THE EFFECTS OF DENSITY-DEPENDENT RESOURCE LIMITATIONS ON THE DEMOGRAPHY OF WILD REINDEER

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SUMMARY

(1) The population dynamics of eight wild reindeer herds in Norway, including the high arctic, were studied in relation to food abundance and population density.
(2) Density-dependent effects were manifested through winter food limitation.
(3) With increasing densities, density-independent factors such as severe weather had additional effects on recruitment, with consequences for population stability.
(4) The density effect took the form of decreased juvenile survival, while adult survival in the most abundant and reproductive age classes was not affected.
(5) At high density, subadult fecundity fell below the threshold body size for maturity.
(6) The fecundity of adults was not affected by density. This finding accords with those made for other large nomadic rather than sedentary ungulates.
(7) Density-dependent food limitation was most apparent at high population density, which conforms with the predictions of density-dependent life history models for large mammals.

INTRODUCTION

The general conclusion of several evolutionary arguments (i.e. Fowler 1981a,b and references therein) is that populations of large animals should show their main density-dependent changes either at high population levels, or close to the carrying capacity. A limitation of food resources can have an important density-dependent effect on populations and is the predominant factor regulating herbivore numbers (Laws, Parker & Johnstone 1975; Sinclair 1977, 1979). The demographic consequences of density dependence, or resource limitation, in most of the recorded instances, has taken the form of a decrease in infant survival, or of a decrease in fecundity, while adult survival has been less affected (Caughley 1970; McCullough 1979; Clutton-Brock, Guinness & Albon 1982; Sinclair & Norton-Giffiths 1982; Sauer & Boyce 1983).

Bergerud (1980) has suggested that populations of North American caribou (*Rangifer tarandus* L.) are mainly regulated by predation by wolves (*Canis lupus* L.), in conjunction with hunting by humans, although Haber & Walters (1980) argued that food supply, wolf predation and hunting by man produce multiple equilibrium states in caribou numbers. Recent studies on other ungulates have stressed the importance of the food supply for migratory populations (Houston 1982; Sinclair & Norton-Giffiths 1982).

In this study I tested the hypothesis that numbers of wild reindeer (*Rangifer tarandus tarandus* L, *R.t. platyrhynchos* L) are regulated by food levels in a density-dependent manner and that these changes occur mainly at high population levels or close to their
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carrying capacity, as is generally predicted for large mammals. No wolf populations were present in any areas included in this study.

Study areas

A description of the study areas (Fig. 1) and of each of the herds on the mainland in Norway is given by Skogland (1983) and of the one in Reindalen on the Svalbard island in the arctic by Alendal & Byrkjedal (1975). The vegetation in the areas included in the study is either typical mountain tundra (Nordhagen 1943) or arctic tundra (Brattbakk & Rønning 1978). Data on habitat characteristics and population sizes are given in Table 1.

The South Norwegian herds are now divided into separate subpopulations (Skogland 1983). The Reindalen subpopulation of the Spitsbergen reindeer (Rangifer t. platyrhynchos) is of particular interest because of its high density and its apparently overgrazed winter pastures. The herd has been protected from hunting since 1920 (Reimers 1983b). The Brattefjell-Vindeggen herd was protected until 1980.

Fig. 1. Map of the location of the reindeer herds studied in Norway. The insert shows the study locality on the island of Svalbard at 78°N. Study herds: (1) Forelhogna; (2) Knutshø; (3) Snøhetta; Sølenkletten; (5) Rondane; (6) Hallingskarvet; (7) Hardangervidda; (8) Brattefjell-Vindeggen; (9) Reindalen.
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TABLE 1. Habitat characteristics of the different study areas

