

Petter Kjellander · Jean-Michel Gaillard
A. J. Mark Hewison

Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations

Received: 1 February 2005 / Accepted: 13 June 2005 / Published online: 8 December 2005
© Springer-Verlag 2005

Abstract We investigated the influence of population density on juvenile body mass in two contrasting roe deer populations, in Sweden (Bogesund) and France (Chizé), in which density was monitored for ≥ 15 years. We investigated the effect of population density and climatic conditions on cohort performance. We predicted that: (1) body mass of growing fawns should be sensitive to environmental changes, showing marked between-year variation (i.e., cohort effects), (2) fawns in the less productive (weakly seasonal, weakly predictable summer weather) habitat of Chizé should show stronger density-dependent responses due to more severe food competition during summer than fawns in the more productive (markedly seasonal, moderately predictable summer weather) habitat of Bogesund, and (3) fawns at Bogesund should be heavier both in absolute terms and relative to their size than their conspecifics in Chizé due to a higher degree of fat accumulation in northern environments. In both study sites we found marked cohort variation and clear effects of density, with body mass varying by as much as 29% over years. While neither summer nor winter climate influenced fawn body mass at Bogesund, fawns tended to be lighter after summers with high temperatures at Chizé. In addition, fawns were heavier after acorn mast years experienced in

utero at Bogesund. As expected, the strength of the density-dependent response of fawn body mass was greater at Chizé than at Bogesund. For a given density, male fawns were consistently heavier than females in both sites. Lastly, both sexes at Bogesund had higher absolute body mass and were larger for a given body size than in Chizé. Our results clearly demonstrate that absolute density is a poor predictor of roe deer performance and supports the view that habitat quality has an overwhelming importance for determining fawn body mass in roe deer populations.

Keywords Cohort effects · Density dependence · Environmental stochasticity · Phenotypic quality · Allometry

Introduction

Changes in population density affect most life-history traits of vertebrates (Fowler 1987; Stearns 1992). Among them, body mass plays a fundamental role in population dynamics (Stubbs 1977; Begon et al. 1990). In ungulates, for example, body mass is a good proxy for individual performance (Clutton-Brock 1991). As a general rule, the heaviest individuals survive better at all ages (Gaillard et al. 1997, 2000) and, starting earlier in life, they produce a larger number of offspring than lighter conspecifics (Albon et al. 1983; Hewison 1996). Among cervids living in temperate areas, there is a consistent inverse relationship between birth weight or early growth and population density (Skogland 1983; Hewison et al. 2002), and birth weight is in turn related to adult body mass (Dooney and Gunn 1981; Albon et al. 1987; Clutton-Brock et al. 1987). Thus, the level of intra-specific competition while in utero and during early growth can determine adult body mass and, hence, the early survival and subsequent reproductive rate of cohorts (Albon et al. 1987; Skogland 1990;

Communicated by Roland Brandl

P. Kjellander (✉)
Department of Conservation Biology, Swedish University of
Agricultural Sciences (SLU), Grimsö Wildlife Research Station,
730 91, Riddarhyttan, Sweden
E-mail: Petter.Kjellander@nvb.slu.se
Fax: +46-581-697310

J.-M. Gaillard
UMR-CNRS 5558,
Laboratoire de Biométrie et Biologie Evolutive,
Université Lyon 1, 69622, Villeurbanne, Cedex, France

A. J. M. Hewison
Comportement et Ecologie de la Faune Sauvage (CEFS),
Institut National de la Recherche Agronomique (INRA),
BP 52627, 31326, Castanet-Tolosan Cedex, France

Rose et al. 1998; Gaillard et al. 2003a for a review on deer).

Inter-annual variation in climate is also known to influence early growth and hence result in the reproduction of large herbivores (Albon et al. 1983; Coulson et al. 2001), possibly through effects on the spatial and temporal quantity and quality of forage (Langvatn et al. 1996). In fact, there is increasing evidence for the delayed effects of conditions during the spring of birth on subsequent life-history traits in temperate vertebrates (see Lindström 1999; Beckerman et al. 2002). Therefore, high population density or severe climatic conditions at birth may have persistent long-term effects on population dynamics because it may not be possible for individuals to compensate later in life (Pettorelli et al. 2002).

Previous studies of cohort effects in ungulates have been restricted to single population studies [e.g., Rose et al. (1998) for red deer (*Cervus elaphus*), Gaillard et al. (1993b) for roe deer (*Capreolus capreolus*) and Forchhammer et al. (2001) for Soay sheep (*Ovies aries*)], without the possibility to make comparisons between contrasting populations over the same density range. To ensure that population studies identify general trends and increase our understanding of biological patterns, it is valuable to adopt a comparative approach. Indeed, a recent analysis using data from 43 previously published meta-analyses revealed that individual ecological and evolutionary studies generally explain a low proportion of variance (mean amount of variance explained was <6%, Møller and Jennions 2002; but see Peek et al. 2003). A comparative approach also ensures that methods are standardized between studies. Here, in this context, we aim to evaluate the influence of population density on fawn cohort body mass in two contrasting roe deer populations.

The roe deer, a small-sized ungulate (adult body mass 20–30 kg; Andersen et al. 1998), is an income breeder (sensu Jönsson 1997), relying on current resource intake for survival and reproduction (Andersen et al. 2000). Environmental factors such as density and weather can have powerful effects on yearly variation in adult body mass of ungulates that stock body reserves (Festa-Bianchet et al. 1996, 1998 in bighorn sheep (*Ovis canadensis*), Mysterud et al. 2002 in red deer). However, these factors are not expected to affect annual variation in adult mass of income breeders such as roe deer to the same extent. In roe deer, adult body mass of individuals varies very little over years since they do not store large fat reserves to compensate for changes in per capita food availability (Andersen et al. 2000). Even so, such fat reserves may provide a greater proportion of energy needs for a population of a given species in more northern and seasonal environments (Lindstedt and Boyce 1985, for roe deer see Holand et al. 1998). Certainly, selection may act to favor those individuals which store extra fat in harsh climates through decreased winter mortality, particularly in years of severe snow conditions (Cederlund and Lindström 1983). We thus predicted that: (1) body mass of growing roe deer fawns

should be highly sensitive to changes in environmental conditions (population density and climatic conditions), and should thereby show marked among-year variation, (2) fawn cohorts in the southern population are expected to show a stronger response to density than those in the north due to increased predictability and higher productivity of the growing season with increasing latitude (Geist 1987; Loe et al. 2005) and (3) roe deer fawns in the more seasonal northern population should be heavier both in absolute terms and relative to their body size than their conspecifics in the southerly population, simply because of higher levels of fat deposited (Lindstedt and Boyce 1985). We tested these predictions using data collected in two long-term studies of marked animals in Sweden (15 years at Bogesund) and France (23 years at Chizé) where density was manipulated experimentally.

