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Key words: *Capreolus*, cohort effect, demography, density dependence, lifetime reproduction, population limitation, predation, roe deer, survival, social system.

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"Livet är sannerlige en berg-och-dalbana.

Alla är fastspända och ingen kan hoppa av. När barnmorskan

daskar dig i baken river hon biljetten, och så bär det av.

När färden övergår från ungdom till vuxen och mogen ålder,

sträcker man ibland upp händerna och tjuter, ibland håller man bara

krampaktigt i stången man har framför sig.

Men det är åkturen som räknas. Det mesta man kan hoppas på i

slutet av livet är nog att håret är rufsigt, att man är anfådd, och att

man inte kräktes."

Jerry Seinfeld

Contents

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I. Kjellander, P. Cederlund, G. and Liberg, O. Experimental evidence for density dependent fecundity in roe deer (*Capreolus capreolus* L.). Manuscript.

II. Kjellander, P. Persistent effects of density-dependent food limitation in roe deer (*Capreolus capreolus* L.) cohorts. Manuscript.

III. Kjellander, P. and Liberg, O. Effects of population density and fox predation on annual and lifetime reproductive success in female roe deer (*Capreolus capreolus* L.). Manuscript.

IV. Liberg, O. and Kjellander, P. Density dependent survival in juvenile and adult roe deer in south-central Sweden. Manuscript.

V. Kjellander, P., Ryberg, U., Liberg, O., Cederlund, G., Pettersson, L. and Roth, L. Effects of sex, season and population density on home range size in Swedish roe deer (*Capreolus capreolus* L.). Manuscript.

Introduction

Populations of many species fluctuate as though regulated, and studies of population fluctuations and what regulates population density have been central to population biologists for decades. However, whether and how most animal populations are regulated remains one of the principal unanswered questions in ecology, despite the many important implications for this knowledge (Sinclair 1989, Murdoch 1994). For example, understanding population regulation is essential for explaining species abundances, predicting the success of biological control, and designing management plans for species conservation as well as sustainable harvesting.

The extent to which populations are regulated by density-dependent factors or persist by less predictable processes has perhaps engendered more debate than any other issue in the history of ecology (Sinclair, 1989). Nicholson (1933) revolutionized thinking about population limitation when he introduced the concept of regulation through density-dependent factors, but was strongly criticized by Andrewartha and Birch (1954). Their disagreement was largely unintentional because they were arguing about different points. Andrewartha and Birch were concerned with limitation and limiting factors, and Nicholson was concerned primarily with regulation (Keith 1974, Sinclair 1989). Lack (1954) became the leading spokesman for the Nicholson view and was one of the first to discuss the subject more theoretically, but was later followed by many others. Failure to understand regulation stems, in part, from ambiguous usage of concepts such as regulation and density dependence. Although defining regulation is problematic, the present consensus is that a regulatory process involves some negative feedback mechanism that increases demographic rates when population size declines (and vice versa), relative to some equilibrium (Sinclair 1989, Murdoch 1994). Thus, this definition assumes the operation of one or more negative feedback mechanisms and a fixed equilibrium. However, Strong (1984) introduced the concept of "density vagueness", described by parameters of birth and death rates that in some cases are only weakly explained by density. Further, density vague population parameters were then argued to be most likely in natural situations at intermediate densities, at which factors such as weather, predation, habitat heterogeneity, and phenology may have a variable influence on demographic rates. This type of modeling has, however, mainly been atributed to stochastic modeling of insect dynamics.

Various mechanisms have consequently been suggested to potentially regulate single populations (Fowler 1987). Most investigations have focused on crowding effects that operate locally via direct and/or indirect interactions among individuals (Sinclair 1989). Other mechanisms proposed include the buffer effect and regulation via territoriality (McCullough 1990) and refuges from predation or parasitism (Andersson and May 1979, Hassel and Andersson 1989). Among these other mechanisms, the common theme is spatial heterogeneity. However, many ecologists believe the ultimate mechanism of feedback, i.e. density dependence, is increased competition for food resources and consequent depletion of the same (Lack 1954, Fowler 1987). The target of density dependence might in that case be any life history trait of importance, such as birth weight, growth rate, body condition, age at maturation, fecundity, or age specific survival. Eberhardt (1977) suggested

that the sensitivity of these rates to increased population density occur in a certain order. For large herbivores, juvenile survival seems to be most sensitive, followed by various aspects of reproduction (Fowler 1987, Gaillard *et al.* 1998). Processes, which show no relation to population size by being either constant or random, are termed density-independent (Sinclair 1989).

Members of the Cervidae family (deer) are the most important large game in the Northern Hemisphere, and are subjected to intensive management (McCullough 1979). Consequently density dependence has received much attention in this taxon, and its occurrence in at least some form has been reported for most species where studied (for reviews see e.g. Fowler 1987, Putman *et al.* 1996, Sæther 1997, Gaillard *et al.* 1998). Several studies have also demonstrated intricate trade-offs between age, growth, maturation, body mass, and reproductive investments that must be considered when density effects are evaluated (McCullough 1979, Albon *et al.* 1983, Sæther and Hagenrud 1983, 1984, Skogland 1985, 1990, Clutton-Brock *et al.* 1987, Gaillard *et al.* 1992, Sand 1996). Roe deer (*Capreolus capreolus* L.) are one of the smaller cervids (adult female body weight 15-30 kg) and are the most wide-spread and common hoofed game species in Europe (Andersen *et al.* 1998). Population density effects have also been documented in roe deer including fawn body weight (Gaillard *et al.* 1996), fawn summer survival (Andersen *et al.* 1995) and fawn production (Liberg *et al.* 1994, Vincent *et al.* 1995). However, it is quite obvious, particularly in the case of roe deer, that we need to have more information both on inter- and intraspecific variation regarding the relative sensitivity of various vital rates to different limiting factors, and especially density, before we can draw firmer conclusions and more importantly, establish the effects of this pattern on population growth and regulation (Gaillard *et al.* 1998).

In 1987 Fowler presented his review of density dependent factors affecting population dynamics in ungulates. Out of 21 species there was no evidence for density dependence in the dynamics of roe deer. This was at that time almost taken as further evidence for the existence of social regulation in this species. Territoriality in bucks was believed to maintain a stable population density at a level where density dependence could not be detected (Bramley 1970, Strandgaard 1972, Bobek 1977). As density dependence has now been demonstrated in several vital rates (Gaillard *et al.* 1998), and dispersal fails to prevent population growth in all populations studied thus far (Linnell *et al.* 1998), this view of the existence of social regulation has been abandoned (Linnell *et al.* 1998).

In this summary, I report on a twelve-year study in a free-living roe deer population, where the population density was experimentally manipulated. I investigate the effect of high population density on individual as well as cohort performance i.e. body weight, growth, reproduction and survival. This was done by first allowing deer density to increase followed by a dramatic reduction, while food availability and browsing pressure was monitored by an exclosure study. Individual deer were studied by an intense long-term radio collaring procedure and effects of density on home range dynamics was examined.

Further, I will focus on synthesizing theory and empirical evidence from the total study to elucidate the most important limiting factors for Swedish roe

deer populations and possibly discern a mechanism of regulation. As such I investigate the relationship between various life history traits (body size, body mass, fecundity, lifetime reproductive success, survival, etc.) and population density, predation, food availability and climatic variables. Finally, I investigate the effect of varying population density on home range size and territory size in roe deer.

The species

The range of the European roe deer covers most of Europe and extends from the Atlantic coast in the west to the Ural Mountains in the east, but it is most abundant in northern continental Europe and southern Scandinavia. The wide variety of habitats occupied by roe deer today is the best evidence of their success. They occur in almost all natural habitats found in Europe, including deciduous, coniferous and Mediterranean forests, shrublands, moorlands and marshes. Only high alpine areas above the treeline and the most open grasslands are rarely occupied (Andersen et al. 1998).

