and evolutionary importance. Yet, it is seldom considered in mammals. I present data on male red deer (*Cervus elaphus*) movements between sub-populations in southern Sweden during the rut. I investigated whether these movements could be breeding dispersal driven by mate competition. During the ruts of 1998–2009, I recorded 91 movements of males. The longest movement distance was 18.5 km. Dispersal was not restricted to yearlings or sub-adults, but also observed among adult stags. Of 91 movements observed, 7 were made by yearlings, 46 by sub-adults and 38 by adults. There was a significant move among yearlings and sub-adults towards areas with a higher ratio of females/adult males and towards areas with more females. The movements between rutting areas thereby seemed driven by sexual competition.

Keywords Breeding dispersal · Deer management · Gene flow · Intra-sexual competition · Reproductive strategy

Introduction

The study of mechanisms and factors affecting dispersal patterns is essential in order to understand gene flow, spatial distribution and range expansion of populations, and thus also of great interest for conservation and management (Stenseth and Lidicker 1992). An individual's permanent

movement away from the birth site to a site for its first attempt of reproduction is commonly referred to as natal dispersal (Howard 1960). Juveniles are generally more inclined to disperse than adults, and sex differences in natal dispersal are common (Greenwood 1980; Lawson Handley and Perrin 2007). Subsequent movements from one site of potential reproduction to another are termed breeding dispersal (Greenwood and Harvey 1982). While natal dispersal has generated numerous studies (Dobson 1982; Wolff 1993; Greenwood 1980; McPeck and Holt 1992; Johst and Brandl 1997), studies on breeding dispersal, particularly in mammals, are rare (Greenwood and Harvey 1982; Paradis et al. 1998). Greenwood (1980) argues that the direction of sex-biased dispersal is a consequence of type of mating system. Dobson (1982) showed a clearly male-biased juvenile dispersal in polygynous and promiscuous mammal species. In a mate-defending system, males are independent of specific site qualities and are in search of areas with available females and as little competition as possible, hence favouring a male-biased dispersal. Of several major causes suggested for natal dispersal (Greenwood 1980; Dobson 1982; McPeck and Holt 1992; Wolff 1993; Johst and Brandl 1997), the one also applicable to breeding dispersal is to improve reproductive success via decreased mate competition (Dobson 1982). This largely agrees with the hypothesis proposed by Greenwood and Harvey (1982) that breeding dispersal is a search for better breeding opportunities via higher quality mates, less breeding competition or a better breeding environment.

Breeding dispersal is frequently observed among primates, where males transfer into groups with cycling females or with more favourable sex ratios (Packer 1979; Jack 2003; Parga and Lessnau 2008). Inbreeding avoidance has been suggested as an explanation for this secondary

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dispersal (Packer 1979), but several studies support that it is driven by intrasexual competition (Olupot and Waser 2001; Jack 2003; Jack and Fedigan 2004; Parga and Lessnau 2008). In comparison, in polygynous ungulates, with strong mate competition and large variations in reproductive success among males, a breeding dispersal similar to that observed for primate males could therefore be expected. Yet, studies on breeding dispersal in ungulates are hard to find. Bighorn (*Ovis canadensis*) rams of intermediate ranking can move to demes with a more favourable female ratio during the rut, seemingly to increase chances of reproduction (Festa-Bianchet 1986; Hogg 2000). Dunham (2000) recorded breeding dispersal of male and female mountain gazelles (*Gazella gazella*). But this was captive-born animals released in a reintroduction programme and it cannot be excluded that the movements were affected by this. Rosenberry et al. (2001) showed that dispersal of yearling male white-tailed deer (*Odocoileus virginianus*) was prompted by sexual competition during the breeding season, and Wahlström (1994) similarly found that dispersal of yearling roe bucks (*Capreolus capreolus*) was driven by aggression from older males. Even if the dispersals in these two studies were natal, they still show that sexual competition during the breeding season can cause dispersal in ungulates, and thus raise the question whether this dispersal is restricted to just yearlings. Older but subordinate or still not prime-aged males could search for areas with less competition. This should especially be the case in long-lived species with a late maturity and a life expectancy of several breeding seasons.