Study area

Bogesund

The study was conducted during 1989–2003 at Bogesund, a 1,200-ha research area located a few kilometers north of Stockholm, (59°23'N, 18°15'E) in the hemiboreal zone in east central Sweden. The entire research area constitutes the major part of a peninsula surrounded by water on all sides except to the north. The area is rather flat with low interspersed ridges. A few people live in small houses, and there are three larger farms associated with the open agricultural areas.

A mosaic of forested and field habitats characterize the landscape. Approximately 65% of the area is forested and 25% is agricultural, while rocky areas and bogs constitute 10%. The forests are dominated by two coniferous species, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), whereas deciduous species including birch (*Betula* spp.), willow (*Salix* spp.) and common oak (*Quercus robur*) are also common in most forest types (Guillet et al. 1996). Associated with the open areas are numerous small meadows and former fields replanted with birch or spruce. Some fields are resown in early autumn or spring with, for example, rape (*Brassica napus*), oats (*Avena sativa*) or wheat (*Triticum* spp.). Dwarf shrubs, primarily bilberry (*Vaccinium myrtillus*), are patchily distributed, while numerous herbs are abundant in most habitats.

The climate is influenced by the Baltic Sea. The warmest month is July with an average temperature of 16.7°C, and the coldest is January with –3.7°C. Annual precipitation is approximately 550 mm, with most falling in July, and the least in February. Snow cover normally lasts for 80 days, usually from late December to early March, with a maximum snow depth of 13 cm in February. During the years of 1990–1992, winters were unusually mild, with little or no snow, and deviated markedly from the long-term means.

Chizé

Chizé is a 2,614-ha reserve of enclosed forest in western France (46°05'N, 0°25'W). The climate is oceanic with mild winters (mean daily temperature in January is 5.5°C) and hot, dry summers (mean daily temperature in July is 20.4°C and total rainfall in July–August is 98 mm). The soils of Chizé are shallow, calcareous, and not very fertile. Three broad vegetation associations of varying quality for roe deer are found at Chizé (Pettorelli et al. 2003a). The richest habitat for roe deer is an oak forest with mainly hornbeam coppice (covering 1,046 ha). About a third of the area (815 ha) is poor roe deer habitat consisting of beech forest on limestone with virtually no coppice. The understory is dominated by woodfalse-brome (*Brachypodium* sp.), butcher's broom (*Ruscus aculeatus*), ivy (*Hedera helix*), wild madder (*Rubia peregrina*) and wood melick (*Melica uniflora*). Neither woodfalse-brome nor butcher's broom are favored forages of roe deer. Ivy, which is highly selected by roe deer in winter, decreased following a peak in the size of the roe deer population in 1983–1984. The remainder of the Chizé forest (758 ha) is a habitat of intermediate quality consisting of oak forest in which the coppice is mainly Montpellier maple (*Acer monspessulanum*). The productivity of the entire forest is quite low (long-term average of 3.77 m³ of wood produced/ha/year versus 5.92 m³ for the same forest type in east France, data from Inventaire National Forestier, unpublished data).

Materials and methods

Roe deer measurements and population estimates

Bogesund

Roe deer were captured since 1988 using trap boxes, nets or as newborns. Live-captured individuals were marked, weighed (kg) and body measurements were recorded (Table 1). In this paper we used total body mass and right-hind foot length from 139 males and 136 females, killed or living deer of known age, shot or caught between November and April at the age of 6–11 months (hereafter called fawns).

Roe deer density was determined by using the Petersen-Lincoln estimate (Caughley 1977) where the capture-mark-recapture procedure constituted observations of the ratio of marked:unmarked animals in a population marked with radio-collars (collar size 50–300 g; Televilt International AB, Lindesberg, Sweden) during the study. In total, 405 individuals were followed by radio tracking, on average constituting 41% of the population during the study (varying between 10% and 70% among years). Visual field observations of deer were made in September each year from 1989 and onwards. The protocol for “field observations” was performed in the same way over the study period. A minimum of two persons performed animal observa-

Table 1 Cohort-specific body mass (kg ± 1 SE) of male and female fawn roe deer at Bogesund, Sweden and Chizé, France measured during winter

Cohort	Bogesund				Chizé			
	Male fawn		Female fawn		Male fawn		Female fawn	
	Weight (kg)	<i>N</i>						
1980					16.29 ± 0.32	30	15.59 ± 0.24	23
1981					14.81 ± 0.36	39	14.71 ± 0.47	30
1982					14.46 ± 0.36	25	13.82 ± 0.42	23
1983					13.75 ± 0.41	23	14.25 ± 0.30	32
1984					13.90 ± 0.64	15	12.88 ± 0.41	20
1985					13.90 ± 0.31	35	12.87 ± 0.29	27
1986					14.29 ± 0.45	22	13.12 ± 0.49	21
1987					15.92 ± 0.40	28	14.69 ± 0.31	27
1988					14.82 ± 0.29	33	14.39 ± 0.31	26
1989	15.71 ± 1.56	6	16.40 ± 0.56	9	13.73 ± 0.38	22	13.10 ± 0.41	26
1990	15.82 ± 1.07	9	14.55 ± 0.44	10	15.07 ± 0.32	29	15.34 ± 0.36	25
1991	15.25 ± 0.68	9	14.57 ± 0.53	9	17.26 ± 0.34	28	15.74 ± 0.32	29
1992	14.38 ± 1.44	3	14.17 ± 0.45	3	15.87 ± 0.36	26	14.91 ± 0.38	15
1993	16.50 ± 0.35	17	15.49 ± 0.67	14	16.97 ± 0.48	11	15.31 ± 0.37	12
1994	16.55 ± 0.75	6	15.62 ± 0.72	7	19.33 ± 0.49	9	16.69 ± 0.45	25
1995	17.90 ± 0.40	7	15.04 ± 0.31	10	16.21 ± 0.40	29	15.55 ± 0.38	31
1996	17.18 ± 0.17	2	15.38 ± 0.47	7	16.61 ± 0.36	38	15.82 ± 0.29	33
1997	14.86 ± 1.44	3	15.98 ± 0.32	7	16.20 ± 0.30	35	15.21 ± 0.39	28
1998	17.26 ± 0.41	8	17.40 ± 0.29	6	16.13 ± 0.42	23	15.48 ± 0.30	24
1999	16.42 ± 0.36	30	15.15 ± 0.52	18	17.38 ± 0.55	19	16.36 ± 0.32	18
2000	16.51 ± 0.61	12	14.58 ± 0.51	11	17.45 ± 0.40	27	16.52 ± 0.30	30
2001	17.73 ± 0.39	7	16.32 ± 0.60	8	16.17 ± 0.50	30	15.98 ± 0.27	43
2002	15.62 ± 0.60	7	15.07 ± 0.65	14	16.09 ± 0.26	53	15.33 ± 0.30	38
2003	14.96 ± 0.41	13	12.31 ± 0.37	3				