The roe deer is a small-sized cervid with weak sexual dimorphism in body size (Andersen et al. 1998). It is a concentrate selector, preferentially feeding on dicots like herbs and deciduous browse, whereas grass and other plants with a high fiber content are taken in small quantities only (Hoffmann 1985). This constraint means that the species is adapted to exploit early stages of forest succession, in which preferred browse are particularly abundant (Liberg and Wahlström 1995). The social system of the species has been examined in a number of previous studies (e.g. Kurt 1968, Bramley 1970, Strandgaard 1972, Ellenberg 1978, Vincent et al. 1995, Wahlström and Kjellander 1995). Female roe deer are non-territorial but live solitarily in overlapping home ranges. Male roe deer, on the other hand, undergo marked seasonal changes. In winter they are non-territorial like the females, whereas from spring (April) until after the rut in late August-early September they defend territories. Males become sexually mature as yearlings but do not defend territories earlier than as 2 yr. old (Liberg et al. 1998).

The reproductive cycle of female roe deer, with embryonic implantation delayed by five months and only one ovulation each year, seems to be unique among ungulates. Despite being monestrous, 98% of females in a population are fertilized (Gaillard et al. 1998). Females give birth to 1-4 neonates in May-June, with twins being most common and four being extremely rare. The fawns accompany their mother until they reach approximately one year of age, when most dispersal takes place (Wahlström and Liberg 1995). Females normally attain sexual maturity as yearlings, but under favorable conditions they may become pregnant already as fawns (Hewison 1996), whereas under poor conditions first reproduction is often delayed one year until the age of 3 yr. (Gaillard et al. 1998, Paper I).

In Scandinavia, the species has occurred since the retreat of ice during the last glaciation, i.e. about 10,000 years before present, but the population has fluctuated widely and gone through at least one severe bottleneck (Ekman 1919, Liberg et al. 1995). In historic time it ranged over approximately the

southern third of the Scandinavian Peninsula, up to 61° N latitude. In the late 18th century, the royal and aristocratic deer hunting monopoly was abolished, and a general permission for peasants to hunt deer was introduced. As a consequence, culling pressure increased and deer populations declined dramatically. In the 1830's the only known remaining population consisted of about 100 animals on one estate in the southernmost part of Sweden. On this estate the landlord protected the deer but it took almost 20 years until hunting was banned on a national level. After the introduction of strict hunting laws, changes in practices by removal of free-ranging and probably competing domestic livestock, and the successive near extermination of wolf (*Canis lupus*) and lynx (*Felis lynx*), the population quickly recovered. Within 60 years it had reoccupied its former range, and today it occurs nearly all over Scandinavia, up to approximately 67° N, except for the alpine region (Liberg *et al.* 1995).

Roe deer are regarded as a valuable game resource (Cederlund *et al.* 1998). In 1984 over 1.6 million roe deer were harvested in Europe (Gill 1990) and in Sweden alone only close to 400,000 roe deer were harvested in 1993 (Swedish Association for Hunting and Wildlife Management, Wildlife Surveillance 2000). Correct management of such a resource clearly requires a good understanding of population dynamics (Andersen *et al.* 1998, Gaillard *et al.* 1998), efficient population monitoring methods, and clear objectives (Cederlund *et al.* 1998). However, high density roe deer populations can also cause conflicts with other human activities, such as commercial forestry, agriculture, collisions with vehicles along roads and last but not least as a noxious animal in gardens, graveyards and parks (Putman and Kjellander, in press). In the latter contexts suburban deer are definitely an increasing phenomenon in Sweden.

Study area

The study was located in a 2,600 ha research area (Bogesund) within the hemiboreal zone in east-central Sweden, a few kilometers north of Stockholm (59° 23' N, 18° 15' E), (Fig. 1). The area was situated on the coast of the Baltic Sea on the inner portion of the Stockholm Archipelago. The study area constituted a major portion of a mainland peninsula surrounded by water on all sides except in the north. Some of the straits bordering the peninsula are rather narrow, in places less than 100 m (Fig. 1). Broad valleys and low ridges intersected the landscape, and altitude never exceeded 60 m above sea level. A mosaic of forested and field habitats characterized the area. Approximately 65% of the area was forested, 25% was agricultural, while bed rock areas and bogs constituted the remaining 10%. The forests were dominated by the coniferous tree species Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but deciduous species like birch (*Betula* spp.), aspen (*Popolus tremulus*), oak (*Quercus robur*), ash (*Fraxinus excelsior*) and willows (*Salix* spp.) were also common in most forest types (Guillet 1994). Dwarf shrubs, primarily bilberry (*Vaccinium myrtillus*), were unequally distributed as ground cover in mature forest stands, while numerous herbs were abundant in most habitats. In a habitat survey of the study area, bilberry was represented in 49% of the study plots, at a mean height of 24 cm ±10 (S.D.) (Guillet 1994). Acorn

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production was recorded in southern Sweden (at a distance of 400 km from the study area) while it is known that mast years occur concomitantly across the entire Swedish range of oak (Gustav Hamilton, Swedish National Board of Forestry unpubl. data). During this study only 1992 was recorded as a true mast year (Swedish Forest Seedlings (Ltd.) (unpubl. data), P. Kjellander, pers. obs.).
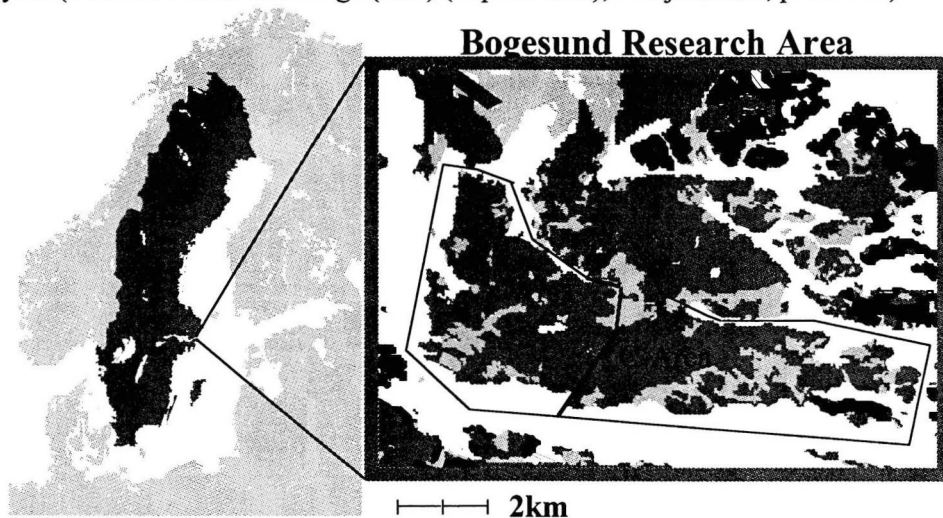
Bogesund Research Area

├──┼──┤ **2km**

Figure 1. The study site "Bogesund research area" (the experimental area (X-area) were the major part of field work was conducted and the control area (C-Area)) with its location in Sweden. The distribution of water (white), forest (dark grey), fields (light grey) and urban areas (black) on the Bogesund peninsula.

Some agricultural fields were resown in early autumn, but most were ploughed after harvest, kept bare during winter and sown in spring. Common crops were rape (*Brassica napus*), oats (*Avena sativa*) and wheat (*Triticum* spp.). Pastures make up less than half of the agricultural land. Associated with the open areas are numerous small meadows and former fields that lay fallow or are replanted with birch or spruce.

The climate was mild and influenced by the Baltic Sea. The warmest month was July with an average temperature of 16.7 °C, and the coldest is January with -3.7 °C. Annual precipitation was approximately 550 mm, with most falling in July, and the least in February. Snow cover normally lasted for 80 days, usually from late December to early March, with a maximum snow depth of 13 cm reached in February. These temperature and precipitation data from Stockholm were long-term means from 1931-60 (Swedish Meteorological and Hydrological Institute (SMHI) 1994). During the years 1989-92 winters were unusually mild with little or no snow, and deviated heavily from long-term means. Data were obtained from a meteorological station situated less than 20 km from the study area.