The European red deer (*Cervus elaphus*) conforms to the pattern of a species adapted to strong competitive conditions in stable and predictable environments (Liberg and Wahlström 1995). They are relatively long-lived: females may reach an age of more than 20 years and still be fertile. Litter size is one and the frequency of multiple ovulations is less than 1% (Mitchell and Lincoln 1973; Langvatn et al. 1996). Red deer are polygynous and commonly display a harem mating system. Hinds are faithful to their natal home range, and dispersal seems more a process of expanding home range than a total abandonment (Clutton-Brock et al. 1982; Albon et al. 1992; Catchpole et al. 2004). Male emigration is more common (Clutton-Brock et al. 1997, 2002; Catchpole et al. 2004) and genetic studies confirm the characterisation of red deer as a species with male-biased dispersal and female philopatry (Nussey et al. 2005; Frantz et al. 2008).

Although a common species in Europe, over-harvesting, habitat fragmentation and translocations have resulted in local extinctions, isolated populations and hybridisation of native populations with deer of foreign subspecies (Lowe and Gardiner 1974; Hartl et al. 2003; Hmwe et al. 2006; Lovari et al. 2008). Concern has been raised over the

negative effects of isolation of sub-populations as well as over the possibilities of establishment of new sub-populations (Simon et al. 1998; Kuehn et al. 2003; Zachos et al. 2007). Remnant populations of endangered subspecies may also risk immigration of introduced non-native conspecifics (Hartl et al. 2003; Feulner et al. 2004). These problems call for detailed behavioural, demographic and quantitative studies on red deer dispersal ecology and how it is affected by various features in the landscape (Patthey 2003, Pérez-Espona et al. 2008).

Using individually identified deer, I present data on male movement between different rutting areas within the same rutting season during a study period of 1998–2009. I test the hypothesis that red deer males move from one rutting area to another in order to increase the chances of reproductive success via decreased mate competition.

Materials and methods

The study was conducted during 1998–2009. The study area covers approximately 400 km² and is situated in the nemoral zone in the southernmost of Sweden in the county of Skåne, approximately 20 km east of Lund, and 600 km south of Stockholm. It is a largely flat lowland area with occasional small rolling hills and small altitudinal variations (elevation ranging from 25 to 160 m above sea level). Climate is mild with a mean temperature of -1°C in January and 16°C in July. Annual snow cover averages 25 days. Annual precipitation averages 700–800 mm with a monthly minimum in February–March with 30 mm and most precipitation in July and August with 60–70 mm per month. The area is dominated by agriculture but mixed with managed forests consisting mainly of Norwegian spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), beech (*Fagus sylvatica*), birch (*Betula pendula*) and oak (*Quercus robur*).

Red deer in the area comprise a part of a free-ranging remnant population of the original nominate red deer subspecies *C. e. elaphus* (Ahlén 1965; Haanes 2008). Pre-harvest size (2009) of this remnant population is believed to be about 1,700–2,000 individuals (A. Jarnemo, unpublished data). The rut lasts from late August to the beginning of October with the peak in mid-September, during which dominant stags hold and defend mobile harems of hinds. To be classified as a harem holder in this study, the stag had to keep and defend a harem. Occasional observations of a stag together with hinds were not enough for a classification as a harem holder. Red deer are not evenly distributed over the area during the rut, but generally confined to 12 rutting areas. These rutting areas are centred at larger estates (size 11–50 km²), probably for historic reasons (Ahlén 1965). Males generally seem to spend most of the

year outside the rutting areas in certain summer and winter areas, sometime tens of kilometres away, to which they return after the rut (Jarnemo 2008).