At both sites, yearly means have been corrected for the influence of the month of capture (standardized to January) and, at Chizé only, for the influence of habitat (standardized in the oak-hornbeam forest stand)

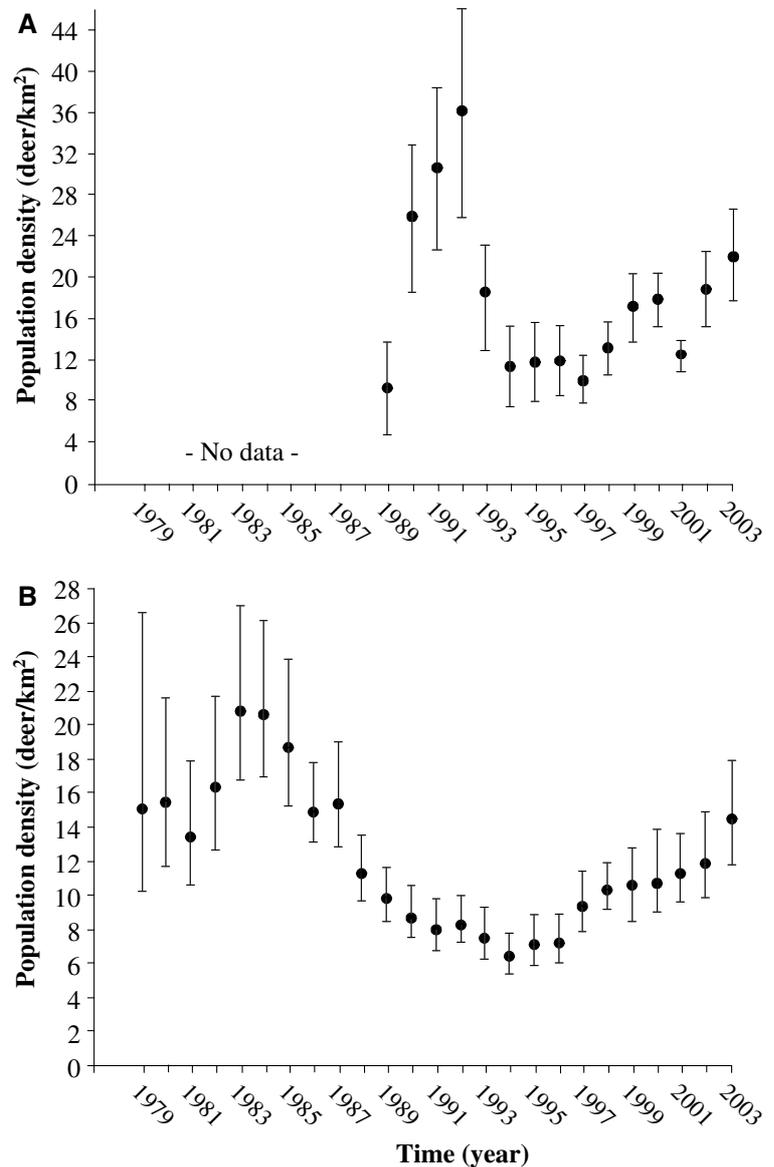
tions at dawn and dusk during on average 13 days (ranging between 7 and 20 days between years) until the pre-monitoring target number of animal observations was obtained (varying between 70 and 372 observations). The observation effort was spread evenly over 20 zones of the study area. Prior to the start of the Bogesund study, the roe deer population was regularly hunted. Then, at the start of the study in 1988, a ban on all hunting was introduced, allowing deer density to increase rapidly. Subsequently, hunting was reinstated from October 1992 to March 1994 to reduce population density once again. Thereafter (1995 and onwards) we allowed population density to increase slowly (Fig. 1a).

Chizé

The roe deer population at Chizé has been intensively monitored for more than 20 years (from 1977 onwards). Each year between 8 and 12 days of captures are orga-

nized in January and February. We used data from 629 male and 606 female fawns that were caught and weighed at least once using an electronic balance (Table 1). For each individual that was captured, year of birth, body mass, sex and hind foot length were recorded. The size of Chizé population has been monitored since 1978 by using recent developments of capture-mark-recapture models (see e.g., Gaillard et al. 2003b). The roe deer population fluctuated markedly during the study period, increasing from 350 individuals > 1-year-old in the study area in 1979 to about 550 in 1983, and then decreasing to less than 200 between 1993 and 1996 (Gaillard et al. 2003b). Since 1996, the population size has increased to densities similar to those of 1979 (Fig. 1b). The population increased because few roe deer were removed annually and decreased due both to high annual culling and density-dependent responses of population parameters (Gaillard et al. 1993). Recruitment decreased from 1.7 to 1.3 fawns per doe

Fig. 1 Population density of roe deer estimated at **a** Bogesund in September and **b** Chizé in March. Bars indicate max and min for 95% CI



following the population peak in 1983 (Boutin et al. 1987). Most does first bred as 2-year-olds, but does born during the population peak first bred as 3- or 4-year-olds (Gaillard et al. 1992b). Without removals, the annual finite rate of increase (λ) would have averaged 1.25 over the study period (Gaillard et al. 1992a).