Other larger mammalian herbivores included a low-density (0.5-1/km^2) moose (*Alces alces*) population. Both mountain and brown hare (*Lepus timidus* and *L. europaeus*) occurred and fluctuated in numbers between years. The only

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roe deer predator of importance is the red fox (*Vulpes vulpes*) which was almost absent during the first half of the study period due to an outbreak of sarcoptic mange in Scandinavia. (Lindström *et al.* 1994). The nearest resident lynx population was for most of the study period more than 100 km to the north, but the lynx (*Lynx lynx*) population in Sweden is expanding south, and occasionally dispersing lynx might occur and hunt in the study area. Human residents in the area are few and dispersed. There were three large farms in the area associated with the open agricultural areas. During weekends and vacations the area was used extensively by the large nearby Stockholm population for recreation. Hunting was controlled by the research project.

Material and methods

There were a number of methods used in each separate study (paper I-V) including body measurements, systematic surveys, counts, field observations, etc. These methods are described in detail in the respective papers (I-V), however, here I present only a brief description, whereas study design and population estimates, critical to the study, are given more detailed attention.

Study design

Previous to the initiation of this study, roe deer were harvested in the study area through non-selective regular hunting by forestry staff and students at the Swedish University of Agricultural Sciences. The annual harvest during this period in the 2,600 ha area averaged 86 deer (37% adult males, 30% adult females, and 33% juveniles). In 1988 population control was initiated where the goal was to manipulate the population density experimentally in one area and keep it constant in another. The research area was divided into two subareas, one 1,250 ha experimental area ("X-area") on the western half of the peninsula, and one 1,350 ha control area ("C-area") in the east (Fig. 1). The two subareas were considered to be equivalent regarding habitat composition and density of roe deer. Beginning in 1988, deer in X-area were completely protected from hunting, which led to a rapid increase in density. In C-area, hunting practices were continued as before and annual harvests increased slowly during 1989-1992, and were on average 67 animals. In autumn and winter 1992/93 a major reduction of roe deer in X-area was performed by harvesting 360 animals, an estimated 75% of the animals present at the time.

Capture and radio marking of roe deer began in the X-area during winter 1988/89. Roe deer were caught, and aged as adults, yearlings, or fawns, using box traps set with livestock forage pellets as bait (n = 335) or nets (n = 4), or as newborns by hand (n = 63). Trapped animals were weighed (Table 1), measured and individually marked with plastic eartags in different colours combinations and equipped with radio collars (maximum life span 3.5 years, 151 MHz, Televilt International, Lindesberg, Sweden) weighing 50-300g before release (Table 2). A minimum of one radio position per month was taken for each radio-marked animal and during winter usually as often as once per week. The animals' status as alive or dead was determined based on

activity indication in the radio signal and movement since the previous position was taken. Suspected deaths were checked by a flushing effort. During the last seven years transmitters with a mortality function were used. Radiot tracking was conducted from the ground with a 3-element Yagi antenna. Animals were located by triangulation from at least three points along roads or hills. Error polygons were < 1 ha (Cederlund *et al.* 1979).

Population density

Annual density of roe deer in X-area was estimated using the Petersen method (Caughley 1977), which was based on the ratio of marked to unmarked animals among a sample of resightings in the field. Density estimates were made in April and September of each year. By summer of 2000, 402 deer had been marked. In April 1993 pellet group count censuses (Neff 1968, Cederlund and Liberg 1995) were performed over the entire research area including both X- and C-area, and continued for the remainder of the study. The density in the C-area was never censused prior to the pellet counts in 1993. Reproductive success in marked females was measured each year and defined as the number of fawns accompanying their mother during fall (September-December). This was accomplished from repeated visual field observations of female-offspring associations during summer and fall.

Density in the X-area in April 1989 was 10.3 ±3.1 (S.E.) deer/km^2 and peaked at 36.1 ±5.2 (S.E.) deer/km^2 in September 1992. In October 1992 the experimental reduction of roe deer by culling was initiated and in April 1994 the population was reduced to 8.2 ±0.8 (S.E.) deer/km^2. Between 1994 and 1996 the intention was to check the population increase by hunting, but the natural rate of increase during these years was so low that not much harvest was necessary, on average 21 animals (7 adult females) annually. Since 1997 the population has been allowed to increase again due to low hunting pressure. In September 1999 deer density was 16.8 ±1.7 (S.E.) deer/km^2 (Tab. 1).

Table 1. Body mass (kg) of roe deer cohorts as fawns and adults (Ad., ≥ 3 yrs.). No. of shot deer in the experimental area (X-area) and population density (deer/km^2) in April and September.

Cohort	Pop. dens.		No shot deer[1]	Mean fawn weight	N	Mean Ad. weight	N
	Apr.	Sept.					
1988	-	-	0	15.85	6	25.92	4
1989	10.3	9.3	0	15.97	15	25.66	6
1990	15.4	25.8	0	15.26	9	25.19	7
1991	28.5	30.6	22	14.79	19	24.95	3
1992	28.1	36.1	356	14.38	6	25.00	6
1993	7.9	18.5	142	16.04	29	26.32	6
1994	8.2	11.4	29	16.21	13	26.00	3
1995	8.7	11.8	17	16.61	13	26.56	4
1996	7.7	11.8	18	16.03	9	25.95	3
1997	7.5	9.9	9	16.35	9	-	0
1998	9.0	13.0	4	16.99	14	-	0
1999	12.0	16.8	19	15.96	32	-	0
2000	15.0	-	-	-	0	-	0

[1] Number of shot deer in the study area during winter, between September and April population censuses.

Table 2. Number of individual radio marked deer alive in the study area each year. M = male, F = female, 0 = fawn, 1 = yearling, 2 = prime age (2-7 yrs.), 3 = old (7+ yrs.).

Year	No. of ind. deer / age and sex category								Σ
	M 0	F 0	M 1	F 1	M 2	F 2	M3	F 3	
1988	5	3	2	1	1	1	0	2	15
1989	6	9	7	3	5	10	0	2	42
1990	10	11	6	8	17	16	0	9	77
1991	9	8	10	14	22	21	0	10	94
1992	3	3	7	5	24	28	0	9	79
1993	14	15	3	3	21	23	2	10	91
1994	5	8	7	8	7	23	3	7	68
1995	5	8	2	7	11	26	4	9	72
1996	2	6	5	7	17	25	5	10	77
1997	8	13	3	5	22	23	1	10	103
1998	14	10	3	8	22	27	2	11	97
1999	22	13	8	6	20	30	5	12	116
2000	7	13	-	-	-	-	-	-	-

Age was estimated to the nearest year in shot deer from tooth eruption and tooth wear patterns (Cederlund *et al.* 1991). Body mass was measured as dressed weight (kg), defined as the weight of the whole animal less heart, lungs and alimentary tract, but with skin, head, and legs included. Body size was estimated using mandible length as an indication of skeletal size (Staines 1978, Skogland 1983, Ratcliffe 1987). Fecundity was measured for shot females as the number of corpora lutea present in the ovaries during the autumn hunt.

Red fox

Population density of red fox was not assessed in the area during the study. However, fox bag records per effort of hunting days in the study area was recorded during 1980-1999 as foxes were shot by chance during regular deer hunting. In addition to this estimate, official county statistics of total fox bag (Swedish Association for Hunting and Wildlife Management, Wildlife Surveillance 2000) were also used as an index of fox density. In total, 104 foxes were shot during 1980-2000 in the study area, with a range from 0 to 20 per year. Hunting effort in the study area during 1980-2000 was in total 4,412 deer hunting days ranging from 190 to 392 days per year.

The two independent indices of fox density were used as a basis for my classification of the period when fox numbers were low due to a sarcoptic mange outbreak (1984–1993). Thus, fox numbers were categorized as "Low fox" during years of high abundance of sarcoptic mange (1984-1993) and as "High fox" during years when foxes had returned (1994-2000), (Paper III).

