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Abstract: We studied both the short- and long-term effects of density on three life history traits of a red deer population inhabiting a temperate forest. Both male and female body mass increased when population density decreased, but male mass changed to a greater extent than female mass. Density did not influence female survival irrespective of age, however, survival of males was lower at high density for all age classes except the prime-age class. Pregnancy rates of primiparous females increased markedly with decreasing density, whereas those of adult hinds were fairly constant and unrelated to density. For both sexes, of the studied life history traits we detected a long-term effect of density at birth (cohort effect) only on body mass. These results suggest that density influences life history traits in the same way as factors of environmental variation such as climate. In this population we did not find any evidence for an influence of climatic conditions on life history traits of red deer. Both mild winters and the absence of summer droughts during the study period could account for such an absence of climatic effects. We interpreted our results to show that 1) as expected for a highly dimorphic and polygynous species such as red deer, male traits showed consistently higher sensitivity to variation in density than female traits, illustrating possible costs caused by sexual selection in males, 2) the female-based Eberhardt's model according to which increasing density should sequentially affect juvenile survival, reproductive rates of primiparous females, reproductive rates of adults and lastly adult survival was only partly supported because we found that pregnancy rate of primiparous females rather than juvenile survival was the most sensitive trait to variation in density. We propose that including variation in male traits would improve the accuracy of models of population dynamics of large mammals, at least for highly dimorphic species. Because the population we studied was not fenced, we only measured apparent survival. We discuss how dispersal, in relation to the phenotypic quality of young deer, might be a potential regulating factor under such conditions.
Sex- and age-dependent effects of population density on life history traits of red deer Cervus elaphus in a temperate forest

Christophe Bonenfant, Jean-Michel Gaillard, François Klein and Anne Leison


We studied both the short- and long-term effects of density on three life-history traits of a red deer population inhabiting a temperate forest. Both male and female body mass increased when population density decreased, but male mass changed to a greater extent than female mass. Density did not influence female survival irrespective of age, however, survival of males was lower in high density for all age classes except the prime-age class. Proportion rates of pithing males increased markedly with decreasing density, whereas those of adult hinds were barely constant and unrelated to density. For both sexes, of the studied life-history traits, we detected a long-term effect of density at birth (except referred only on body mass). These results suggest that density influences life-history traits in the same way in factors of environmental variation such as climate. In this population we did not find any evidence for an influence of climatic conditions on life-history traits of red deer. Both mild winters and the absence of winter stress during the study period would account for such an absence of climatic effects. We interpreted our results to show that 1) an expected for a highly demic and sedentary species such as red deer (male traits showed consistently higher sensitivity to variations in density than did female traits), destroying possible units caused by recent selection in males, 2) the female-based model of the density effects of survival, reproductive rate of pithing females, reproductive rate of adult males and pithing rates of adults was only partly supported because we found that pithing rate of pithing females rather than juvenile survival was the most sensitive trait to variation in density. We propose that including variation in male traits would improve the accuracy of models of population dynamics of large animals, at least for highly demic species. Because the population we studied was not limited, we only measured apparent survival. We discuss how dispersal, in relation to the phenotypic quality of young deer, might be a potential regulating factor under such conditions.

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Regulation of mammal populations, through density dependent responses of life history traits (Hansol Messier 1994) plays a central role in modern ecological theory (Canfield 1997, Fowler and Smith 1981). Recent studies have highlighted the difficulty in distinguishing density dependence and density independence (Leison and Langvatn 1998, Coulson et al. 2000) because not all age and sex classes have similar responses to variations in density or weather. Indeed, the two processes both primarily affect juvenile survival and reproductive rates rather than adult survival (Gallard et al. 2000b). Fowler (1987) and then Sotherton