Data analysis

Because roe deer show some sexual dimorphism in size (Andersen et al. 1998), we analyzed cohort body mass in relation to sex to test our first prediction of widespread cohort effects in both populations. Between-year (i.e., cohort, $n=15$ and 23 respectively, for Bogesund and Chizé) variation in fawn body mass was analyzed by standard analysis of variance (ANOVA). To test our second prediction of higher density-dependence at Chizé than at Bogesund, accurate estimates of population density based on the capture-mark-recapture (Gaillard et al. 1993) or capture-mark-resighting monitoring were available between 1980 and 2002 at Chizé and 1989–2003 at Bogesund. We tested for possible effects of density on yearly variation in fawn body mass using the observed sex-specific mass of each roe deer fawn cohort with linear models (one per site), including climatic variables as covariates (to account for possible confounding effects), sex as a factor (to account for the weak sexual size dimorphism of roe deer). To control for fawn growth over the winter catch season (Pettorelli et al. 2001; Hewison et al. 2002), we included the months of capture in the models (6 and 2 modalities at Bogesund and Chizé, respectively). In addition, we controlled for known effects of habitat quality at Chizé (i.e., fawns are heavier in the rich oak-hornbeam forest stand than in the oak-maple and beach forest stands, Pettorelli et al. 2001) and mast availability at Bogesund (i.e., fawns are heavier during mast years, Kjellander 2000) by fitting habitat quality (three classes) and mast occurrence (two classes), respectively, while in utero as additional factors of variation in fawn body mass. Acorn mast production was recorded by a commercial seedling producer (Svenska Skogsplantor AB) at several different locations in southern Sweden, but not in the study area itself. Mast harvest varied between 0 and 500 kg in a poor year and 1.5–4 tonnes in true mast years. Mast years occur concomitantly across the entire Swedish range of oak (Hamilton, Swedish National Board of Forestry, unpublished Data). In temperate areas, both winter severity and summer weather have been found to correlate with temporal variation in demographic traits of ungulates (Sæther 1997; Gaillard et al. 2000). In order to assess density-dependent responses of fawn body mass without any confounding effect of climatic variation, we used proxies of both winter (at Bogesund only because winters are very mild at Chizé) and summer (at both sites) conditions. To index winter conditions, we used the number of days per

year with snow lying deeper than 10 cm. We did not use the winter NAO often reported to have a strong influence on several life-history traits, including body mass (Post and Stenseth 1999; Coulson et al. 2001; Mysterud et al. 2002) because NAO did not correlate to local climatic factors at our study sites. To index summer conditions, we used mean daily temperature in June–July because it has been previously reported to negatively affect winter fawn body mass of roe deer fawns (Gaillard et al. 1996). Interactions between covariates were fitted by using the product of interacting covariates of their main effects (see Portier et al. 1998 for further explanations). We then tested various effects of explanatory variables using Wald tests. The best model was selected using the Akaike Information Criterion (AIC) following Burnham and Anderson (1998). Then, to measure accurately the population-specific response of fawn body mass to changes of density, we standardized our density estimates for both populations so that density had a mean of zero and a standard deviation (SD) of 1 in order to explore density-dependent responses over a density range common to both sites. Lastly, to test our third prediction that fawns should be heavier at Bogesund than at Chizé for a given size, we fitted allometric relationships between fawn body mass and hind-foot length. We regressed body mass on hind-foot length after log-transformation and tested for the effects of sex and site, as well as their interaction, on both the slope and the intercept of the regression using Wald tests. We used R software (R-Development Core Team 2004) for all the statistical analyses.

Results

Cohort differences

At Chizé, when we accounted for possible confounding effects of month of capture (male and female fawns were on average 0.221 and 0.285 kg heavier in February than in January) and habitat type (male and female fawns were on average 1.023 and 1.108 kg heavier in the oak-hornbeam stands than in the beech stand), there was significant variation among cohorts in mean body mass for both sexes during the study period (males from 13.7 kg in 1984 and 1990 to 19.3 kg in 1995: $F_{22, 606} = 10.339$, $P < 0.0001$, females from 12.9 kg in 1985 and 1986 to 16.7 kg in 1995: $F_{22, 583} = 9.987$, $P < 0.0001$; Table 1). At Bogesund, when we accounted for possible confounding effects of month of capture (male fawns were on average 1.94 kg heavier in November than in February and female fawns were on average 1.85 kg heavier in November than in December), we found significant differences among cohorts in females only, although the range of cohort variation observed in males was similar to that observed at Chizé (males from 14.4 kg in 1992 to 17.9 kg in 1995: $F_{14, 119} = 1.66$, $P = 0.073$, females from 12.3 kg in 2003 to 17.4 kg in

1998: $F_{14, 116} = 1.96$, $P = 0.027$; Table 1). The lack of a significant difference among cohorts in male fawns at Bogesund was likely a consequence of small sample size in some years (see Table 1).

Effects of density and climate

At Bogesund, models including two-way interactions performed less well than models including only main effects (Table 2a). From the additive model, the main effects of sex, density, and mast occurrence were significant and accounted for 56.3% of the variation observed in cohort-specific fawn body mass. Male fawns were 0.97 kg (SE=0.307) heavier than female fawns, fawn body mass decreased by 0.064 kg (SE=0.022) per increase of 1 roe deer/100 ha, and fawns were 0.82 kg (SE=0.362) heavier following mast years. Although the relationships were in the expected direction, the additive effects of snow conditions (cohort-specific body mass tended to decrease by 0.019 kg (SE=0.014) per increase of one snow day) and of summer temperature (cohort-specific body mass tended to decrease by 0.173 kg (SE=0.135) per increase of 1°C) were not retained in the final model (Table 2a).