As part of management practice, red deer were counted annually from 1998 to 2009. The count was performed 7 days a week in the rutting season during a continuous period of 42–46 days from 23–25 August to 5–9 October. Given the general behaviour of these red deer to forage in agricultural fields during the night and to seek cover in dense forest during the day, the counting was performed during evenings, nights and mornings, applying the same method over the entire study. Observation was made from car as well as by foot, either from fixed points or by moving in the areas (driving or stalking). Throughout the study period, the same person (A. Jarnemo) performed the counting, but additional assistance was provided in mornings and evenings by one highly experienced red deer photographer (L. Jarnemo). During the night-time, 2nd generation night-vision scopes with 4× and 5.6× magnification were used. The traditional rutting areas were visited repeatedly throughout the whole rutting season. Animals were also localised through listening for roaring, through tracking and through contacts with wildlife managers, hunters and landowners. The night-vision scopes made it possible to also observe, count and identify deer during the dark hours, thus prolonging the working shift and meaning that several rutting areas could be visited the same night (travel by car between rutting areas) and thereby also increased the number of possible visits in each rutting area. The morning shifts usually started at 0230–0430 hours and ended at 0800–1000 hours. The evening shifts usually started at 1700–1800 hours and ended at 2100–2400 hours. For each work shift, from one to five rutting areas were visited. The assisting photographer normally visited one rutting area per working shift and did not use a night-vision scope. For each visit in a rutting area, the numbers of females, calves and males were recorded. The maximum number of females obtained for each rutting area during a rut was the figure used in the analysis in the present study, whereas for males, the total number for each rutting area during a rut was based on identification of individuals (see below).

The harem size for each rutting area in 2009 varied from 2 to 65 hinds with a mean of 21.3 (SD = 22.3, median = 10.5). The movement of females between the rutting areas during the period of counting is probably low. In 2007–2008, for another study, 12 adult females were marked with GPS-collars: 8 within the present study area, and 4 approximately 18 km outside. All 12 individuals have been stationary in each respective rutting area during the rutting season (A. Jarnemo, unpublished data). During the study period 1998–2009, the counted number of deer has shown a two-fold increase in the study area, and the

2009 population, estimated at 600 deer, was comprised of 42% adult females, 27% calves, 20% stags categorised as yearlings and sub-adults, and 11% stags categorised as adults. The number of counted males each year varied between 66 and 185 (mean = 124, SD = 45.4). Hunting is allowed from the second Monday in October to 31 January, falling outside the rut (Jarnemo 2008).

Based on body morphology and antler characteristics, stags were classified as yearlings, sub-adults or adults (Hetschold and Vorreyer 1968; Krebs 1969). The young stag gives the impression of being long-legged and is characterised by a short and slender body, a thin high stretched neck, a pointed nose and a head held high. With increasing age, the body gets increasingly massive, the neck thicker and the head is held lower. The adult, full-grown stag is characterised by a heavy body, a thick neck and strong forequarters. The head seems larger relative to the body. The nose is obtuse and a “double chin” is developed, which gets more and more pronounced the older the stag. Red deer males reach their full body-weight at an age of 6–8 years (Langvatn and Albon 1986; Wagenknecht 1986; Meisingset and Langvatn 2000). The sub-adults in this study should in general be less than 6 years old and the adults older than that, but it is important to bear in mind that the maturity process and the morphological features can differ between individuals and may not reflect the exact year of age. To distinguish between stags on the margin between sub-adults and adults, I thus used a combination of body morphology and antler size, where body was given more weight, especially concerning heaviness and signs indicating a mature stag.

Individual stags were identified by antler shape and photo-documented or sketched and described in detail. Especially for yearlings, but also for 2–3 year olds, the antlers are comparably undeveloped and it might therefore be difficult to distinguish between different individuals. Unless there were photographs, or good drawings, of these younger stags ensuring identification, only stags whose antlers had some unusual and distinguishing feature were included in the dataset. Stag identification and age classification were performed by the same person (A. Jarnemo) throughout the whole study.

In the observed movements by stags between rutting areas, the two visited areas were compared by (1) number of counted females that year, (2) the ratio females/all males that year, and (3) the ratio females/adult males that year, in order to investigate whether the stags moved towards areas with more females and higher female/male ratios. For statistical testing, I used Wilcoxon signed-rank test. The values of females and males to which an observed movement was related were the ones obtained for the same year as the movement took place. The number of females (including both adult females and yearling females) used in