<table>
<thead>
<tr>
<th>Herd area</th>
<th>Total area (km²)*</th>
<th>Mean winter habitats (proportion of total area)± S.E.</th>
<th>Ratio of winter:summer grazing area</th>
<th>Mean lichen dry biomass g⁻² ± S.E.</th>
<th>Biomass sample sizes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Knutshø</td>
<td>1600</td>
<td>31.7 ± 7.3</td>
<td>0.79</td>
<td>557 ± 17</td>
<td>46</td>
</tr>
<tr>
<td>Forelhogna</td>
<td>1600</td>
<td>27.7 ± 8.6</td>
<td>0.67</td>
<td>500</td>
<td></td>
</tr>
<tr>
<td>Snohetta</td>
<td>2750</td>
<td>14.3</td>
<td>0.23</td>
<td>30 (1966)†</td>
<td></td>
</tr>
<tr>
<td>Solenkletten/</td>
<td>1200</td>
<td>34.5/</td>
<td>2.35/</td>
<td>97.4 ± 2.9</td>
<td>59</td>
</tr>
<tr>
<td>Rondane Sør-</td>
<td>1500</td>
<td>20.3 ± 16.6</td>
<td>0.7</td>
<td>500</td>
<td></td>
</tr>
<tr>
<td>Hardangervidda</td>
<td>8000</td>
<td>12.1</td>
<td>0.3</td>
<td>134 ± 62(1970)§</td>
<td>44</td>
</tr>
<tr>
<td>Brattefjell–Vindeggen</td>
<td>445</td>
<td>23.8 ± 4.8</td>
<td>0.7</td>
<td>290 ± 21</td>
<td>39</td>
</tr>
<tr>
<td>Hallingskarvet</td>
<td>2384</td>
<td>27.1 ± 9</td>
<td>0.57</td>
<td>194 ± 37</td>
<td></td>
</tr>
<tr>
<td>Reindalen</td>
<td>115</td>
<td>14.9</td>
<td>0.15</td>
<td>25±</td>
<td></td>
</tr>
</tbody>
</table>

* Only vegetated areas included, data from the area records on file at DVF.
† From Skogland (1984); Skogland (1983).
‡ From Gaare & Skogland (1980).
§ From Gaare & Skogland (1979). Lichen density calculated from volumes as given therein.
¶ From Brattbakk & Renning (1978) and this study.

METHODS

Population size

Herd size was estimated by making total counts from small aeroplanes. Complete coverage of each study area was obtained by flying along a number of parallel traverses across the area. All herds were photographed and the number of animals visible on the enlarged photographs were counted. Owing to its scattered distribution, the Reindalen herd was counted on the ground once every year, during the first week of August, instead of by the aerial method. The aerial counts were done by either members of the research staff at DVF, or in cooperation with the local game wardens.

Fecundity

Fecundity was estimated by (i) culling does in the winter during the gestation period and (ii) counting live does considered to be pregnant just prior to the calving time. The counts involved checking the external appearance of the does, particularly antler possession, size of abdominal region as well as swollen udders. Approximately 1% of all the does in each of the study herds never developed antlers. Non-pregnant does dropped their antlers prior to the calving period (see also Espmark 1971). During seventeen calving seasons less than 1% of the does that gave birth were without antlers (T. Skogland unpublished).

Recruitment and calf survival

Recruitment was estimated by field counts of the ratio of the number of live calves to the number of live does ≥1 year of age. The counts were done 1 month after calving, during the autumn composition counts in the rut, and at the end of the calf’s first winter. Calf survival was estimated by the change-in-ratio (CIR) method. The degree of variance of the survival rate estimates given by the CIR method was calculated by Ricker’s (1975) method. The confidence limits for all the survival rates were calculated on a basis of binomial sampling (Snedecor & Cochrans 1978). Recruitment rates were also calculated from age-specific survival rates (see below).
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Ageing and age structures

Age was estimated from tooth eruption patterns for animals 1–3 years of age, and for older animals by microscopic inspection of the annuli in the stained incisors from each jawbone, according to the method of Reimers & Nordby (1968).

Age structures were constructed for the doe cohorts ≥ 2 years of age from collections of jawbones from animals shot by hunters during the regular hunting season. Because of the impossibility of ageing a doe from her external appearance I assumed that does would be shot in direct proportion to their availability in the herd (see also Burgoine 1981). Age structure of the protected herd in Reindalen was constructed from pick-up samples from natural deaths of adults ≥ 1 year of age during field searches.