Table 2 Model selection procedure for the analysis of the effects of population density, climatic conditions, and sex on cohort-specific body mass

Model term	AIC
A. Bogesund	
Sex + Mast + Density + Snow	80.374
Sex + Mast + Density	80.475
Sex + Mast + Density + Temperature	80.561
Sex + Mast + Density × Snow	80.856
Sex × Mast + Density	81.922
Mast × Density + Sex	82.241
Sex × Density + Mast	82.404
Sex + Mast + Density × Temperature	82.540
Sex + Density	83.843
Sex × Density + Mast × Density	84.170
Sex × Mast + Sex × Density + Mast × Density	85.680
Sex + Mast	86.718
Mast + Density	88.275
Density	90.227
Mast	92.438
Sex	95.767
B. Chizé	
Sex + Density + Temperature	132.123
Sex + Density	133.405
Sex × Density + Temperature	133.493
Sex + Density × Temperature	133.994
Sex × Temperature + Density	134.111
Sex × Density + Sex × Temperature	135.492
Density	139.382
Sex	158.497

(A) Bogesund, Sweden and (B) Chizé, France. At both sites, yearly means have been corrected for the influence of the month of capture (standardized to January) and, at Chizé only, for the influence of habitat (standardized in the oak-hornbeam forest stand). The selected model (i.e., the model with the lowest AIC value) is indicated in bold type

Likewise at Chizé, models including two-way interactions performed less well than models only including main effects (Table 2b). The model including additive effects of sex and density was selected and accounted for 49.8% of the variation observed in cohort-specific fawn body mass (Table 2b). Male fawns were 0.823 kg (SE=0.282) heavier than female fawns and fawn body mass decreased by about 0.207 kg (SE=0.034) per increase of 1 roe deer/100 ha. As previously reported in this population, fawns tended to be lighter following hot summers (cohort-specific body mass decreased by 0.225 kg (SE=0.128) per increase of 1°C).

Sites combined

To combine our data sets, we used cohort-specific values that had first been corrected for those confounding environmental factors which we had shown to significantly affect fawn body mass variation (mast occurrence at Bogesund). When we standardized population density (mean of 14.18 roe deer/km² and SD of 6.55) to assess the site-specific response of body mass to given absolute changes of roe deer density, the model including the three-way interaction between site, sex and density was not retained (Table 3). However, the between-site difference in slope (0.604, SE=0.285) was significant (Wald test, $P=0.04$), indicating that the density-dependent response of fawn body mass differed between the study sites. This shows that the density-dependent response of roe deer at Chizé was greater than that observed at Bogesund (Fig. 2), as expected from our second prediction. The strength of the density-dependent response of body mass over this standardized density range did not differ between sexes (difference of slope = 0.061, SE=0.268, Wald test, $P=0.820$). The selected model

Table 3 Model selection procedure for the analysis of the effects of standardized population density, sex and site on cohort-specific body mass

Model term	AIC
Sex + Density × Site	226.248
Sex × Site + Site × Density	228.143
Sex × Density + Site × Density	228.243
Sex + Density + Site	228.920
Sex × Density + Site × Density + Sex × Site	230.086
Sex × Site + Density	230.822
Sex × Density + Site	230.915
Sex × Density × Site	231.550
Sex × Density + Sex × Site	232.768
Density × Site	238.008

At Chizé, confounding effects of month of capture and habitat were accounted for by standardizing mass to January in the oak-hornbeam stand. At Bogesund, confounding effects of month of capture and mast occurrence while in utero were accounted for by standardizing mass to January during non-mast years. Density was standardized to have a mean of zero and a SD of 1. The selected model (i.e., the model with the lowest AIC value) is indicated in bold type

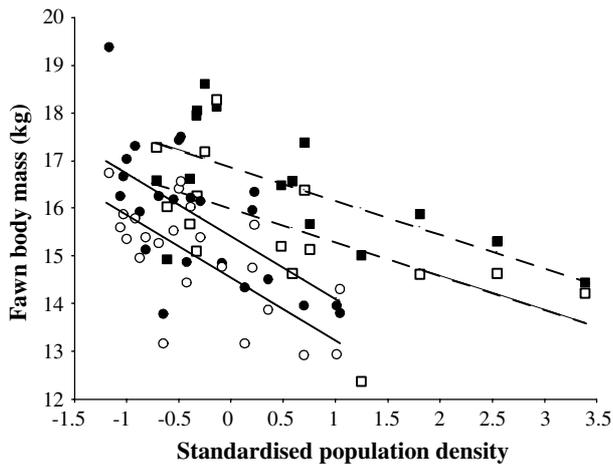


Fig. 2 Standardized population density in the year of birth versus mean fawn cohort body mass in male (filled symbols) and female (open symbols) roe deer at Bogesund (squares, broken lines) and Chizé (circles, unbroken line). Population density was standardized to have a mean of zero and a SD of 1. For each site the upper regression line corresponds to males while the lower one corresponds to females

(Table 3) accounted for 50.0% of the variation observed in cohort-specific fawn body mass. Male fawns were 0.883 kg (SE = 0.235) heavier than female fawns.

Allometric relationships

Data inspection revealed that while the lightest fawns were found at Chizé (11.1 and 8 kg at Chizé vs. 13.1 and 11.1 kg at Bogesund for males and females, respectively), the smallest measurements of hind-foot length were reported from Bogesund (275 and 253 mm at Bogesund vs. 294.5 and 279.5 mm at Chizé for males and females, respectively). Including these individuals in the analysis led to a poor fit of the allometric model (skewed distribution of residuals and marked underestimation of the allometric slope with estimates of 0.983 and 1.869 for males and females, respectively, compared to the expected value of 3 based on the equation-dimension, i.e., volume/length ratio, Peters 1983). Hence we removed the smallest males ($N=3$) and female ($N=1$) measured at Bogesund to perform the analysis. We did not find any statistical evidence for a two-way interaction between sex and site on the slope of the allometric relationship between hind-foot length and body mass (Table 4). Further, we did not find any support for a model including interaction terms (Table 4). There was, as expected, a strong allometric relationship between hind-foot length and body mass. The allometric exponent (2.735 ± 0.154 (SE)) did not differ significantly from the expected coefficient of 3. The intercept of the allometric relationship differed highly between sites (difference of 0.079, SE = 0.013 in favor of Bogesund) but did not differ between the sexes (difference of 0.010, SE = 0.012 in favor of males). For a given