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(1997) reviewed empirical evidence of density de-
pendence in several life history traits of large mammals. In ungulates, negative effects of density have been re-
ported for body mass (red deer Cervus elaphus; Gray,
1834); Chiquinet 1991; simirers R. Aguirr, laurad Hamil-
ton-Smith, 1968; Ale er Capreolus capreolus; Grey, Chiquinet et al. 1998), age at first reproduction (red deer
Cervus elaphus; Linnawe. Albon et al. 1983, 1987; re
deer Cervus elaphus; Guilard et al. 1992; simirers: Skoglund 1990; bighorn sheep Ovis canadensis; Linnawe. Jorgesen et al. 1987; and adult survival (wag. sheep Ovis aries; Linnawe. Milner et al. 1990; African buffalo Syncerus caffer Hudsonian Sinclair 1994). However, the effects of density can differ within a given species depending on environmental conditions (Guillard et al. 1996; Coulson et al. 1997; Porteret al. 1998).

Actually, it is also established that large mammal populations respond to density independent factors in-
cluding local climatic variations (Peron 1984, Albon and Clutton-Brock 1988, Sæther and Heie 1993; Lei-
son and Langvatn 1997, Post and Stenseth 1999, Coul-
son et al. 2000; more recently, several studies reported an influence of large-scale climatic trends like the North
Atlantic Oscillation (Hurrell 1995) on ungulate individ-
ual life history traits (Post et al. 1997, Post and Stenseth
1997, Forchhammer et al. 1998, Leisner et al. 1999; Møller et al. 1999). However, life history traits re-
sponses induced by climate are often associated with extreme conditions like high density, particularly harsh
weather or weather patterns at the boundary of their distribution (Clutton-Brock and Albon 1989, Grenfell et al. 1998). Coulson et al. (2000) suggested that the modifications in vital rates from intrinsic and extrinsic factors were better explored using a process-oriented approach on long-term data. Here we used such a process-oriented approach to investigate the influence of marked variations in density on sex and age-specific body mass, pregnancy rate and survival from a red
deer population in a temperate forest. More particularly, we aimed to test the following six predictions.

Because of the widespread occurrence of density de-
pendence in ungulate populations (see above), we ex-
pected 1) components of individual fitness to be lower at high density than at low density in each age and sex-class. Body size early in life partly accounts for variations in sex fitness traits (Doney and Gaunt 1981, Clutton-Brock et al. 1982, Biggerman and Eivalt 1997, Petit-Blanc et al. 2000). Therefore, environ-
mental conditions during the early stage may have long-term effects on fitness components (Albon et al.
1997, Lindstrøm 1989). Such cohort effects have been reported for red deer (Albon et al. 1993, Ross et al. 1998), roe deer (Guillard et al. 1997), and reindeer (Gaundal et al. 1999). We thus expected that 2) population density at birth would have long-
term effects on body mass, survival and pregnancy rate in our red deer population.

The Pierre Peir National Reserve (PPNR) popula-
tion lives at low density under moderate climatic con-
ditions. In ungulate populations snow accumulation and duration have been reported as the main population
cause of mortality in winter (Moeh et al. 1987, Albon
and Clutton-Brock 1988, Goodson et al. 1991, Post and Stenseth 1998, Leisner et al. 1998) and annual varia-
tion in body mass replenishment/growth in spring (Post
and Stenseth 1999). Over the past 20 yr, the longest
period with snow cover recorded in our study area was
only 5 d. We thus expected that 3) body mass would not be affected either by the NAO or by the local weather.

Eberhard (1977) suggested that density dependent effects are predictable, sequential and additive. Because
small animals are less competitive than large ones dur-
ing food shortage (Begon 1984), juveniles, who are also subject to growth constraints (Sharma 1993), should be
influenced first by density. Then in turn, after further increase of population density, the performance of adults should decrease. Therefore, we expected that when the red deer population varied markedly in size, juvenile survival would vary more and adult survival the least, and 5) pregnancy rates of parous females would vary to a greater degree than those of adult females (Guillard et al. 2000).