Table 1 Summary of red deer (*Cervus elaphus*) male dispersals during the rut

Age and status	Observations	Date of confirmation			Distance (km)			
		First	Median	Last	Mean	SD	Min	Max
Young								
Yearlings	7	12 September	23 September	01 October	9.9	3.1	6.0	15
Sub-adults	46	08 September	24 September	05 October	8.3	3.5	3.0	18.5
Adult								
Non-harem	19	06 September	23 September	06 October	7.9	3.8	3.0	15.5
Harem	15	05 September	24 September	08 October	5.6	1.9	2.5	8.5
Ex-harem	4	15 September	26 September	05 October	13.4	3.6	8.0	15.5
All combined	91	05 September	23 September	08 October	8.1	3.6	2.5	18.5

the analysis was the maximum number observed at the rutting area during the rut for that year. The number of males used in the analysis was the number of individuals that were identified at the rutting area that particular year. The moving stags were registered in the rutting area where they were first observed. Each movement by a stag was treated as one independent observation. If a stag made a second movement, this was also treated as one independent observation.

Results

Over the 12 years of study (1998–2009), movements between rutting areas during the rut were observed 91 times (Table 1). The longest distance was 18.5 km (mean = 8.1 km, range 2.5–18.5 km, SD = 3.6). Of the 91 movements, 7 were made by yearlings, 46 by sub-adults and 38 by adult stags. Of the 38 adult stag movements, 19 were made by stags that had not been observed as dominant harem holders, 4 by former harem holders that had lost their position, and 15 by dominant harem holders. Movements were observed multiple times in some individuals. Seven individuals were observed to have made a second movement within a rutting season, and of these, two individuals also made a third movement. Three harem holders were observed to have made movements in different rutting seasons. All rutting areas in the study area were networked to at least two other rutting areas via the observed male movements (Fig. 1). No definite trend was observed in the timing of movements (Table 1).

For all males combined, as well as for the young males, the number of females in the second area observations were significantly higher than in the first areas, and the ratio females/adult males was significantly higher in the second visited area than in the first (Table 2). For adult males, there were no significant differences between first and

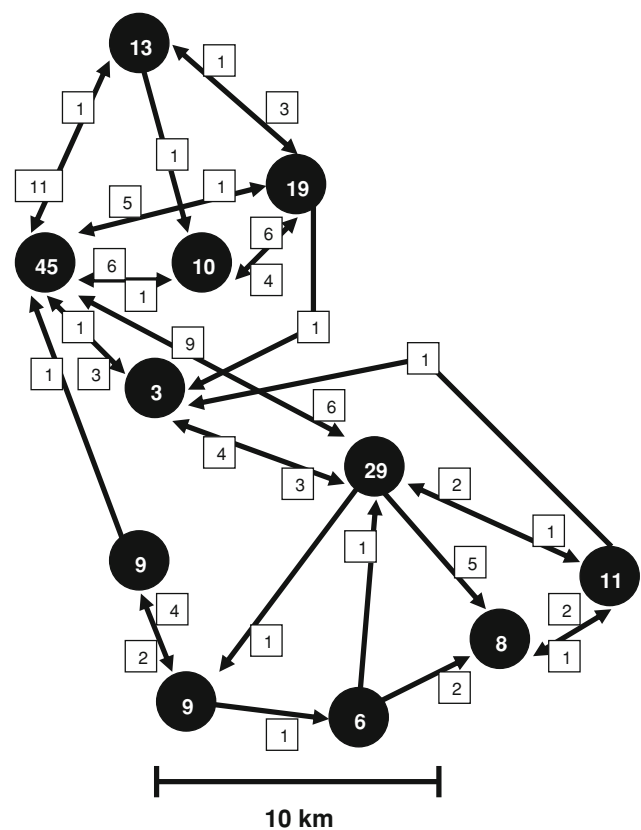


Fig. 1 Observed movements of male red deer (*Cervus elaphus*) between rutting areas during 1998–2009. Black circles are rutting areas with average number of females during the period of study. Arrows show exchange of males between rutting areas with numbers in squares showing how many males have entered the area

second rutting areas regarding the number of females or the ratio females/adult males. With one exception, separate tests of adult harem holders and non-harem holders did not give any significant differences. The exception was adult harem holders for which the ratio females/all males was significantly lower in the second visited area.