Table 4 Model selection procedure for the analysis of the effects of sex and site (as well as of their interactions) on the intercept and slope of the allometric relationship between fawn body mass and hind foot length at Bogesund and Chizé

Model term	AIC
Hind-foot length \times Site	-446.900
Hind-foot length + Site	-446.217
Hind-foot length \times Site + Sex	-445.612
Hind-foot length + Site + Sex	-444.836
Hind-foot length \times Site + Site \times Sex	-444.013
Hind-foot length \times Sex + Hind foot length \times Site	-443.679
Hind-foot length \times Sex \times Site	-442.086
Hind-foot length \times Sex + Hind foot length \times Site + Site \times Sex	-442.021
Hind-foot length \times Sex + Site \times Sex	-440.921

The selected model (i.e., the model with the lowest AIC value) is indicated in bold type

size, fawns at Bogesund reached a higher body mass than at Chizé, as expected from our third prediction. Finally, no difference was found between males or females; i.e., male and female fawns followed the same allometric relationship (difference of slope = 0.078, SE = 0.306, Fig. 3, Table 4).

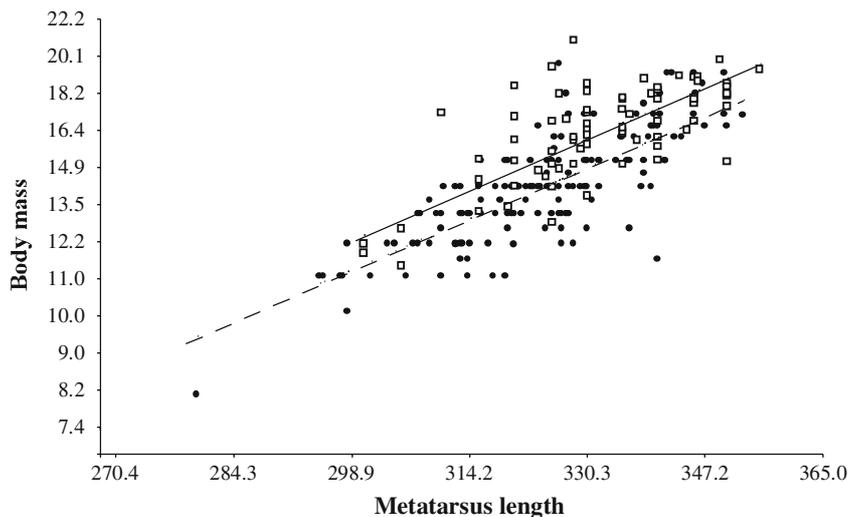
Discussion

We found support for all our three predictions. In both study sites, when we accounted for other possible sources of environmental variation, a clear and consistent effect of population density occurred on cohort-specific body mass of fawns such that fawns born at high density weighed less during their first winter compared to those born at low density (*Prediction 1*). In support of our second prediction (*Prediction 2*), we found a much stronger density-dependent response at Chizé than at Bogesund. Lastly, as expected from the third prediction (*Prediction 3*), fawns at Bogesund were heavier than at Chizé, both in absolute (i.e., higher body mass) and relative (i.e., heavier for a given body size) terms, due to a higher degree of fat accumulation in northern environments. Below we discuss these findings in further detail.

Marked cohort effects on fawn body mass

The body mass of fawns was strongly dependent on the year of birth, with mean weights varying by between 3.5 and 5.6 kg depending on sex and site (Fig. 2). This represents a between-cohort difference in mean body mass of up to $\pm 29\%$. There was a clear pattern in both sites whereby cohorts that were born in years of high density were relatively lighter during their first winter than those born during years with lower density. Such effects of density on juvenile size have been reported in other species of large mammals (Fowler 1987; see

Fig. 3 The allometric relationship between body size (metatarsus length) and body mass at Bogesund, Sweden (*open squares*) and Chizé, France (*filled circles*) in male and female roe deer fawns



Gaillard et al. 2000 for a review on ungulates) and could be caused by differential early growth rates, both in utero and during the first summer of life (Skogland 1983; Clutton-Brock et al. 1992; Cook et al. 1996; Gaillard et al. 1996; Hewison et al. 1996, 2002). In addition to population density, we confirmed the negative effect of summer temperature on body mass previously reported at Chizé for cohorts born before 1993 (Gaillard et al. 1996). However, the absence of a climatic influence on fawn body mass at Bogesund indicates that changes in population density rather than climatic variations predominate in shaping fawn body mass of roe deer.

Population-specific responses of fawn body mass to changes in density

Either when considering the whole range of density observed in the two populations, or when standardizing the between-site comparison to the same relative range of density, the density-dependent response of fawn body mass was more marked at Chizé than at Bogesund. Increasing roe deer density by 10 animals per km² led to a decrease in mean cohort body mass of 0.64 kg at Bogesund versus 2.07 kg at Chizé. This pattern is striking and, if not a coincidence, requires explanation.

Density-dependent effects are typically related to the interaction between population density and habitat quality (e.g., Sinclair 1989 for a review; Pettoelli et al. 2003b for a case study on roe deer). Roe deer seem to fit that pattern closely. Roe deer at the relatively high latitude of Bogesund have access to high quality habitat during spring and summer. At high latitude, resources should be richer and more predictable during the growing season than at low latitude (Geist 1987; Loe et al. 2005) and, in the absence of severe limitation during winter (as suggested by the absence of an effect of snow conditions), roe deer at Bogesund are expected to experience highly favorable conditions for body

growth. In contrast, at Chizé the availability of resources is limited by summer drought, is more spread over the year (less seasonality compared to Bogesund) and is less synchronized with the short time during which roe deer fawns require high energy input (May–June, Maugey et al. 1999). Therefore, habitat quality during spring and summer time is likely superior at Bogesund in comparison to Chizé and, for a given density, we expect the per capita resources to be higher in the more productive habitat. Thus, the higher productivity during late spring and summer time at Bogesund compared to Chizé will support more individuals. This demonstrates the fact that absolute density has no biological meaning by itself. Only the density relative to the habitat quality is expected to influence population performance (see Van Horne 1984). We report here that the marked between-site differences in the density-dependent response of fawn body mass to identical changes in population density allows us to reject any social regulation suggested to occur in roe deer (Strandgaard 1972) which would be independent of habitat quality. Hence, as Andersen et al. (1998), our results support the view that habitat quality rather than social pressure is the regulating mechanism for roe deer populations.