The age of bucks 1·5–3·5 years old was estimated from their external appearance during the autumn composition counts in the rut. Because of the wide variation in the size and shape of adult bucks, most hunters were unable to distinguish clearly in the field their different age-groups. Therefore, I have assumed that ageing bucks as ≥ 4·5 years from the jaw collections provided a fairly representative picture of the age composition of adult bucks.

Analysis of density effects on recruitment was by least squares regressions of recruitment rates against population densities. Furthermore, a multiple least squares regression was calculated with recruitment rate against winter density and lichen biomass.

Life-table analyses

The age-class frequency data for the adults were converted into logarithmic values. The reasons for using log values are given by Varley & Gradwell (1970). The data for the standing age-classes yielded age-specific survival rates. Since population growth rates were known for all the herds, based on the counts, the age-specific rates were converted into time-specific rates by the \( N_x e^{rx} \) conversion method (Caughley 1977 and see Table 3), where \( N_x \) is the log of the standing age-class frequency and \( r \) is the population growth-rate. The resulting time-specific rates were further smoothed by making polynomial regression analyses for best fit. The critical assumption made in these calculations is that all herds showed stable increase, or decrease, or that their numbers remained stable over a period of time that included most of the age-classes present. When population development was more unstable, the age-specific survival rate (s) was calculated from the equation:

\[
    s = J \left( 1 - \frac{z}{\lambda} \right)
\]

where \( J \) = annual hunting rate (proportion of the population shot); \( \lambda \) = finite population increment; \( z \) = instantaneous age-class decrement; \( z \) was derived from the age-specific rates by calculating either the regression coefficient for decrement against age (for large samples), or the value

\[
    N_2 \sum_{x=2}^{\infty} N_x
\]

for samples that were either too small, or that were too variable in size owing to fluctuating annual recruitment rates. The resulting coefficients (b) were converted into instantaneous rates from the equation \( z = (1 - e^{-b}) \) (Ricker 1975, see Table 3).

A buck survival curve could be constructed only for the Brattefjell-Vindeggen herd, because after many years of buck shooting, the adult sex ratios of other mainland herds had become skewed in favour of does.
Winter food availability was assessed by noting the plant composition and the height of the plant cover within 33 × 100 cm plots. The plots were randomly placed within the typical wintering areas. Due to the snow cover on the tundra, only one particular vegetation type, the *Loiseleurio Arctostaphyliion* (see Nordhagen 1943), is available to the reindeer for grazing in late winter. The thickness and height of the lichen mats on the xeric, chionophobous heaths therefore give a good indication of the actual foraging conditions. From the degree of coverage and the height of the lichen mats I calculated the forage volume. I converted this to biomass by the methods given by Gaare & Skogland (1979).

**RESULTS**

**Fecundity rates**

Data from culls do not show any density effect on the fecundity of the adult does, but with increasing population density the 1.5 and 2.5 year-old cohorts gradually become less productive (Fig. 2). Since a heavy decline in calf productivity is found over the same density gradient (see Fig. 4), the youngest cohorts represent a smaller proportion of the total population of does at increasingly higher densities. Field counts of pregnant does show only a small, but still significant, decline in overall fecundity with increasing density ($R^2 = 0.43; F = 12.49$; d.f. = 1,20; $P < 0.01$; Fig. 3). The decline is slight mainly because of the absence of such a density effect on the fecundity rate of the adult does.

It is thus clear that the difference between the fecundity rate and the recruitment rate becomes significantly greater with increasing herd density. The difference was of the order of 67% (Table 2).