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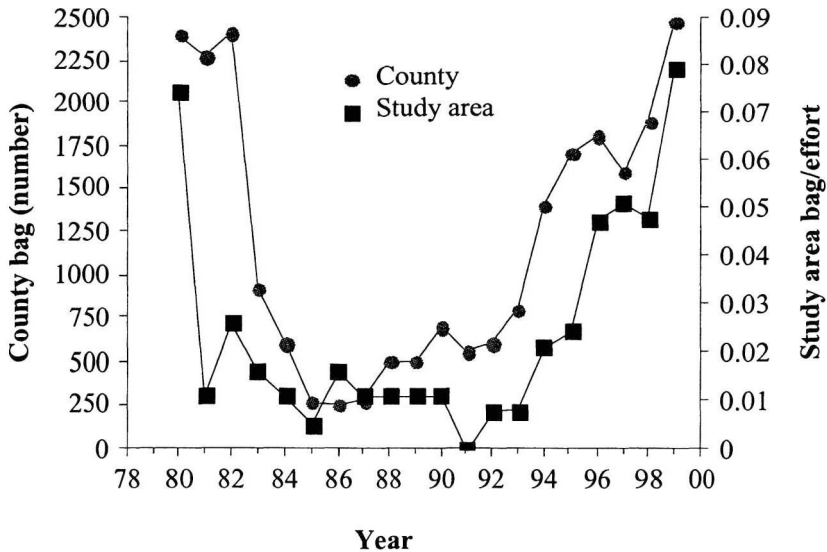
Figure 2. Total yearly county fox bag and fox bag per effort of hunting days in the study area (1,200 ha) during 1980-1999.

Exclosure study

Ten control exclosure plots (CX-plots) and 10 browsing or experiment plots (BR-plots) were monitored twice a year, in mid-November and early April, for examining browsing effects on the main food plants of roe deer. Three different measurements were taken directly in the plots, i.e. average height of bilberry, number of ramets, and number of fresh bites on this species. Each measurement was taken in four random subplots (25 x 25 cm) within each CX- or BR-plot (31.5 m^2 each). Furthermore, during each visit, one of the 25 x 25 cm subplots was harvested with regard to all above ground live bilberry ramets visible. Each sample was divided into two fractions, i.e. twigs and older woody parts, dried at 60° C for 48 hours, and weighed (0.01g). The proportion of twig biomass (%) of total ramet biomass in the BR-plots was used as an estimate of browsing pressure, or when measured in November, as available winter food. This estimate corrected for annual variation in growth will be refered to as "Food abundance (%)".

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Result and Discussion

In this study density dependence has been demonstrated in all important components of demography of the Bogesund roe deer population, i.e. fecundity and survival (dispersal has not been investigated). Further, I demonstrate that negative effects of high population density that roe deer might suffer during the first two years of life will affect them for the remainder of their lives (cohort effects).

Density dependent fecundity and emerging cohort effects

It has not been a straightforward to draw such conclusions. First, fecundity (number of corpora lutea) and body weight was found to decrease in all age classes in the experimental area after density increased, while they remained unchanged in the control area (Fig. 3). Body size decreased in those age classes that were raised during the experimental period with increasing density. Much of the effect of density on the fecundity of deer was coupled to corresponding effects on body mass and body size, and I concluded that the latter may cause persisting effects in affected animals (Paper I).
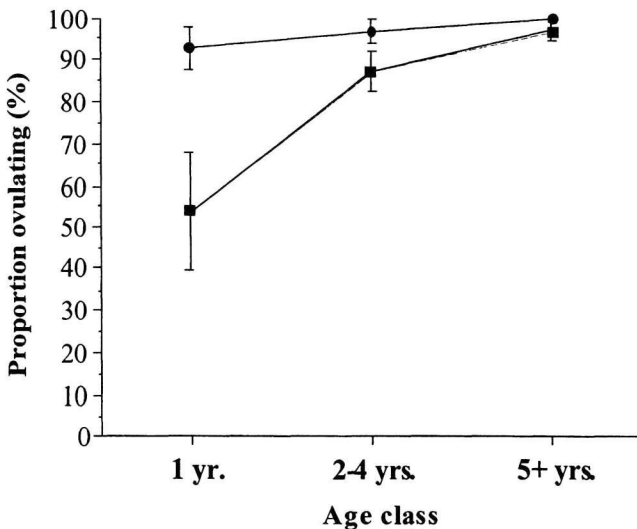
Figure 3. The age specific effect of density on the probability of ovulation (0 vs. 1-4 ova) for two contrasting population densities. Bold bullets represent low density and bold squares represent high density. Error bars represent the Standard Error.

This results led to the realization that whole cohorts might be negatively affected by high population density. It has recently been demonstrated that environmental conditions experienced during early development will affect both future survival and reproductive performance in many mammal species (Lindström 1999) and thus can have a strong effect on individual development. Individuals which get a good start in life will perform consistently better during life than their less lucky conspecifics. If between-

year variation in external conditions affects the early development of whole cohorts in a consistent way, this may also have strong effects on the demography of a population (Lindström 1999). One such type of external condition that might affect a whole cohort is population density. Cohorts born during high density might perform poorly, even after density has declined. This will prolong negative effects of high density, and may also confound studies of density dependence.

Effects of early development on lifetime reproductive success

Longitudinal studies that follow the breeding success of the same individuals throughout their life have an advantage over the usual practice of just comparing the survival and reproductive performance of different age classes (Clutton-Brock 1988). In this thesis I present a study of the former type and significant negative effects of population density and food abundance on several examined traits (fawn cohort body mass, cohort growth rate and final adult body mass, Paper II)(Fig. 4). Although body mass is not the only determinant of expected future reproduction, it is definitely the most important factor (Begon *et al.* 1996). Birth weight is known to affect both adult body size and reproductive performance (Dooney and Gunn 1981, Albon *et al.* 1987, Clutton–Brock *et al.* 1987). It is consequently probable that the annual variation in body mass demonstarted in this study also should generate differences in reproductive performance and survival between cohorts, even though measured at 20-22 months of age. Therefore long-term consequences of early development on lifetime reproduction was examined and significant effects of population density during early development in life on age-specific reproduction as well as on lifetime reproductive success (LRS, Paper III) were found. Much of the effect of density on LRS of deer was coupled to corresponding effects on longevity and body mass (Fig. 5). However, density still contributed to LRS even after the other two factors were controlled for. This result likely has its basis in the effect of body size that was investigated in Paper I. When born under severe conditions i.e. high population density, both body mass and growth are negatively affected and those unfortunate individuals born under severe conditions seem predestinated to become small low-performing deer.
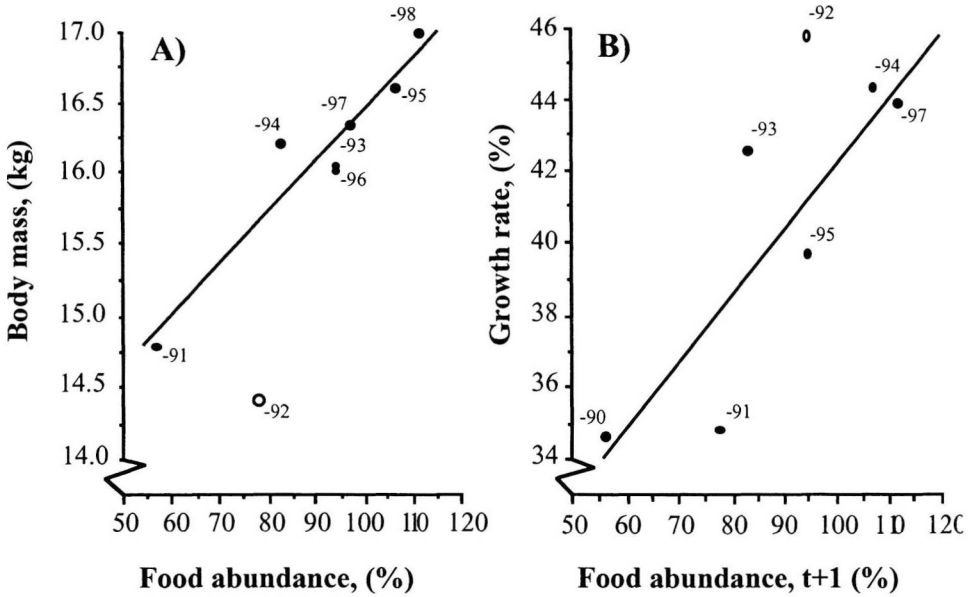
Figure 4. A). Food abundance (%) in the year of birth vs. mean fawn cohort body mass. Y = 12.9 + 0.4x. B). Food abundance (%) the second fall in life (food abundance, t+1) vs. mean cohort growth rate from their first to their second winter. Y = 23.6 + 0.2x. The mast year of 1992 (open symbol) is not included in the regression lines.
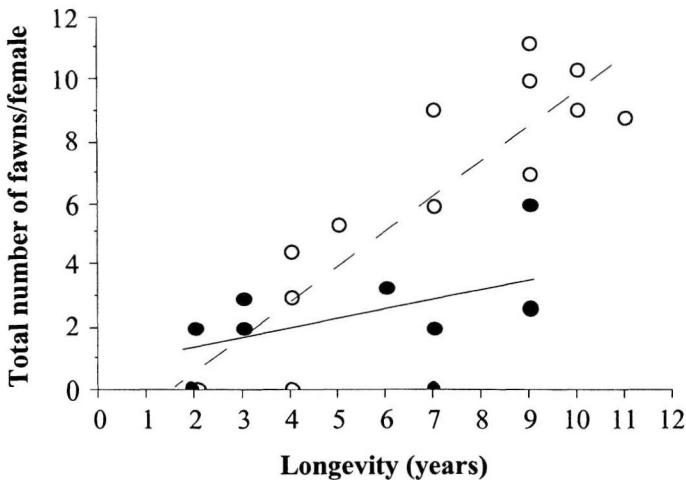
Figure 5. Lifetime reproductive success (LRS) in individual female roe deer in relation to longevity. Females are categorised according to population density during early development (first year in life), low density (open circles) and high density (black dots).