Between-population differences in absolute and relative mass

Roe deer in the northern Bogesund (Sweden) study site were heavier than those in the more southern Chizé (France) study site (Fig. 2). This result seems to support the predicted pattern (*Prediction 3*) of higher accumulation of body fat in the northern population, even if fawns were also larger in absolute terms. Indeed, comparative studies of roe deer mass across the European range also support such a pattern (Andersen et al. 1998), although it may reflect adaptation to increasingly seasonal environments towards the north rather than to

cold climates per se (Lindstedt and Boyce 1985). Further, fawns at Bogesund were heavier for a given body size than at Chizé, but at each site both sexes had the same mass for a given body size. This result is in agreement with the low level of sexual selection exhibited by roe deer (Andersen et al. 1998). However, it is not possible to distinguish the causes of the between-site differences observed in size and body mass (Fig. 3). Lesage et al. (2001) have previously shown that body mass and size of white-tailed deer (*Odocoileus virginianus*) fawns were higher in populations experiencing severe winter conditions. Further, large animals are able to accumulate a disproportionately larger amount of fat than smaller individuals (Peters 1983), and since individuals with the largest fat reserves and fasting endurance will suffer least winter mortality, there will be strong selection towards larger body size in northern areas (Lindstedt and Boyce 1985). Alternatively Geist's 1987 suggestion that food resources in northern latitudes are of generally higher quality than in more southern temperate areas might account for our findings, especially because we are concerned here with growth during the short summer period when mothers require high food quality for lactation. As a consequence, roe deer may use the vegetation flush in northern latitudes to increase growth rate and thereby reach higher body mass and larger size. A reverse pattern is expected during winter because of the high degree of seasonality in more northern areas. Summer conditions should therefore be more limiting at Chizé than at Bogesund, while winter conditions should limit access to high-quality food at Bogesund, e.g., because of snow conditions. Both these seasonal effects should operate through an effect on body mass or growth (Albon et al. 1987; Gaillard et al. 1996; Sand et al. 1996).

Acknowledgements We are grateful to Johan Månsson, Jonas Nordström, Lennart Pettersson, Leif Rooth, Gunnar Schön and Pia-Lena Widén for doing most of the field work in Sweden and to Olof Liberg for suggestions and ideas on earlier drafts of the manuscripts. The Bogesund study in Sweden, is a part of a long-term study of population demography in roe deer, initiated, lead and supervised by Olof Liberg and later together with P. Kjellander both at SLU, Grimsö, Sweden. The Swedish study was financed by the Swedish Association for Hunting and Wildlife Management and by the private foundations of "Oscar och Lilli Lamm stiftelser", "Olle och Signhild Engkvist stiftelser" and FORMAS. We are grateful to Bernard Boisauvert, Jean-Marie Boutin and Carole Toigo for organizing the capture sessions, Daniel Delorme and Guy Van Laere for help in the field and we thank all volunteers who had helped us to catch roe deer at Chizé for more than 20 years. We also thank Atle Mysterud, Tim Coulson and an anonymous referee for useful comments on previous drafts of this work.

References

- Albon SD, Guinness FE, Clutton-Brock TH (1983) The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *J Zool* 200:295–298
- Albon SD, Clutton-Brock TH, Guinness FE (1987) Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *J Anim Ecol* 56:69–81
- Andersen R, Gaillard JM, Liberg O, San José C (1998) Variation in life-history parameters in roe deer. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 285–307
- Andersen R, Gaillard JM, Linnell JDC, Duncan P (2000) Factors affecting maternal care in an income breeder, the European roe deer. *J Anim Ecol* 69:672–682
- Beckerman ATG, Benton T, Ranta E, Kaitala V, Lundberg P (2002) Population dynamic consequences of delayed life-history effects. *TREE* 17:263–269
- Begon M, Harper JL, Townsend CR (1990) *Ecology individuals, populations and communities*, 2nd edn. Blackwell, Cambridge
- Boutin JM, Gaillard JM, Delorme D, Van Laere G (1987) Suivi de l'évolution de la fécondité chez le chevreuil (*Capreolus capreolus*) par l'observation des groupes familiaux. *Gibier Faune Sauvage* 4:255–265
- Burnham KP, Anderson DR (1998) *Model selection and inference: a practical information-theoretic approach*. Springer, Berlin Heidelberg New York
- Caughley G (1977) *Analysis of vertebrate populations*. Wiley, London
- Cederlund G, Lindström E (1983) Effects of severe winters and fox predation on roe deer mortality. *Acta Theriol* 28:129–145
- Clutton-Brock TH (1991) *The evolution of parental care*. Princeton University Press, Princeton
- Clutton-Brock TH, Albon SD, Guinness FE (1987) Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) *Reproductive success*. University of Chicago Press, Chicago, pp 325–343
- Clutton-Brock TH, Price OF, Albon SD, Jewell PA, (1992) Early development and population fluctuations in Soay sheep. *J Anim Ecol* 65:675–689
- Cook JG, Quinlan LJ, Irwin LL, Bryant LD, Riggs RA, Thomas JW (1996) Nutrition–growth relations of elk calves during late summer and fall. *J Wildl Manag* 60:528–541
- Coulson T, Catchpole EA, Albon SD, Morgan BJT, Pemberton JM, Clutton-Brock TH, Crawley MJ, Grenfell BT (2001) Age, sex, density, winter weather and population crashes in Soay sheep. *Science* 292:1528–1531
- Dooney JM, Gunn RG (1981) Nutritional and other factors in breeding performance of ewes. In: Gilmore D, Cook B (eds) *Environmental factors in mammal reproduction*. Macmillan, London, pp 169–177
- Festa-Bianchet M, Jorgenson JT, King WJ, Smith KG, Wishart WD (1996) The development of sexual dimorphism: seasonal and lifetime mass change of bighorn sheep. *Can J Zool* 74:330–342
- Festa-Bianchet M, Gaillard JM, Jorgenson JT (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am Nat* 152:367–379
- Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD (2001) Climate and population density induce long-term cohort variation in a northern ungulate. *J Anim Ecol* 70:721–729
- Fowler CW (1987) A review of density dependence in populations of large mammals. In: Genoways HH (ed) *Current mammalogy*. Plenum, New York, pp 401–441
- Gaillard JM, Lebreton JD, Pontier D, Landry P (1992a) Demographic sensitivity and population management: an application to roe deer (*Capreolus capreolus*). In: *Proceedings of the International Union of the Game Biologists Congress* 18:547–550
- Gaillard JM, Sempéré AJS, Boutin JM, Van Laere G, Boisauvert B (1992b) 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
- Gaillard JM, Delorme D, Jullien JM (1993) Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* 94:57–61
- Gaillard JM, Delorme D, Boutin JM, Van Laere G, Boisauvert B (1996) Body mass of roe deer fawns during winter in 2 contrasting populations. *J Wildl Manag* 60:29–36