Table 2 Wilcoxon signed-rank tests for male movements

Age and status	1st area	2nd area	Z value	P value
No. females \pm SD (min–max)				
All males ($n = 91$)	20.2 \pm 17.7 (3–65)	26.7 \pm 19.2 (4–65)	2.71	0.0067
Yearlings and sub-adults ($n = 53$)	19.1 \pm 15.1 (3–65)	25.0 \pm 17.2 (4–65)	2.14	0.0324
Adults ($n = 38$)	22.6 \pm 19.4 (4–65)	29.4 \pm 21.6 (4–65)	1.67	0.0951
Non-harem ($n = 19$)	25.4 \pm 18.7 (4–65)	24.2 \pm 22.6 (4–65)	0.13	0.896
Harem ($n = 15$)	13.4 \pm 14.9 (4–64)	28.3 \pm 17.6 (6–54)	1.92	0.0553
No. females/no. adult males \pm SD (min–max)				
All males ($n = 91$)	6.2 \pm 3.4 (1.9–16.0)	7.8 \pm 4.1 (2.4–16.0)	2.99	0.0028
Yearlings and sub-adults ($n = 53$)	6.4 \pm 3.7 (1.9–16.0)	8.5 \pm 4.1 (3.1–16.0)	2.96	0.0031
Adults ($n = 38$)	5.9 \pm 3.0 (2.5–16.0)	6.7 \pm 3.8 (2.4–16.0)	1.06	0.2889
Non-harem ($n = 19$)	5.7 \pm 3.3 (2.8–16.0)	6.2 \pm 2.9 (3.1–14.0)	0.57	0.5687
Harem ($n = 15$)	6.7 \pm 2.6 (3.7–12.0)	6.6 \pm 4.6 (2.4–16.0)	0.94	0.3453
No. females/no. all males \pm SD (min–max)				
All males ($n = 91$)	1.8 \pm 1.6 (0.4–9.0)	1.7 \pm 0.9 (0.6–5.0)	1.24	0.2131
Yearlings and sub-adults ($n = 53$)	1.5 \pm 1.0 (0.6–6.5)	1.7 \pm 0.8 (0.8–5.0)	2.29	0.0221
Adults ($n = 38$)	2.2 \pm 2.1 (0.4–9.0)	1.7 \pm 1.0 (0.6–5.0)	0.59	0.5555
Non-harem ($n = 19$)	1.8 \pm 1.9 (0.8–9.0)	1.9 \pm 1.3 (0.6–5.0)	0.92	0.3551
Harem ($n = 15$)	3.2 \pm 2.3 (1.1–9.0)	1.3 \pm 0.5 (0.7–2.8)	2.79	0.0052

P values in bold are significant at <0.05

Discussion

The results showed a frequent exchange of red deer males between the different rutting areas during the breeding season, suggesting a significant potential of breeding dispersal in red deer. The observations also suggest a high capacity of gene flow between established red deer sub-populations. As the movements were discovered by chance, it is likely that a large number of movements between different rutting areas remained undetected, suggesting that the observed movements by far underestimate the real number. With an apparent highly skewed mating success for red deer males (Clutton-Brock et al. 1982; Pemberton et al. 1992), there is strong competition forcing males to adopt various strategies in order to reach reproductive success. Males moved towards areas with more females and towards areas with a higher female/adult male ratio, as predicted.

Although the exact age of males was unknown, the determination of adult males in this study should be reasonable because red deer stags seem to assess opponents by their appearance (Clutton-Brock et al. 1982) and roaring (Reby and McComb 2003; Reby et al. 2005). The classification may thus to some extent reflect stage of maturity, size and apparent strength, rather than exact age. Male age and size are, however, often closely related (Myserud et al. 2001). Despite this weakness of the data, I conclude that the movements seem related to sexual competition and

were conducted in an effort to improve the chances of reproductive success, and thereby indicating breeding dispersal among male red deer. The study thereby also gives support to Greenwood's (1980) hypothesis of sex-biased dispersal as a consequence of mating strategy. There was, however, no tendency for males in any age category to immigrate into areas with a higher ratio females/all males. This could reflect that it is the presence of dominant adult males that deters other stags and persuades them to move on. Young males may very well join in pairs or groups during the rutting season, which further indicates that the presence of young stags do not deter other stags, neither the young ones nor the adults.