Red deer are highly polygynous and dimorphic in sex (Clutton-Brock et al. 1982). Thus, because of both
behavioural constraints (Peterson 1985) and sexual selection (Flock 1970, Clutton-Brock et al. 1982), males are expected to have greater energy requirements than fe-
males and are therefore more sensitive to food shortage (Glickman 1994, Clutton-Brock et al. 1989, Leiberg
et al. 1999, Olsson et al. 1999). Such patterns might account for the low survival of males compared to females that is often reported in ungulates (red deer: Clutton-Brock et al. 1989; greater kudu Tragelaphus strepsiceros De Blainville: Owen-Smith 1993; bighorn sheep: Jorgesen et al. 1997; reindeer: Skoglund 1990). We thus expected that 6) density variations would influ-
ence male traits more than female traits.

Study area

The Peirre Peir National Reserve (PPNR) is a 2600 ha
forest located in southeastern France (44°37′N, 7°7′E) in the Yongs areas at an elevation of 300 m. The climate is continental with oceanic influences (mean January and mean July temperatures are 6.0°C and
18.4°C respectively) characterized by mild winters and
cold summers. The studied red deer population inhabits
a temperate forest of silver fir Abies alba, Douglas-fir
Pseudotsuga douglasii, Norway spruce Picea abies and
European beech Fagus sylvatica. The soils are poor
because of the acidity of the parent rock (sandstone).

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suggesting relatively poor food availability, and as a consequence, the reserve cannot be considered as a
favourable habitat for red deer. In addition, the red deer and
wild boar share the same territories within the reserve.
All the traps snares are hunted, either based on
quota (deer or strictly wild boar). During the last 10
years 50 red deer and 100 wild boar were hunted annually.
The study area is free of predators that could have an influence on deer survival.

Methods
Since 1977 the red deer population has been estimated by the Office National de la Chasse (ONC) and hunted in autumn each year by both professionals and sport
hunters. Every deer shot was scored and aged (N = 9500);
ONC managers recorded dressed weight and for horns
reproductive status. If the pregnancy was assessed be-
fore mid-November, the result was not included in our
analysis to avoid risk of diagnostic errors. Between
1977 and 1999 there were a total of 1621 hinds for which
we obtained fecundity data. Only singles were pro-
duced. Sample sizes were lowest for yearling hinds (i.e.,
primiparous) because of selective shooting. As hinds
were not all marked, we considered two age-classes:
only yearlings (1 and 2 years old) and adult (3 or
more years old). Deer were aged by dental eruption
and tooth wear. Because tooth wear estimates of age
may be biased (Hamlin et al. 2000) and dental eruption
allows reliable age assessment for red deer to 3
years of age only, we used three age classes: calf (< 1 yr),
yearling (between 1 and 2 yr) and adult (> 2 yr). As
calves were hunted over a period of ~ 4 months,
we accounted for possible growth, within the sampling
period by correcting call body mass for shoot date
using a regression from Sickler and Mazur (1978) and
standardized values to 5 December (mean shoot date, see
Jorgenson et al. 1993 for a similar procedure).

Although we did not know population size precisely,
the managers of the PPNR population have monitored
relative density by using an Abundance Index (AI,
Caughley 1977, Seber 1982) derived from road night
counts. The method consisted of driving the same road
twice a month from December to April and counting
every deer seen with a powerful spotlight (100 W) to
give an index of abundance sensitive enough to detect
major density fluctuations (Caughley 1977). Hunting
pressure increased markedly just before 1983 (87 and
66 deer were shot in 1981 and 1982 vs an average of 27
deer after 1983) and peaked the population density to
decrease drastically without a transient stage (Fig. 1)
together with a possible change in age structure. We
used this reduction in density as an experimental test
of density dependent responses in life history traits of red
deer (Sinclair 1989). However we did not use the AI as
a continuous variable in the analyses because of its low
accuracy (CV = 25.9%) likely due to changes in climatic
conditions (rain, fog), observer experience and sampling
errors (Caughley 1977, Seber 1982). Instead, two levels
of density were considered explaining 78% of the total
variance in the AI (AI = 74.53, p < 0.0001): a high-
density from 1977 to 1983 and a low-density from 1984
to 1999 (Fig. 1). Additionally, this marked change in
density allowed us to classify red deer into two types
of "cohorts" (e.g., Festa-Bianchet et al. 1998): individuals
born at high density (H type) and individuals born at
low density (L type).