- Gaillard JM, Boutin JM, Delorme D, Van Laer G, Duncan P, Lebreton JD (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* 112:502–513
- Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J (2000) Body mass and individual fitness in female ungulates: bigger is not always better. *Proc R Soc Lond B* 267:471–477
- Gaillard JM, Duncan P, Delorme D, Van Laere G, Pettorelli N, Maillard D, Renaud G (2003b) Effects of Hurricane Lothar on the population dynamics of European roe deer. *J Wildl Manag* 67:767–773
- Gaillard JM, Loison A, Toigo C, Delorme D, Van Laere G (2003a) Cohort effects and deer population dynamics. *Ecoscience* 10:312–320
- Geist V (1987) Bergmann's rule is invalid. *Can J Zool* 65:1035–1038
- Hewison AJM (1996) Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriol* 41:187–198
- Hewison AJM, Vincent JP, Bideau E, Angibault JM, Putman RJ (1996) Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. *J Zool (Lond)* 239:573–581
- Hewison AJM, Gaillard JM, Angibault JM, Van Laere G, Vincent JP (2002) The influence of density on post-weaning growth in roe deer (*Capreolus capreolus*) fawns. *J Zool (Lond)* 257:303–309
- Holand Ø, Myrsterud A, Wannag A, Linnell JDC (1998) Roe deer in northern environments: physiology and behaviour. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 117–137
- Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *OIKOS* 78:57–66
- Kjellander P (2000) Density dependence in roe deer population dynamics. PhD Thesis. Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Uppsala. *Silvestria* 154
- Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *J Anim Ecol* 65:653–670
- Lesage L, Crête M, Huot J, Ouellet JP (2001) Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia* 126:30–41
- Lindstedt SL, Boyce MS (1985) Seasonality, fasting endurance, and body size in mammals. *Am Nat* 125:873–878
- Lindström J (1999) Early development and fitness in birds and mammals. *TREE* 14:343–348
- Loe LE, Bonenfant C, Myrsterud A, Gaillard JM, Langvatn R, Stenseth NC, Klein F, Pettorelli N (2005) Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *J Anim Ecol* (in press)
- Mauget C, Mauget R, Sempere A (1999) Energy expenditure in European roe deer fawns during the suckling period and its relationship with maternal reproductive cost. *Can J Zool* 77:389–396
- Møller AP, Jennions MD (2002) How much variance can be explained by ecologists and evolutionary biologists. *Oecologia* 132:492–500
- Myrsterud A, Langvatn R, Yoccoz NG, Stenseth NC (2002) Large-scale habitat variability, delayed density effects and red deer populations in Norway. *J Anim Ecol* 71:569–580
- Peek MS, Leffler AJ, Flint SD, Ryel RJ (2003) How much variance is explained by ecologists? Additional perspectives. *Oecologia* 137:161–170
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Pettorelli N, Gaillard JM, Duncan P, Ouellet JP, Van Laer G (2001) Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* 128:400–405
- Pettorelli N, Gaillard JM, Van Laer G, Duncan P, Kjellander P, Liberg O, Delorme D, Maillard D (2002) Density at birth and habitat quality affects adult body mass in roe deer. *Proc R Soc Lond B* 269:747–753
- Pettorelli N, Dray S, Gaillard JM, Chessel D, Duncan P, Illius A, Guillon N, Klein F, Van Laere G (2003a) Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia* 137:363–369
- Pettorelli N, Gaillard JM, Duncan P, Maillard D, Van Laere G, Delorme D (2003b) Habitat quality influences both survival and movements of juvenile roe deer. *Ecology* 84:3307–3316
- Portier C, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Yoccoz NG (1998) Effects of density and weather on survival of big-horn sheep lambs (*Ovis canadensis*). *J Zool Lond* 245:271–278
- Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology* 80:1322–1339
- R-Development Core Team (2004) *R: a language and environment for statistical computing*. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org> <http://r.project.org/>
- Rose KE, Clutton-Brock TH, Guinness FE (1998) Cohort variation in male survival and lifetime breeding success in red deer. *J Anim Ecol* 67:979–986
- Sæther BE (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *TREE* 12:143–149
- Sand H, Pehrson Å, Cederlund G (1996) Annual variation in body mass and reproductive traits in mouse *Alces alces*—the effects of weather conditions and food quality. In: *Life history strategies in moose (Alces alces): geographical and temporal variation in body growth and reproduction*. PhD Thesis. Swedish University of Agricultural Sciences, Uppsala
- Sinclair ARE (1989) Population regulation in animals. In: Cherrett JM (ed) *Ecological concepts*. Blackwell, Oxford, pp 197–241
- Skogland T (1983) The effects of density dependent resource limitation on size of wild reindeer. *Oecologia* 60:156–168
- Skogland T (1990) Density-dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. *Oecologia* 84:442–450
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Strandgaard H (1972) The roe deer (*Capreolus capreolus*) population at Kalø and the factors regulating its size. *Dan Rev Game Biol* 7:1–205
- Stubbs M (1977) Density dependence in the life-cycles of animals and its importance in K- and r-strategies. *J Anim Ecol* 46:677–688
- Van Horne B (1984) Density as a misleading indicator of habitat quality. *J Wildl Manag* 4:893–901