**Differences between herds in recruitment**

The difference between the least and the most productive herds (Reindalen and Forelhogna-Knutshø, respectively) was almost fourfold (Table 2). The variance in the recruitment rates increased with decreasing overall productivity (Table 2). Since differences

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**Fig. 2.** Age-specific fecundity rates for four population densities. Numbers above the graphs indicate sample herds: (1), Knutshø-Forelhogna, $n = 44$; (2), Hallingskarvet, $n = 295$; (3), Hardangervidda, $n = 73$; (4), Snøhetta, $n = 53$. For (4) rates are calculated from Reimers (1983a).
Fig. 3. The ratio of antlered to unantlered does prior to calving, as an estimate of population fecundity rates at different population densities. N indicates the number of years in which data were collected. See also Table 2. The mean and range (vertical bars) are given.

existed in the age and level of first-time fecundity of the herds, the calf recruitment rates were analysed in relation to the proportion of the first-years that were fecund to see whether this was the factor accounting for the variation. It accounted for most of the year-to-year variation only in the highly productive herds (Forelhogna-Knutsho, $R^2 = 0.84; n = 6; P < 0.02$), creating a cycle of productivity. For the less productive herds (Hardangervidda, Snohetta, Reindalen), no such statistically significant relationship was found ($R^2 = 0.1; n = 6; P > 0.1$). Apparently, environmental perturbations in addition to other factors affect herds of low productivity. Disregarding both this cycle generated by the age-structure, and the oscillations in recruitment caused by other external factors, the overall difference in recruitment between the highly and the less-productive herds was not accounted for by this analysis.

The recruitment rates, obtained from direct field observations (Table 2) can be compared with those calculated by the age-specific survival method, i.e. from the standing age-classes of does (Table 3), divided by an average sex ratio of 0·5. For all herds, except the Hallingskarvet one, the rates given by the two methods overlapped. Calf production by the Hallingskarvet herd collapsed in 1982, following a period of overgrazing of the winter pastures that culminated in 1981. Before then calf production of this herd had been much higher, around sixty calves: 100 does $\geq$ 1 year of age (J. Vik & O. Dusegard personal communication). The standing age-class distribution of this herd therefore did not reflect a lowering of the recruitment rate.

**Effects of density on recruitment**

The recruitment rates were lowest at high overall densities ($R^2 = 0.87; F = 221.4$, d.f. $= 1.32; P < 0.001$; Fig. 4), and were related to both winter density and lichen biomass (see Table 1) in the multiple regression ($R^2 = 0.87; P < 0.001$). The correlation coefficient for both winter density and lichen biomass with recruitment rate was significant ($P < 0.05$). For two populations the recruitment rate was significantly lower at high winter population densities ($R^2 = 0.88; F = 93.6$, d.f. $= 1.12; P < 0.001$; Fig. 5).

The herds of Reindalen on Svalbard had a low finite rate of increase of 6·4% (Table 3). In another part of Svalbard, Nordenskioldkysten on Nordenskiold Land, a herd of eleven immigrant reindeer increased to c. 1000 in 17 years, with a finite rate of increase of 27%
<table>
<thead>
<tr>
<th>Herd</th>
<th>Fecundity rate, does</th>
<th>Mortality rates</th>
<th>Recruitment rate</th>
<th>Survival rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Post-natal rate</td>
<td>Autumn rate§</td>
<td></td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>C.V.</td>
<td>N</td>
</tr>
<tr>
<td></td>
<td>(N)</td>
<td>(Mean)</td>
<td>(C.V.)</td>
<td>(N)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Post-natal rate</td>
<td>Autumn rate§</td>
<td></td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>C.V.</td>
<td>N</td>
</tr>
<tr>
<td>Reindalen♂</td>
<td>0.5 (0.16–0.18)</td>
<td>0.44 N.S. (0.03–0.18)</td>
<td>0.18*** (0.11–0.23)</td>
<td>0.36 (0.28–0.61)</td>
</tr>
<tr>
<td>Hardangervidda</td>
<td>0.64 (0.03–0.07)</td>
<td>0.34*** (0.02–0.1)</td>
<td>0.32 N.S. (0.02–0.09)</td>
<td>0.5 (0.4–0.73)</td>
</tr>
<tr>
<td>Snohetta</td>
<td>0.6 (0.03–0.08)</td>
<td>0.34*** (0.06–0.09)</td>
<td>0.33 N.S. (0.07–0.13)</td>
<td>0.55 (0.48–0.71)</td>
</tr>
<tr>
<td>Hallingskarvet</td>
<td>0.57 ± 0.01†</td>
<td>0.44*** ± 0.06</td>
<td>0.16*** ± 0.03</td>
<td>0.23 ± 0.03†</td>
</tr>
<tr>
<td>Brattefjell</td>
<td>0.57 0.06 (0.1–0.16)</td>
<td>0.49 N.S. (0.1–0.16)</td>
<td>0.86 ± 0.096†</td>
<td></td>
</tr>
<tr>
<td>Knutsho</td>
<td>0.67 (0.06–0.09)</td>
<td>0.64 N.S. (0.05–0.14)</td>
<td>0.6 N.S. (0.7–0.11)</td>
<td>0.9 (0.88–0.99)</td>
</tr>
</tbody>
</table>