We performed an analysis of covariances (ANCOVA)
for examining the response of red deer to weather-
variables, the mean dressed body mass as the dependent
variable, the NMD index (available from: http://
www.cdq.aucr.edu/clus/demind/), the mean precipita-
tion and temperature, in January–February and
May–June as the covariables and density as a two-level
factor. We replicated these analyses for each class of
sex and age. All the climatic data were obtained from
Météo-France.

The effects of mass and density on the proportion of
pregnant females were analyzed with a GLM proced-
ure. We used a logistic regression with pregnancy
status as the binary dependent variable, mass as covari-
ate and density and age as factors (ANCOVA-like
procedure, see Festa-Bianchet et al. 1998 for further
details). Because of the unbalanced sampling design,
we used a backward stepwise selection procedure, testing
successively the two-way interaction and then the main
effects of factors against the most general model (Steel
1977). A factor was considered significant when p <
0.05. All calculations were performed using S-plus soft-
ware (Venables and Ripley 1994).

We investigated the effects of population density on
survival by using deer that were marked every year with
our tags, their collar and radio-collars in the PPNR.

Bibliography

Fig. 1. Yearly variation in the Abundance Index from 1977 to
1999 for the PPNR red deer population (France). The marked
downward trend at the index observed in 1983 resulted from
an increase in hunting pressure.
population (M = 56 males and N = 109 females); for a given year, between 15 and 20% of the population was individually identified. This allowed us to estimate appre- ciation more or less from a lake-long Mark-Recapture model (CMR; see Lebreton et al. 1992). We had only access to apparent survival as the study area was not fenced, permanent immigration was possible and could not be distinguished from death. Because this method is now widely used, we will not describe it at length in the present work (Lebreton et al. 1992 for general approach and Gaillard et al. 1993, 1997, Leisler et al. 1994, Cornette et al. 1997, Jorgensen et al. 1997, Töller et al. 1997 for applications to ungulates). As physical recapture data were not available for our study, we used shooting and/or weighing of marked deer during the rutting period or during autumn counts as reca- pture data. To satisfy the underlying assumptions of the CMR model, we limited the period of recapturing to 4 months during which we assumed a mortality rate close to zero. The median date of the sex-specific observa- tions was used as the starting date in the CMR analysis. In order to get the narrowest confidence intervals of the estimates (Lebreton et al. 1992) the timing of obser- vations differed according to sex: males were mostly seen during rutting activities from July to October whereas females were better seen during winter nights- counts from January to April. Furthermore we as- sumed that the loss of marks was negligible and that there was an equal catchability for all animals within one age and sex class. We tested first the fit of the Cormack-Jolly-Seber model (CJS, the time-dependent model) to our data as a starting point in our survival analyses (see Lebreton et al. 1992). High p-value ob- tained (P = 0.01) for the Goodness-of-Fit (GOF) tests by Redhorse (Burhans et al. 1987) revealed sponso- rship problems. We therefore used the U-Care package (Choquet et al. 1997) that propose robust GOF tests accounting for sparseness, transience and trap depen- dence for each sex separately. Since the CJS model could be rejected because of the occurence of between-age differences in survival (e.g., Jorgensen et al. 1997), we used the Bootstrap GOF (that accounts for age structure) available in Mark software (White and Burnham 1999). In a second step, we applied different constraints to the survival and recapture probabilities by using Sarge (Pradel and Lebreton 1991). We successively fitted the age-dependent model, the Caughley-like model (Caughley 1966), a three age-class model (that is well-suited to ungulate survival patterns; Gaillard et al. 1993, 2000b, Leisler et al. 1995a) using 1 and 7 yr as threshold ages and a model in which survival is a linear function of age (with a linear decrease in survival beginning either from the 1st yr or from the 5th yr of life). In each case, additive and interactive effects of time were examined. Finally, we used the best age-de- pendent model to test for additive and interactive ef- fects of density on survival. In this third step model