Effects of population density on survival

As the next step, the second investigated component of demography in the Bogesund population was survival patterns (Paper IV). There were significant effects of increased population density on survival in all age classes including

the prime age class. The lowest survival, and also the strongest density effects, was found in the juvenile age class. The negative effect on survival persisted in all age classes at least for three years after peak density. Again, there was a significant negative effect of population density in the year of birth, but this time on survival, at least up to the age of 2 yrs., (Fig. 6). I hypothesize that much of the effect of density on cohort survival was coupled to corresponding effects on body mass, since there is a good correlation between body weight and survival in ungulates in general (Paper III). In this context, a mechanism for lag effects on survival is suggested.
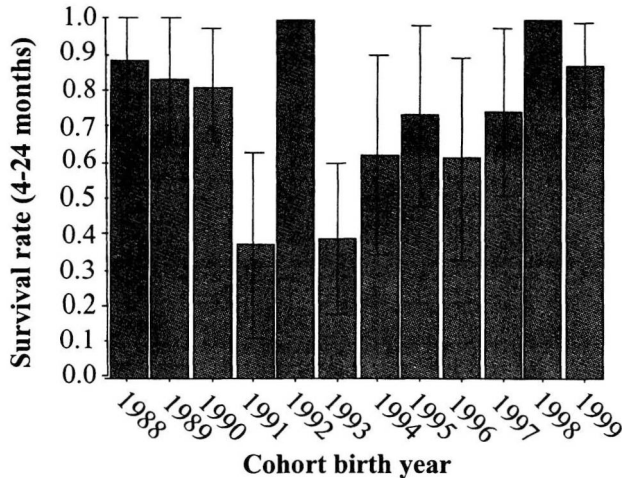
Fig. 6. Figure 5. Survival between 4 and 24 months of age for roe deer cohorts born 1988-1998. In 1999 survival is estimated between 4 and 15 months only. Error bars represent 95% C.I. Upper limits for the 95% C.I. are cut at survival 1.0.

Effect of the social system

An unintentionall discovery was made concerning the potential effect of population density on spatial dynamics of the Bogesund roe deer population that might influence vital rates. In conjunction with environmental heterogeneity socially dominant individuals might occupy the best home ranges and lower ranked individuals are forced to occupy lower quality home ranges. Relatively small increases in density might in that way result in declining average home range quality and as such have a fortifying negative effect on rate of increase (r)(Lomnicki 1988, McCullough 1990). However, significant effects of sex, season and population density on home range size was found in the Bogesund population. Male territory size decreased significantly with increasing population density and winter range size in both sexes became smaller when population density increased (PaperV). It is suggest that much of the effect of deer density on winter home range size was coupled to the solitary behaviour and social system of roe deer, with possible effects of dominance rank also outside the mating season.

Effects of fox predation

Predation as a cause of mortality was not investigated specifically in this study. However, at the onset of the study, the only predator of juvenile roe deer present, red fox, was down to an extremely low density due to an outbreak of epizootic sarcoptic mange. Fortunately, the red fox population did recover during the study period, which gave us an opportunity to also analyze the combined effects of density and predation on annual offspring recruitment in the roe deer population. Significant effects of maternal age on roe deer reproductive success (mean number of fawns/female) was found in years of high fox density but not in years of low fox density, and an inverse density dependent relationship between annual reproductive success and population density in years of high fox density but the opposite in years of low fox density (Paper III). The inverse density dependent relationship in annual reproductive success to population size in years of high fox density seems to be an obvious example of how easily concealed responses in reproduction may be to various external conditions (McCullough 1990). Without knowledge of the sarcoptic mange outbreak and subsequent recovery in the fox population, the current data set could have been completely misinterpreted. Further, this inverse density dependence in predation indicates no numerical response by foxes to increased numbers of roe deer fawns, but rather a constant kill. This seems plausible since fox numbers are limited 10 months of the year by factors other than the supply of roe deer fawns (Fig. 7). The effect of a mother's age on summer survival of fawns has not been demonstrated previously for roe deer. On the contrary, roe deer generally are considered to show no differential distribution of maternal care over age classes, except during senescence (Andersen *et al.* 1998). This age effect appeared only in years after fox recovery, indicating a learning behavior by female roe deer. Once a female has suffered losses of fawns due to fox predation she might behave differently in consecutive reproductive seasons.
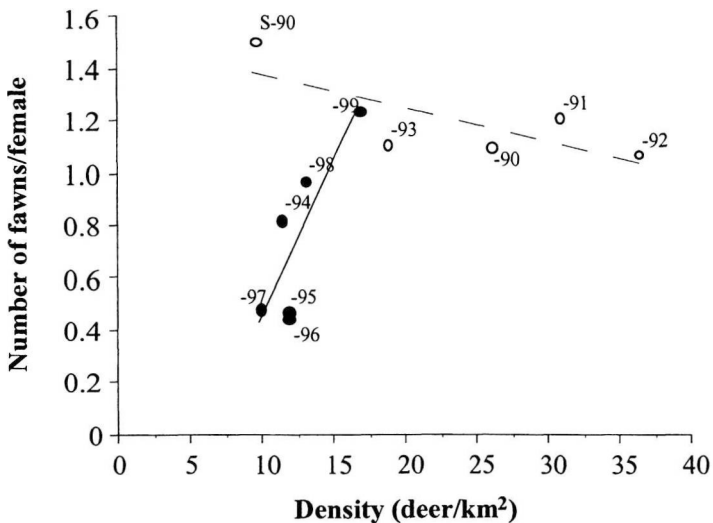
Figure 7. Number of roe deer fawns per adult marked female during fall (except fall 1989 = S-90) in relation to roe deer population density in September at low (open circles) and high (black dots) fox density.