In 46 of the 91 observations, the stag was classified as sub-adult. In comparison, Clutton-Brock et al. (2002) found that male natal dispersal was most common among males aged between 2 and 5 years. Avoidance of inbreeding has been suggested as an ultimate factor driving natal dispersal (Wolff 1993) as well as secondary dispersal (Packer 1979). Place of birth or relatedness to individual females were, however, not known for the stags in this study. The possibility that some of the observed stags were leaving their natal area in order to avoid inbreeding can therefore not be excluded. This might especially be the case with younger stags. By visiting different areas, the young stags may also prepare for later in life by exploring the area and gaining experience.

It was the young stags that were observed to move to rutting areas with more females and higher female/adult male ratios. Males are sexually mature as yearlings, but they usually cannot hold a harem before the age of 5–6 years (Clutton-Brock et al. 1982). By going to areas with higher female/adult male ratios, the young stags might have a greater chance of a sneak copulation. For these young stags, however, the chances of mating success are probably small, partly because of competition from adult males (the percentage of adult males in the population varied between 6 and 11% during the study; A. Jarnemo, unpublished data), but also because it has been suggested that red deer hinds may try to avoid mating with males younger than 5 years (Clutton-Brock et al. 1982). The more adult dominant males that are present, the greater energy exerted by young males as they get harassed and the lesser chance to get a sneak copulation. Aggression from adult males could in fact be a proximate cause for the dispersal of young males (Wahlström 1994; Neuhaus 2006). Harem holders are frequently seen attacking young stags that come too close to the harem. This kind of harassment is rarely seen between adult stags. Knowing that any close contact infers a high risk of injury or even death, adult stags normally keep a safe distance and carefully measure each other up before possibly starting a fight (Clutton-Brock et al. 1982).

Among the dispersing stags, however, were also 38 stags classified as adult of which 19 had not been observed as harem holders. Adult stags may also search harems where there are possibilities to use a sneak mating tactic (Clutton-Brock et al. 1982). However, stags old enough to compete over females are likely to seek rutting areas unoccupied by dominant mature stags or areas where they have a chance to beat the resident harem holder. For the adult stags, it might not be the number of competing stags, or even the number of females, that are given highest priority. Being full-grown, they might try to take over a harem rather than having occasional matings as their primary goal. Instead of focusing on the number of females, they are perhaps more interested in the quality of the harem holder to see if it is worth to challenge him. This could offer one explanation for why adult stags were not observed to move to rutting areas with more females or a higher female/adult male ratio.

The reasons for harem holders to visit other rutting areas may seem more difficult to understand, especially when considering the significant move to areas with a lower females/all males ratio! However, six of the moving harem holders were seen in another rutting area towards the end of the rut. It could be that these stags stop by in another rutting area on their way back to the over-wintering areas (Jarnemo 2008). Two visits made early in the rutting season were made by harem holders known from the previous

year. These two stags were observed in another rutting area before entering the area where they were harem holders the previous year, and therefore seemed to stop by at the other area on their way from the summer quarters. Another harem holder appeared to have left his rutting area as a response to a decreasing number of females. During two consecutive rutting seasons, the fields in this area did not offer anything to eat; the majority of the females then seemed to leave for other areas. This harem holder, who was seen in his rutting area at the beginning of both these ruts, later left for a neighbouring area that was larger, where he also managed to become a harem holder; in the second year, he was not observed holding a harem. One special case was a dominant harem holder that seemed to commute between two rutting areas, doing so during three rutting seasons. There was also one case where a harem holder made an excursion to a neighbouring area and then returned to his harem place. Temporary stops on the way to and from the site of the harem, shifts to an area with more preferable food conditions, commuting and excursion therefore seemed to be the behavioural explanations behind these visits by harem holders to other areas. These other factors may, at least partly, explain the seemingly odd result of the significant move towards areas with a less preferable female/male ratio.

Consequently, it seems as if breeding dispersal in red deer is not a behaviour restricted to young males (yearlings and sub-adults), but also continues among prime-aged individuals, even among those that have become harem holders. The pattern that emerges is one where stags, especially those that have not reached prime breeding potential, move around between different rutting areas in the search for improved mating opportunities, and doing this in a manner similar to what has been found for bighorn rams (Festa-Bianchet 1986; Hogg 2000) and for primate males transferring between different groups (Parga and Lessnau 2008).