N = number of sample years and C.V. = range of values of the coefficient of variation
N.S. = insignificant decrement in rate compared to that for the preceding sampling period in the same year
*** = p < 0.001
* = total count
† = 95% confidence level on sample mean
‡ = significant in 1 year
§ = rates adjusted for hunting losses
♂ For the Reindalen herd, data from Alendal & Byrkjedal (1975) and Gossow (1980) are included.
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Table 3. Estimated survival and recruitment rates for the studied herds

<table>
<thead>
<tr>
<th>Herd</th>
<th>Sample year</th>
<th>n§</th>
<th>z</th>
<th>P</th>
<th>Age-classes in least squares regression (years)</th>
<th>Finite rate of increase (r)‡</th>
<th>Time-specific survival rate (p,)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forelhoga</td>
<td>(1980)</td>
<td>30</td>
<td>-0.281*</td>
<td></td>
<td></td>
<td>0.28</td>
<td>0.97</td>
</tr>
<tr>
<td>Forelhoga</td>
<td>(1969)</td>
<td>169</td>
<td>-0.302†</td>
<td></td>
<td></td>
<td>0.995</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Knutshø</td>
<td>(1981)</td>
<td>62</td>
<td>-0.31†</td>
<td>0.995</td>
<td>&lt;0.001</td>
<td>0.3</td>
<td>0.954</td>
</tr>
<tr>
<td>Rondane Sør-</td>
<td>(1981)</td>
<td>184</td>
<td>-0.27†</td>
<td>0.995</td>
<td>&lt;0.001</td>
<td>0.254</td>
<td>0.949</td>
</tr>
<tr>
<td>Solenkletten</td>
<td>(1981)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hallingskarvet</td>
<td>(1981)</td>
<td>295</td>
<td>-0.275†</td>
<td>0.995</td>
<td>&lt;0.001</td>
<td>0.28</td>
<td>0.931</td>
</tr>
<tr>
<td>B. Vindeggen</td>
<td>(1981)</td>
<td>78</td>
<td>-0.267†</td>
<td>0.959</td>
<td>&lt;0.001</td>
<td>0.23</td>
<td>0.963</td>
</tr>
<tr>
<td>Hardangervidda</td>
<td>(1979)</td>
<td>188</td>
<td>-0.224†</td>
<td>0.985</td>
<td>&lt;0.001</td>
<td>0.19</td>
<td>0.936</td>
</tr>
<tr>
<td>Snohetta</td>
<td>(1981)</td>
<td>349</td>
<td>-0.19†</td>
<td>0.959</td>
<td>&lt;0.001</td>
<td>0.23</td>
<td>0.963</td>
</tr>
<tr>
<td>Reindalen</td>
<td>(1981)</td>
<td>29</td>
<td>-0.124*</td>
<td></td>
<td></td>
<td>0.064</td>
<td>0.92</td>
</tr>
</tbody>
</table>

* Age-specific rate = N₁/N₀, N₀ is the standing age-class frequency.
† From the regression coefficient (b). z is given by z = (1 - e⁻ᵇ)
‡ From Fig. 6.
§ n is sample size.