Results

Body mass

Most body mass varied among age classes and levels of density in support to our first prediction: deer living at high density were lighter than those living at low den- sity (Fig. 2). For males, mean dressed body mass of calves was 30.6 kg at high density vs 34.8 kg at low density (standardized to 5 December, P = 0.001), 47.3 kg at high density vs 56.3 kg at low density for year- old males (P < 0.001) and 72.8 kg at high density vs 80.6 kg at low density for adults (P = 0.12). Similarly, mean dressed body mass of female calves was 29.3 kg at high density vs 31.2 kg at low density (P = 0.03), 43.0 kg at high density vs 48.4 kg at low density for yearlings (P < 0.001) and 56.0 kg at high density vs 59.7 kg at low density for adults (P < 0.001). Sexual dimorphism in body mass was more marked at low than high density for each age class (1.3 kg for calves, 4.3 kg for yearlings and 16.8 kg for adults at high density com- pared to 0.7 kg for calves, 7.8 kg for yearlings and 20.7 kg for adults at low density).

In support of our second prediction, high density at birth negatively influenced the body mass of yearling sibs (48.2 kg vs 56.6 kg, F<sub>1,11</sub> = 14.6, P = 0.001) but not adult males (78 kg vs 72 kg, F<sub>1,11</sub> = 3.3, P = 0.15) but management policies biased the sampling towards young of young animals (Fig. 3). On the other hand, both yearlings (43.2 kg vs 48.8 kg, F<sub>1,11</sub> = 14.6, P = 0.001) and adults (71.5 kg vs 59.7 kg, F<sub>1,11</sub> = 5.06, P = 0.016) females were lighter when born in years of high density (Fig. 3).

Whatever the sex and the age of the PNPN red deer, neither the NAO index nor the local weather (January–February and May–June average temperature and pre- cipitation) had a significant effect on body mass (Table 3) as expected from the mild climatic conditions of the PNPN.

Pregnancy rate

The level of density did not influence the shape of the relationship between body mass and pregnancy rate and heavier females were more likely to be pregnant in both age classes (Table 4), though body mass had a
Calves

Male
Female

Yearlings

Male
Female

Adults

Male
Female

stronger effect in the young class. On the other hand, for a given body mass, the pregnancy rate of adult bars was not significantly change in relation to density (0.79 ± 0.09 at high density vs 0.90 ± 0.06 at low density), pregnancy rate of first-breeding bars (yearlings) was significantly lower at high density compared to low density (0.06 ± 0.11 vs 0.63 ± 0.15, Fig. 4 and Table 4). These results support our fifth prediction, that primiparous females would be more sensitive to population density than prime-aged females.

Contrary to our second prediction, the pregnancy rates of adult bars was high and quite constant (χ² = 0.46, DF = 2, p = 0.79) at 0.65 (p < 0.05), irrespective of the level of density during the year of birth.

Survival
To fit the CSS model, we separated the data into two data sets. One data set contained all males of known age (53 males and 30 females) and the second data set pooled adults (>2 yr old) for which the exact age was not known. There were 33 samples and 59 males. None of the GOF tests rejected the CSS model (denoted p, following Latourette et al. 1992 notations, see Table 1 for biological significance) with all p > 0.80. We used a constant sex-age probability for modeling survival.

Fig. 2. Short-term density effects on age- and sex-specific annual body mass (after log-transformation) for the red deer population of PPNR (France). Sample sizes are Nbar vs Nbar density: male calves (29 vs 50), female calves (17 vs 50), male yearlings (73 vs 4), female yearlings (73 vs 2), male adults (42 vs 33) and female adults (105 vs 94).