Food

Lastly, no relationship was found between population density and the main winter food, standing bilberry biomass, but a significant effect on the bilberry twig abundance (Paper II), (Fig. 8). Further, I found indications of food limitation that might be both dampened and fortified by density independent changes in the environment. In 1992 (peak density), growth rate was higher than expected in relation to density and the coefficient of variation in growth rate lower than expected in relation to density. Further, the radio-marked cohort born in 1992 had an extraordinary good survival both as fawns, yearlings and adults in spite of high population densities during those years. Several independent indices point in the same direction, supporting the assumption of an exceptional density independent effect of the acorn mast year of 1992, dampening the negative effect of high population density (Paper II).
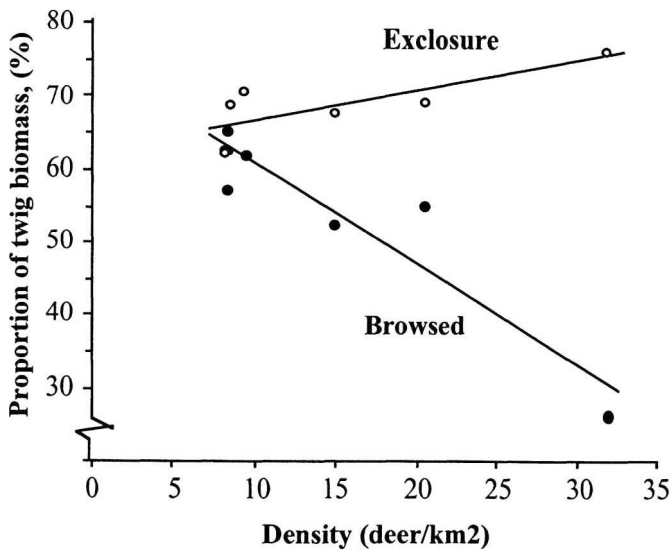
Figure 8. Relative twig biomass out of total biomass measured in the bilberry exclosures (open symbols) and unfenced browsing plots (solid symbols) vs. roe deer density in spring, measured in April.

Competition for food, the regulating factor?

Generally, food seems to be the main factor behind population regulation in ungulates. The bulk of density dependent changes presented in the literature are attributed to food resources at high population densities. Even when other factors such as predation and disease are considered, these factors are often observed to occur in response to the weakened condition of animals faced with limited food resources. Based on the data presented in this thesis, and even though sample sizes contrained to one (n = 1), I suggest that the Bogesund roe deer population ultimately is regulated by intraspecific competition for limiting food resources. Additionally, the behavioral and social factors previously suggested to operate in roe deer population regulation (Bramley 1970, Strandgaard 1972, Bobek 1977) I believe are secondary responses to food limitation. I thereby define regulation as a process that retards population increase at high densities and relaxes it at low densities, but that there is not necessarily a fixed equilibrium level ("K") to which the population returns after deviations (Sinclair 1989). More likely there is a density range within which K oscillates. Also, the kinds of dynamic patterns generated by predators and parasites could theoretically be similar to those observed in the present study (Sinclair 1989). They all tend to depress the abundance of their prey or hosts, to an extent that depends on the degree to which they reduce survival or reproductive rates. The reduced populations can then persist around a "stable" equilibrium or may show cyclic behavior.

In the absence of large mammalian predators, most ungulate populations studied in Europe are probably capable of overexploiting forage and subsequently becoming limited by food shortages as also found in this study. However, the nearest resident lynx population was for most of the study period not more than 100 km to the north, and expanding south. What will happen if lynx establish in the Bogesund area? Wherever lynx coexist with roe deer, the latter almost always become the major prey species even in areas with low roe deer densities (0.5 deer/km^2, east Norway, Aanes *et al.* 1998) and lynx was estimated to remove 41% of available roe deer in that area annually (Linnell *et al.* 1996). At Grimsö Wildlife Research Area in south central Sweden, at a roe deer density between 5 and 10 deer/km^2, preliminary estimates give an annual roe deer mortality of 15-20% caused by lynx (Andrén *et al.* unpubl. data). In more northern areas than Bogesund, lynx predation and snow mediated mortality therefore seems to be able to cause population decline. On the other hand, in a high density (> 20/km^2) roe deer population in Switzerland Liberek (1992), estimated that lynx remove 4% of the population annually. Thus, there are no published studies yet which provide evidence for high density roe deer population decline caused by lynx predation and the initially asked question therefore has to remain unresolved.

Conversely, if variation in vital rates were random, the probability of extinction would be extremely high. But, population persistence is dependent upon survival, reproductive rates, etc. not being random when N is low, i.e. density dependence tends to operate strongly at low density and this reduces the probability of extinction. Further, there seems to be a general pattern, supported by this study, that adult survival rates are less likely to vary with population density than juvenile survival (Eberhardt 1977). Even though density dependence on adult mortality is rarely reported, less likely and

appears to be buffered against density effects, it was significant in this study but varied much less between years than did fawn mortality.

McCullough (1979) subtitled his famous and seminal book about the George Reserve white-tailed deer herd in Michigan "Population ecology of a K-selected species". However, when making comparisons within the Cervidæ family this is somewhat misleading since white-tailed deer, like its European ecological equivalent, the roe deer, is a polytocous species, with an ability to produce quadruplets, in contrast to the great majority of species in the family that only produce one young, i.e. being monotocous. Reproductive rates therefore are among the highest recorded within the Cervidæ. Both species (white-tailed and roe deer) has evolved in rapidly changing and unpredictable environments, created particularly by forest fires. These deer have probably responded to this type of environment through a great capacity for dispersal and ability to exploit exceptionally rich browse production that occurs after large scale destruction of mature forest (McCullough 1979, Liberg and Wahlström 1995). By evolving an inherent flexibility in reproductive parameters, such as age at maturity and number of offspring (0-4), both species are actually slanted to the "*r* - end" of the *r* - K continuum within the Cervidæ.

The general conclusion of many evolutionary arguments (Fowler 1981) is that populations of large animals should show density dependent changes at high densities close to carrying capacity. Further, species with large physiological capacity to reproduce can show a pronounced response to changes in density, as the roe deer in this study, while species with small physiological range (e.g. litter size constrained to one) can show a less pronounced response. Stubbs (1977) and Fowler (1981, 1987) have presented theoretical arguments and literature reviews suggesting that K-selected species should show the strongest density dependent response close to K, whereas *r*-selected species should show the strongest response when N is low. Because of large birth weight and small litter size, physiological and morphological limitations exist on the reproductive rate for strongly K-selected species, thereby constraining *r*. Thus, once a stable age distribution has been achieved, growth tends to be fairly constant up to a level close to K for these species, after which a decline in *r* occurs relatively rapidly. In this context and considering Eberhardts (1977) proposed sequence of effects on poulation growth of increasing density (juvenile survival, age of first reproduction, adult reproductive rate and lastly adult survival), I now in the case of the decicive Bogesund roe deer can conclude that Eberhardt (1977) probably was right.

The existence of pronounced differences in reproductive performance between successive cohorts, as demonstrated by Albon *et al.* (1987) in red deer (*Cervus elaphus*) as well as in this study on roe deer, has important implications for our understanding of population biology. It predicts that population size and recruitment will continue to oscillate after populations have reached carrying capacity, as good and poor cohorts progress through their lifespan. Thus I suggest this phenomenon to play a role in the paradigm of "irruptive population behavior" (Leopold 1943) critically reviewed by McCullough (1997). The concept of irruptive behavior in ungulate populations could briefly be described as a reduction in K as a result of a drastic population increase, overshoot and following crash. Subsequently, the population would grow to an equilibrium or dampened oscillations at a

substantially lower number than the first population peak (Leopold 1943, modified by Caughley 1970). However, despite its great intuitive appeal and being widely believed by deer biologists it has mostly anecdotal support and well-documented cases are rare (McCullough 1997). In this study, such negative effects of the first initial peak (1992-1993) creating cohort effects might very well cause a population to become more sensitive to natural or anthropogenic factors simply by a lower r not related to K. Even if not examined explicitly in this thesis, the lag phase in the Bogesund population (1994-1996) is most likely an effect of low performing cohorts dominating in numbers. If instead of inducing the experimental reduction a natural crash had been awaited, the effect of low performing cohorts would have been even greater and probably could have caused further oscillations in future dynamics. This hypothesis is supported by the fact that no effect was found of of population density on standing bilberry biomass, even though it is only one of several important food species. The present findings suggest that the Leopold-Caughley paradigm is in need of revision. In the long run I predict such a pattern to gradually disappear as low-performing cohorts die out and are replaced by better conditioned subsequent generations. However, the reason for inducing the reduction in the present study was because other components of population dynamics were in focus and from a population already at equilibrium, little can be learned about either the density dependent processes that culminate in zero rate of increase or the intensity of resource limitation. The most revealing studies involve natural experiments with either growing populations or populations deliberately reduced from equilibrium (Caughley 1970, Sinclair 1977, McCullough 1979, Bayliss 1985), whereas such manipulative studies of ungulates are uncommon.