Fig. 4. The effects of different population densities on the ratio of calves recruited per 100 does ≥1 year-old. Open circles (O) indicate data from mainland Norway while triangles (△) indicate data from Svalbard. The data sources are the same as those in Tables 1 and 2.

(K. Bye personal communication; N. Øritzland personal communication, own observations; Alendal & Byrkjedal 1975). A third group, of thirteen reindeer, was transplanted by N. Øritzland from the overgrazed habitats near Longyearbyen on Svalbard to the Ny Ålesund area, where no reindeer have ever been recorded. This herd has grown at a finite rate of more than 30%, since the start.

The physiognomy of the vegetation cover of all these three areas of Svalbard is similar, but each is at a different stage of winter grazing pressure. In the Reindalen area all the lichens have been eliminated and soil erosion has reached an advanced stage. At Nordenskioldkysten extensive mats of lichens (Cetraria spp.) are still present (I. Brattbakk personal communication; own observations) and at Ny Ålesund the winter forage biomass of the habitat is of the order of 5–12 times greater than that in the Reindalen area (Brattbakk & Rønning 1978).
These results on recruitment support the hypothesis that there is a density-dependent food limitation effect acting on the productivity of the wild reindeer herds included in this study.

**Calf survival rates**

Neonatal mortality was, on average, about 40%, being consistently high for herds living on overgrazed pastures (Table 2). All mainland herds calved during winter and were probably vulnerable to limitations in the availability of lichens at this time. Significantly, in only 2 out of 10 years did I find mortality to be related to the foraging conditions following the neonatal period (Table 2). Neonates were most at risk. For the Hardangervidda herd, living on overgrazed winter ranges, in only those years with exceptionally extreme winter conditions did I detect any mortality associated with winter weather among calves of the previous year. Furthermore, in those herds with a consistently high productivity (Knutshø, Forelhognå), recruitment did not fluctuate from year to year, regardless of extreme summer or winter conditions, as it did in the herds living on more limited food.

Mortality of older calves during summer or winter was only recorded for those herds having a significant neonatal mortality. Mortality associated with the adverse summer weather was about 30–40% (Hardangervidda and Hallingskarvet) and with winter weather about 10% (Hardangervidda, Hallingskarvet), but up to more than 50% in Reindalen.

The correlation between first-year mortality (Table 2) and the average availability of forage during late winter (Table 1) was highly significant \( r = -0.95; n = 6; P < 0.001 \). The data suggest that limited food supply in late winter results in an increase in neonatal mortality. Furthermore, as shown above, the magnitude of this neonatal mortality is related to a large extent to the magnitude of all subsequent mortality in response to adverse climatic conditions occurring at other times during the calves' first year of life.

**Primary to secondary sex-ratios**

The pre-natal sex ratio was slightly skewed in favour of males, but did not differ significantly from equality (Table 4). This agrees in general with data about other ungulates (Verme 1983). The secondary sex ratio, however, was skewed in favour of females and differed significantly from equality. Thus, for those herds that experience neonatal and
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**Table 4.** Changes in the sex ratio (males:females) from the pre-natal to adult stages (data from Hardangervidda and Brattefjell-Vindeggen)

<table>
<thead>
<tr>
<th>Sample size</th>
<th>P</th>
<th>1-5 years</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prenatal</td>
<td>101*</td>
<td>1418†</td>
<td>815‡</td>
</tr>
<tr>
<td>Ratio</td>
<td>53:49</td>
<td>0-18</td>
<td>0-9</td>
</tr>
<tr>
<td></td>
<td>&gt;0-9</td>
<td></td>
<td>&lt;0-005</td>
</tr>
</tbody>
</table>

* Sample of culled does.
† Survivors of the 1971 cohort born on Hardangervidda during the period when hunting was prohibited (1971–72).
‡ Sample of the Brattefjell–Vindeggen herd that emigrated from Hardangervidda and lived there, without being hunted, until 1980.