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References

- Ahlén I (1965) Studies on the red deer *Cervus elaphus* L., in Scandinavia. *Swed Wildl* 3:1–376
- Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH (1992) Density-dependent changes in the spacing behavior of female kin in red deer. *J Anim Ecol* 61:131–137

- Catchpole EA, Fan Y, Morgan BJT, Clutton-Brock TH, Coulson T (2004) Sexual dimorphism, survival and dispersal in red deer. *J Agri Biol Env Stat* 9:1–26
- Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behaviour and ecology of two sexes. Edinburgh University Press, Edinburgh
- Clutton-Brock TH, Rose KE, Guinness FE (1997) Density-related changes in sexual selection in red deer. *Proc R Soc Lond B* 264:1509–1516
- Clutton-Brock TH, Coulson TN, Milner-Gulland EJ, Thomson D, Armstrong HM (2002) Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415:633–637
- Dobson FS (1982) Competition for mates and predominant male juvenile dispersal in mammals. *Anim Behav* 30:1183–1192
- Dunham KM (2000) Dispersal pattern of mountain gazelles *Gazella gazella* released in central Arabia. *J Arid Env* 44:247–258
- Festa-Bianchet M (1986) Site fidelity and seasonal range use by bighorn rams. *Can J Zool* 64:2126–2132
- Feulner PGD, Bielfeldt W, Zachos FE, Bradvarovic J, Eckert I, Hartl GB (2004) Mitochondrial DNA and microsatellite analyses of the genetic status of the presumed subspecies *Cervus elaphus montanus* (Carpathian red deer). *Heredity* 93:299–306
- Frantz AC, Hamann J-L, Klein F (2008) Fine-scale genetic structure of red deer (*Cervus elaphus*) in a French forest. *Eur J Wildl Res* 54:44–52
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Ann Rev Ecol Syst* 13:1–21
- Haanes H (2008) Genetic variation and structure in Norwegian red deer. PhD thesis, Norwegian School of Veterinary Science, Oslo
- Hartl GB, Zachos F, Nadlinger K (2003) Genetic diversity in European red deer (*Cervus elaphus* L.): anthropogenic influences on natural populations. *C R Biol* 326:37–42
- Hetschold W, Vorreyer F (1968) Das Ansprechen des Rotwildes. Paul Parey, Hamburg
- Hmwe S, Zachos FE, Sale JB, Rose HR, Hartl GB (2006) Genetic variability and differentiation in red deer (*Cervus elaphus*) from Scotland and England. *J Zool (Lond)* 270:479–487
- Hogg JT (2000) Mating systems and conservation at large spatial scales. In: Apollonio M, Festa-Bianchet M, Mainardi D (eds) Vertebrate mating systems. World Scientific, Singapore, pp 214–252
- Howard WE (1960) Innate and environmental dispersal of individual vertebrates. *Am Mid Nat* 63:152–161
- Jack K (2003) Males on the move: evolutionary explanations of secondary dispersal by male primates. *Primate Rep* 67:61–83
- Jack KM, Fedigan L (2004) Male dispersal patterns in white-faced capuchins *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. *Anim Behav* 67:771–782
- Jarnemo A (2008) Seasonal migration of male red deer (*Cervus elaphus*) in southern Sweden and consequences for management. *Eur J Wildl Res* 54:327–333
- Johst K, Brandl R (1997) Evolution of dispersal: the importance of the temporal order of dispersal and reproduction. *Proc R Soc Lond B* 264:24–30
- Krebs H (1969) Schießen oder schonen?. Mayer, München
- Kuehn R, Schroeder W, Pirchner F, Rottmann O (2003) Genetic diversity, gene flow and drift in Bavarian red deer populations (*Cervus elaphus*). *Conserv Gen* 4:157–166
- Langvatn R, Albon SD (1986) Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Hol Ecol* 9:285–293
- Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age of first reproduction of a temperate herbivore. *J Anim Ecol* 65:653–670
- Lawson Handley LJ, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. *Mol Ecol* 16:1559–1578