Finally, in an ideal deterministic world, there is often little problem. Average or total population size could be used to study density dependent relationships, even when the regulatory process stems from heterogeneity (Hassel 1986). The actual problem is that such determinism rarely applies since so much environmental noise often hides density dependent relations (May 1989). The detection of regulation in such cases is then advised to be done by a more "flexible" approach to field studies. Long-term population studies combined with experiments and observations remain crucial, but more effort should be devoted to studying the individual variability (Hassel 1986, Lomnicki 1988).

Management implications

Irruptive ungulate populations is a common problem confronting nature conservation, and a certain loss of biodiversity has recently been suggested as an effect of overbrowsing by dense ungulate populations in Sweden (Berquist 1998, Angelstam *et al.* 2000). This negative effect could be reduced by increasing offtake while irruptions may be stabilized by management decisions to achieve goals based upon given values. However, if decisions are not based on scientifically tested and empirically sound paradigms, result of management will be populations shaped in artificial ways rather than along a natural course (McCullough 1997). In the absence of large natural predators from most of the Scandinavian Peninsula, estimates of appropriate offtake of roe deer are crucial. Harvesting is a complex activity whose product is as much

sports and recreation as it is meat or trophies. Whether or not one considers it is appropriate or ethical to harvest a population of roe deer depends more on one's view of life than what may be happening in the forest. But there is an ethical aspect that is fundamental to all wildlife harvesting, i.e. culling must result in a sustainable offtake, a yield that can be taken year after year without jeopardizing future yields or ecosystem function. In most game species the strategy of harvesting is simple, i.e. to harvest the population at the same rate as it is increaseing. Hence, a roe deer population increasing at 35% per year can be harvested at around 35% per year. This simple model of harvesting is sometimes applicable in reality (Caughley and Sinclair 1994). However, sustainable harvest of a wildlife species can rarely be achieved without at least some knowledge of the form and magnitude of density dependence (Caughley 1977, Caughley and Sinclair 1994). In that contex this study should be extremely useful. Density dependence may, however, operate through several mechanisms, such as the facilitated spread of contagious diseases, parasites with increasing density or as a functional response in predators or as suggested in this study, by competition for food. Offtake is then set by the desired management goal in relation to the population's growth pattern, which in turn is determined by the relationship between the population and its limiting factors.

This study should have clarified several steps towards an ecologically sound management model for roe deer based on scientifically tested hypotheses and has possibly shed some light on the importance of cohort effects in population dynamics. However, what we have not done is to evaluate the separate effect of early development on population growth, which might have profound effects in harvest models. But in such "realistic models" of populations it is necessary to also understand stochasticity and the important role it plays in natural systems. I hope this work leads towards better understanding in future modeling, not only in roe deer management but also in ungulate management in general, and hopefully such models will become accessible to the people who need them, i.e. conservation biologists and wildlife managers.

Litterature Cited

Aanes, R., Linnell, J.D.C., Perzanowski, K., Karlsen, J. & Odden, J. 1998. Roe deer as a prey. In: Andersen, R., Duncan, P. & Linnell, J.D.C. (eds). The European Roe Deer: the Biology of Success. Scandinavian University Press, Oslo.

Albon, S. D., Mitchell, B. & Staines, B. W. 1983. Fertility and body weight in female red deer: a density dependent relationship. J Anim Ecol, 52:969-980.

Albon, S. D., Clutton-Brock, T. H. & Guinnes, F. E. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. J Anim Ecol, 56:69-81.

Andrewartha, H. G. & Birch, L. C. 1954. The distribution and abundance of animals. University of Chicago press, Chicago. Cited in, Cherret; Ecological concepts. 1989. Blackwell scintific publ. Camebridge.

Andersen, R., Gaillard, J-M., Liberg, O. & San José, C. 1998. Variations in life history parameters in roe deer. In: Andersen, R., Duncan, P., Linnell, J.D.C. (eds). The European Roe Deer: the Biology of Success. Scandinavian University Press, Oslo.

Andersen, R., Linnell, J.D.C. & Aanes, R. 1995. Rådyr i kulturlandskapet. Slutrapport. NINA Fagrapport 10:1-80.

Andersson, R. M. & May, R. M. 1978. Regulation and stability of host-parasite population interactions:I. Regulatory processes. J Anim Ecology, 47:219-247.

Angelstam, P., Wikberg, P.E., Danilov, P., Faber, W.E. & Nygren, K. 2000. Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. Alces 36:133-145.

Bayliss, P. 1985. The population dynamics of red and western grey cangaroos in arid New South Wales, Australia. I: Population trends and rainfall. J Anim Ecol, 54:125-129.

Begon, M., Harper, J.L. & Townsend, C.R. 1996. Ecology. Third edition. Blackwell Scientific, Boston, Mass. USA.

Bergquist, J. 1998. Effects of large herbivores on plant community and early succession in south Swedish spruce forests. In: Influence by Ungulates on early plant succession and forest regeneration in South Swedish spruce forests. PhD Thesis. Swedish University of Agricultural Scienses, Uppsala, Sweden.

Bobek, B. 1977. Summer food as the factor limiting roe deer population size. Nature, 7.47-49.

Bramley, P. S. 1970. Territoriality and reproductive behaviour of roe deer. J Repr and Fert, 11:43-70.

Caughley, G. 1970. Population statistics of chamois. Mammalia, 34:194-199.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London.

Caughley, G. & Sinclair, A.R.E. 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Boston. 334 pp.

Cederlund, G. Bergqvist, J., Kjellander, P., Gaillard, B., Boisaubert, P., Ballon, P. & Duncan, P. 1998. Managing roe deer and their impact on the environment. (In: The European roe deer: The biology of success, Andersen, R., Duncan, P. & Linnell, J. Eds.). 14:337-372. Scandinavian University Press. Stockholm.

Cederlund, G., Dreyfert, T. & Lemnell, P. A. 1979. Radiotracking techniques and the reliability of systems used for larger birds and mammals. Swedish Environment Protection Board, Solna, Sweden, Report, 1136:1-102.

Cederlund, G., Kjellander, P. & Stålfelt, F. 1991. Age determination of roe deer by tooth wear and cementum layers - tests with known age material. Trans XX IUGB Gödöllö. 540-545.

Cederlund, G., Kjellander, P. & Liberg, O. 1993. Effects of buck hunting on spatial distribution among roe deer (Capreolus capreolus L.). Trans XXI IUGB Halifax, Kanada. 271-278.

Cederlund, G. & Liberg, O. 1995. Rådjuret. Viltet, ekologin och jakten. Almqvist & Wiksell, Uppsala.

Clutton-Brock, T.H. 1988. Reproductive Success. In "Reproductive Success". Ed. T. H. Clutton-Brock, Univ of Chcago Press, Chicago. 472-485.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. J Anim Ecol, 56:857-871.

Clutton-Brock, T. H., Major, M., Albon, S. D. & Guinness, F. E. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. J Anim Ecol, 56:53-67.

Dooney, J.M. & Gunn, R.G. 1981. Nutritional and other factors in breeding performance of ewes. Environmental factors in mammal reproduction (Ed. D. Gilmore & B. Cook), Macmillan, London. pp. 169-177.

Eberhardt, L.L. 1977. Optimal management policies for marine mammals. Wildl. Soc. Bull. 5:162-169.

Ekman, S. 1919. Några jaktbara djurarters historia under senare tid. 3. Rådjuret (In Swedish with English summary: The dispersal of roe deer in recent time.). Svenska Jägareförbundets Tidskrift, pp. 11-51.

Ellenberg, H. 1978. The population ecology of roe deer, Capreolus capreolus (Cervidae) in Central Europe. Spixiana Suppl. 2: 5-211.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology, 62:602-610.