**Table 5.** Adult sex ratios (males:females) of herds protected from being hunted

<table>
<thead>
<tr>
<th>Year</th>
<th>1-5 ratio</th>
<th>n</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Reindalen</td>
<td>1978</td>
<td>39:8:60:2</td>
<td>102*</td>
<td>4:24</td>
</tr>
<tr>
<td>Reindalen</td>
<td>1979</td>
<td>35:65</td>
<td>351†</td>
<td>31:59</td>
</tr>
<tr>
<td>Reindalen</td>
<td>1982</td>
<td>42:58</td>
<td>363‡</td>
<td>9:59</td>
</tr>
</tbody>
</table>

* counted during the rut.
† counted during late summer.

Post-natal mortality, the males suffer a high mortality rate. This trend continued into adulthood (Table 5). We shall therefore turn our attention to the survival rates of adults.

**Adult survival rates**

For the least productive herds, there is a slight decline in mean survival rate of adult does (Table 3), but the life-table analysis method does not permit any statistical test being made of the sampling error involved.

The survival curves shown in Fig. 7, calculated from population growth rates (Fig. 6), and the standing age classes (Fig. 7), indicate that the survival rates of the strongest, most productive, age classes (those between 2 and 10 years-old), were high in all the herds. Survival rates of adult does in the different herds may differ because of a change in the age-structure of the population in these herds whose productivity was lowered by calf losses.

Because the age-class sample for the Reindalen herd in 1981 was very small, owing to the irregularity in the annual losses, it is difficult to draw valid conclusions for this herd. During the 5-year study period, a total of fifty-one carcasses of adults 1 year-old or older were found, twenty-nine of which were found in 1981. This means that, on average, ten animals out of a total population of 550 died each year, in which case the actual survival rate for adults in the Reindalen herd was 0.98 which is similar to the calculated value of 0.92 (Table 3). The mean recruitment rate was 0.18 during the entire 11-year period for which data exist. Since roughly half of the recruitment was of does, then the doe recruitment rate, less the adult mortality rate, yields a population growth rate of 0.07. This growth rate compares favourably with the population growth rate estimated from field observations (Fig. 6). This result suggests that the adult mortality rate does not differ from that of mainland herds.

In an analysis of variance the mean adult survival rate was not significantly related to the winter population density for the mainland herds ($F = 4.62$; d.f. = 1,5; $P > 0.05$),

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which suggests that doe survival is not affected by population density. The decline in the survival rate with increasing age takes place more rapidly for bucks than for does (Fig. 8). The mean survival rate of bucks was 93% of the value for does. This higher mortality rate for males thus explains the discrepancy shown in Tables 4 and 5 between the secondary and the adult sex ratios.

DISCUSSION

Reproductive life history strategy

From my results it is clear that the effects of food limitation at a high population density are mainly through the pregnant doe’s chances of success in giving birth to a viable offspring. If food is scarce, she apparently abandons her foetus, or young, in preference to putting her own survival at stake and halt her own body growth after reproduction. The gradual decline in fecundity of the youngest cohorts with increasing herd density is caused by a decrease in body-size, to a value below the threshold at which maturity takes place (Reimers 1983a). Once this minimum size has been attained, fecundity remains high
Fig. 7. Age-specific and time-specific age-class frequencies for the does of different ages in the studied herds (see Methods for calculation details). Dashed lines (---) indicate age-specific and solid lines (---) time-specific frequencies. Sample sizes are given in Table 3.
throughout adulthood, regardless of actual body size. The average body size of the Hardangervidda does was only 60% of that of the Knutshø does (Skogland 1983), yet adult fecundity rates were similar. These findings do not support Reimers’ (1983a) suggestion that fecundity is related to body size.