- Liberg O, Wahlström K (1995) Habitat stability and litter size in the *Cervidae*, a comparative analysis. In: Wahlström K (ed) Natal dispersal in roe deer. PhD thesis, Stockholm University
- Lovari S, Herrero J, Conroy J, Maran T, Giannatos G, Stubbe M, Aulagnier S, Jdeidi, T, Masseti M, Nader I, de Smet K, Cuzin F (2008) *Cervus elaphus*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>. Accessed on 16 May 2009
- Lowe VPM, Gardiner AS (1974) A re-examination of the subspecies of red deer (*Cervus elaphus*) with particular reference to the stocks in Britain. *J Zool (Lond)* 174:185–201
- McPeck MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. *Am Nat* 140:1010–1027
- Meisingset EL, Langvatn R (2000) Variasjon i vekt og reproduksjon hos hjort i Norge: resultater knyttet till overvåkningsprosjektet for hjort. *Hjorteviltet* 2000:52–56
- Mitchell B, Lincoln GA (1973) Conception dates in relation to age and condition in two populations of red deer in Scotland. *J Zool (Lond)* 171:141–152
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2001) The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proc R Soc Lond B* 268:911–919
- Neuhaus P (2006) Causes and consequences of sex-biased dispersal in Columbian ground squirrel, *Spermophilus columbianus*. *Behaviour* 143:1013–1031
- Nussey DH, Coltman DW, Coulson T, Kruuk LEB, Donald A, Morris J, Clutton-Brock TH, Pemberton J (2005) Rapidly declining fine-scale genetic structure in female red deer. *Mol Ecol* 14:3395–3405
- Olupot W, Waser PM (2001) Correlates of intergroup transfer in male grey-cheeked mangabeys. *Int J Primatol* 22:169–187
- Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim Behav* 27:1–36
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. *J Anim Ecol* 67:518–536
- Parga JA, Lessnau RG (2008) Dispersal among male ring-tailed lemurs (*Lemur catta*) on St. Catherines Island. *Am J Primatol* 70:650–660
- Patthey P (2003) Habitat and corridor selection of an expanding red deer (*Cervus elaphus*) population. PhD thesis, Faculté des Sciences de l'Université de Lausanne, Lausanne
- Pemberton JM, Albon S, Guinness FE, Clutton-Brock TH, Dover GA (1992) Behavioural estimates of male mating success by DNA fingerprinting in a polygynous mammal. *Behav Ecol* 3:66–75
- Perez-Espona S, Perez-Barberia J, McLeod JE, Jiggins CD, Gordon IJ, Pemberton JM, Perez-Barberia FJ (2008) Landscape features affect gene flow of Scottish Highland red deer (*Cervus elaphus*). *Mol Ecol* 17:981–996
- Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Anim Behav* 65:519–530
- Reby D, McComb K, Cargnelutti B, Darwin C, Tecumseh Fitch W, Clutton-Brock T (2005) Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc R Soc Lond B* 272:941–947
- Rosenberry CS, Conner MC, Lancia RA (2001) Behavior and dispersal of white-tailed deer during the breeding season. *Can J Zool* 79:171–174
- Simon O, Kugelschaffer K, Mörschel F (1998) Effects of hunting on dispersal of red deer—implications for deer management in Germany. In: Zomborszky Z (ed) Advances in deer biology, Proc 4th Intern Deer Biol Congr, Kaposvar, pp 32–35

- Stenseth NC, Lidicker WZ (1992) Animal dispersal. Small mammals as a model. Chapman & Hall, London
- Wagenknecht E (1986) Rotwild. Neumann-Neudamm, Berlin
- Wahlström LK (1994) The significance of male-male aggression for yearling dispersal in roe deer (*Capreolus capreolus*). Behav Ecol Sociobiol 35:409–412
- Wolff JO (1993) What is the role of adults in mammalian juvenile dispersal? Oikos 68:173–175
- Zachos FE, Althoff C, Steynitz YV, Eckert I, Hartl GB (2007) Genetic analysis of an isolated red deer (*Cervus elaphus*) population showing signs of inbreeding depression. Eur J Wildl Res 53:61–67