Fowler, C. W. &. 1987. A review of density dependence in populations of large mammals. Genoways, (Ed.) Current Mammology Plenum, 1:401-441

Gaillard J-M., Delorme, D., Boutin, J-M., Van Laere, G. & Boisaubert, B. 1996. Body mass of roe deer fawns during winter in 2 contrasting populations. J Wildl Manage. 60:29-36.

Gaillard, J-M., Festa-Bianchet, M. & Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. TREE 13:57-63.

Gaillard, J.M., Liberg, O., Andersen, R., Hewison, A.J.M. & Cederlund, G. 1998. Population dynamics of roe deer. In "The Euorpean roe deer - Studies of adaptation and variation". Eds. Andersen, R., Duncan, P. & Linnell, J. Scandinavian University Press. 309-335.

Gaillard, J. M., Sempréré, A. J., Boutin, J. M., Van Laere, G. & Boisaubert, B. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (Capreolus capreolus). Can J Zool, 70:1541-1545.

Gill, R.M.A. 1990. Monitoring the status of European and North American cervids. GEMS Information Series Global Environment Monitoring System., pp. 277. United Nations Environment Programme. Nairobi, Kenya.

Guillet, C. 1994. Winter home range and habitat use of roe deer in two forest environments of Sweden. –Mémoire de stage 3éme anné Formation des Ingénieurs Forestiers de l'E.N.G.R.E.F., Nancy, France, 79 pp.

Hassel, M. P. 1986. Detecting density dependence. TREE, 1: 90-93.

Hassel, M. P. & Andersson, R. M. 1989. Predator-prey and host-pathogen interactions. Ecological concepts (ed. by J.M. Cherrett). Blackwell Scient. Publ., Oxford pp:147-196.

Hewison, A.J.M. 1996. Variation in the fecundity of roe deer in Britain: Effects of age and body weight. Acta Theriologica. 41:187-198.

Hofmann, R. R. 1985. Digestive physiology of deer – their morpho-physiological specialisation and adaptation. In: Fennessy, P.F.&Drew, K.R. (eds.): Biology of Deer Production. Royal Society of New Zealand. Pp. 393-407.

Keith, L. B. 1974. Some features of population dynamics in mammals. Trans, IUGB, Stockholm, 11:17-57.

Kurt, F. 1968. Das Sozialverhalten des Rehes (Capreolus capreolus L.). Paul Parey, Hamburg, 101 pp.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon press, Oxford. Cited in, Cherret; Ecological concepts. 1989. Blackwell scintific publ. Camebridge.

Leopold, A. 1943. Deer irruptions. Wisconsin Conservation Bulletin 8:3-11.

Liberek, M. 1992. Analyse du prélevement du lynx (*Lynx lynx* L.) dans le Jura vaudois (Suisse): premiere approche de l'influence se ce predateur sur les populations d'ongules. Diploma thesis, University of Neuchâtel, Switzerland.

Liberg, O., Cederlund, G., & Kjellander, P. 1994. Population dynamics of roe deer in Sweden: A brief review of past and present. Milne, J. A. & Reid, H. W. Proc third Internat Congr Biol Deer. Edinburgh.

Liberg, O., Johansson, A., Andersen, R. & Linnell, J.D.C. 1998. Mating systems, mating tactics and the function of male territoriality in roe deer. In "The Euorpean roe deer - Studies of adaptation and variation". Eds. Andersen, R., Duncan, P. & Linnell, J. Scandinavian University Press.

Liberg, O. & Wahlström, K. 1995. Habitat stability and litter size in the Cervidae; a comparative analysis. In: Wahlström, K.: Natal dispersal in roe deer. Thesis, Stockholm University, Stockholm.

Lindström, E. R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P-A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994. Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. Ecology, 75:1042-1049.

Lindström, J. 1999. Early development and fitness in birds and mammals. TREE, 14:343-348.

Linnell, J.D.C., Duncan, P. & Andersen, R. 1998. The European roe deer: A portrait of a successful species. In "The Euorpean roe deer - Studies of adaptation and variation". Eds. Andersen, R., Duncan, P. & Linnell, J. Scandinavian University Press.

Linnell, J.D.C., Støen, O.G., Odden, J., Ness, E., Gangås, L., Karlsen, J., Eide, N. & Andersen, R. 1996. Gaupe og rådyr i østre deler av Hedmark. (Lynx and roe deer in eastern Hedmark. In norwegian with english abstract). NINA Oppdragsmelding, 414.

Lomnicki, A. 1988. Population ecology of individuals. Princeton university press, Princeton, New Jersey. 223pp.

May, R. M. 1989. Detecting density dependence in imaginary worlds. Nature, 388:16-17.

May, R. M. & Andersson, R. M. 1979. Population biology of infectious diseases: Part II. Nature, 280:455-461.

McCullough, D. R. 1979. The George reserve deer herd. Population ecology of a K-selected species. Univ of Michigan press, Ann Arbor, 271pp.

McCullough, D. 1990. Detecting density dependence: Filtering the baby from the bathwater. Trans NA Wildl Natural Resources Conf, 55:534-543.

McCullough, D.R. 1997. Irruptive Behavior in Ungulates. In: McShea, W.J., Underwood, H.B. & Rappole, J.H. (eds.). The Science of Overabundance. Deer ecology and population management. Smithsonian Instituion. p. 69-98.

Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology 75:271-287.

Neff, D.J. 1968. The pellet-group count technique for big game trend, census and distribution: A review. J Wildl Manage 32:597-614.

Nicholson, A. J. 1933. The balance of animal populations. J Anim Ecol, 2:132-178.

Putman, R. & Kjellander, P. In Press. Deer damage to cereals: Economic significance and predisposing factors. Biol J of Linnaean Society.

Putman, R.J., Langbeinm J., Hewison, A.J.M. & Sharma, S.K. 1996. Relative roles of density-dependent and density-independent factors in population dynamics of British deer. Mamm Rev 26:81-101.

Ratcliffe, P.R. 1987. Red deer population changes and the independent assessment of population size. Symposia of the Zoological Society (London). 58:153-165.

Sand, H. 1996. Life history strategies in moose (*Alces alces*): geographical and temporal variation in body growth and reproduction. Ph.D. thesis. University of Agricultural Sciences, Uppsala.

Sæther, B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. TREE 12:143-149.

Sæther, B-E. & Hagenrud, H. 1983. Life history of the moose (*Alces alces*): Fecundity rates in relation to age and carcass weight. J Mamm. 64:226-232.

Sæther, B-E. & Hagenrud, H. 1984. Life history of the moose (*Alces alces*): relationship between growth and reproduction. Holarct Ecol. 8:100-106.

Sinclair, A. R. E. 1977. The African buffalo. University of Chicago press, Chicago.

Sinclair, A. R. E.1989. Population regulation in animals. Ecological concepts (ed. by J.M. Cherrett). Blackwell Scient. Publ., Oxford pp. 197-241.

Skogland, T. 1983. The effect of density dependent resource limitation on size of wild reindeer. Oecologia, 60:156-168.

Skogland, T. 1985. The effects of density dependent resource limitations on the demography of wild reindeer. J Anim Ecol 54:359-374.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. Oecologia, 84:442-450.

SMHI (Swedish Meterological and Hydrological Institute). 1994. Väder och vatten. Monthly reports. (In Swedish).

Staines, B.W. 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). J of Zool. 184:403-419.

Strandgaard, H. 1972. The roe deer (Capreolus capreolus) population at Kalø and the factors regulating its size. Danish Rev Game Biol. 7: 1-205.

Strong, D.R. 1984. Density-Vague Ecology and Liberal Population Regulation in Insects. In: A new ecology. Price, P.W., Slobodchikoff, C.N. & Gaud, W.S. (Eds.) Wiley & Sons, New York. pp.313-327.

Stubbs, M. 1977. Density dependence in life-cycles of animals and its importance in K- and r-strategies. J Anim Ecol, 46:677-688.

Vincent, J.P., Bideau, E., Hewison, A.J.M. & Angibault, J.M. 1995. The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (Capreolus capreolus). Journal of Zoology 236:371-382.

Wahlström, L.K. & Kjellander, P. 1995. Ideal free distribution and natal dispersal in roe deer. Oecologia 103:302-308.

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