High adult fecundity rates are compatible with a nomadic reproductive life history strategy (Geist 1981), as shown by the migratory wildebeest (Connochaetes gnou) (Sinclair 1979), the reindeer (R.t. tarandus) Klein 1968; Leader-Williams 1982; this study) and the caribou (R.t. groenlandicus, R.t. arcticus) (Bergerud 1971; Dauphiné 1976; Parker 1981). This particular strategy, as opposed to that of having a fixed home range, entails movement in order to locate better foraging areas. The North American caribou can still practice their migration unhindered by habitat obstructions. In Norway, however, this is normally no longer the case, and when interference with this life history strategy occurs, food may become a limiting factor to reproductive success (as shown in this study). Species having home-ranges, like the North American deer (Odocoileus virginianus, O. hemionus) or the Scottish red deer (Cervus elaphus) show a size-fecundity relationship, and the fecundity rate falls with increasing population density (Gross 1969 and references therein; Albon, Mitchell & Staines 1983; Clutton-Brock, Guinness & Albon 1983; Mitchell & Brown 1974). In respect to reproductive life history strategy, the migratory North American elk (Cervus canadensis) appears to be intermediate, because the fecundity rates of middle-aged females (3–9 years old) are unaffected by changes in population density (Houston 1982).

Survival

In this study, the greater part of the mortality of reindeer was due to neonatal losses probably caused by food limitation prior to, or at calving. Furthermore, herds with a limited food supply were not buffered against adverse climatic effects at other seasons of the year. This led to fluctuations in the recruitment rate and, in turn, to unstable population growth. The effects of years of low recruitment clearly show up in the age structure data, i.e. the 1969 and 1971 cohorts in both the Hardangervidda and Snohetta age-class distributions (Fig. 7).

My results suggest that the survival rate of does during their reproductive life-span was unaffected by herd density (or by limitations of the food supply). Unfortunately,
Reindeer population regulation

comparable adult survival rate data at both high and low densities are lacking for other cervids.

Population regulation

As Ricklefs (1973) pointed out, density is critical for a population only when viewed in the context of resource availability. Therefore, a valid evaluation of a density-dependent factor must be based on data gathered under identical environmental conditions, to eliminate the effects of density-independent factors on population size. In this study identical environmental conditions for comparison were ensured by using only the actual winter habitat densities for the mainland herds of reindeer for the analysis of density-dependence, since winter food availability was found to be the most critical factor for survival.

The data from Svalbard show that the intrinsic growth rate of reindeer on this island is identical to that for mainland reindeer ($r = 0.3$). When plotted against winter habitat density the Svalbard data would fall on the slope of the mainland data shown in Fig. 5. Leader-Williams (1982) concluded that three introduced herds of reindeer at different population densities on South Georgia were at different stages of food resource limitation although lichens do not form a part of the winter diet of reindeer on these islands.

Density-independent factors such as (a) those related to climate (i.e. snow depth, ground ice or suppressed plant growth), and (b) harassment by insects (also climatically dependent), man or predators have been shown (or suggested) to affect body composition as well as growth in Peary caribou (Thomas 1982) and wild reindeer (Reimers 1983b,c). Ground ice in winter, following overgrazing of the lichen, was the most likely cause of the population crashes of several introduced reindeer herds on arctic islands off the coast of Alaska (Scheffer 1951; Klein 1968).

Reimers (1983b,c) suggested that the population size of reindeer was regulated by climate on Svalbard and by harassment on the mainland. From the above discussion and the presented results however, I suggest that the primary factor in population regulation of wild reindeer herds is density-dependent food limitation in winter, and that density-independent effects are most likely to be a contributory factor only at high population density.

Low density populations are characterized by a lower mean age than those at higher density, because of a higher population growth rate. Older age classes play an increasing role in the reproduction of high density populations. This is evident from the slope of the curves for the standing age-class frequencies shown in Fig. 7. One would therefore expect to find that the longer reproduction is delayed, the greater the degree of non-linearity of the density-dependent relationship. The slight delay in attaining reproductive age at high densities in this study is in accordance with the finding that the curvilinearity of the recruitment-density relationship is slight.

The results presented in this study thus support the hypothesis that density-dependent food limitation occurs at densities near to, or above, one half the ecological carrying capacity, in conformity with the predictions of large-mamall population models.

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