Fig. 3. Long-term density effects on age- and sex-specific annual body mass (after log-transformation) for the red deer population of PPNR (France). Sample sizes are (Nbar vs Nbar density) vs Nbar density: female yearlings (64 vs 62), male adults (67 vs 150), male yearlings (64 vs 30), male adults (11 vs 42).

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because the model $\Phi$ had the lowest AICc ($p = 0.59$ [95% CI: 0.50, 0.67] for females and $p = 0.48$ [95% CI: 0.33, 0.61] for males, Table 2). Mean survival excluding hunting mortality and irrespective of age differed significantly between the sexes (0.80 [95% CI: 0.80, 0.83] for females vs 0.72 [95% CI: 0.66, 0.81] for males, Wald test [Bieden et al. 1995], $W = 3.88$, $p = 0.05$).

Female survivorship (Table 3): the Caughley-like model (model $\Phi$) was the most parsimonious descriptor of the survival pattern for females, with a minimal survival for prime-age deer (0.84 [95% CI: 0.76, 0.92] for calf, 0.92 [95% CI: 0.89, 0.94] for prime-age and 0.89 [95% CI: 0.83, 0.92] for antemortem stage). In spite of its low AICc, model $\Phi$ ($\Phi_{acc}$, i.e., a linear decrease in survival probability with age from the first year) did not fit the data as the slope did not differ from 0 ($t = -0.17$ [95% CI: $-0.62$, 0.149]).

Male survivorship (Table 3): so that the data were directly comparable, we needed a common model that could be used for all age-sex classes. Based on AICc selection procedures, the common model that provided an accurate description of survivorship for both sexes was the Caughley-like model $\Phi$. Using this latter, apparent survival estimates were $0.88$ [95% CI: 0.84, 0.92] for calf, 0.67 [95% CI: 0.54, 0.78] for prime-age and 0.82 [95% CI: 0.76, 0.91] for antemortem deer.

Contrary to our first prediction, population density did not influence significantly female survivorship of any age class: calves: $0.90$ [95% CI: 0.83, 0.99] vs $0.83$ [95% CI: 0.72, 0.92] for 0.96 [95% CI: 0.47], 0.99 [95% CI: 0.94, 0.99] for 0.93 [95% CI: 0.47] and 0.93 [95% CI: 0.48] vs 0.73 [95% CI: 0.49] for high vs low density respectively ($\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 0.389$, $DF = 1$, $p = 0.56$; $\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 0.187$, $DF = 3$, $p = 0.91$; Table 3, Fig. 5). In contrast, survival of red deer stags varied according to density ($x^2 = 3.89$, $DF = 2$, $p = 0.05$, one-side t-test, Table 3). Calf survival increased markedly from 0.54 at high density to 0.99 at low density. Likewise, the mortality of adult males increased with decreasing density (0.45 to 0.59). Prime-age stags, however, survived apparently much better at high density (0.92) than at low density (0.58, Fig. 5). These results support our fourth hypothesis of a juvenile survival more sensitive than adult survival to environmental variation. In addition, between-sex differences in response to survival to density support our last prediction that males would be more sensitive than females to density effects.

Contrary to our second prediction, when using the second data set we did not find any evidence for long-term cohort effects on survival. Hinds born at high density had similar survival rates as hinds that were born and lived at low density (respectively 0.94 [95% CI: 0.88, 0.965] vs 0.84 [95% CI: 0.75, 0.94], $\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 1.287$, $DF = 1$, $p = 0.25$; $\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 1.405$, $DF = 1$, $p = 0.23$, Table 3). Hinds > 2 yr had a constant survival over time (0.92 [95% CI: 0.88, 0.95]) $\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 15.331$, $DF = 19$, $p = 0.59$) irrespective of density. Male survival followed the same pattern as, when accounting for immediate density effects, the long-term cohort effect was not significant ($\Phi_{acc}$ vs $\Phi_{acc}$ $x^2 = 0.389$, $DF = 1$, $p = 0.56$).
Table 1. Notation and biological significance of models used to assess the pattern of variation in survival and capture probabilities of red deer in PPNR (Frankot).

<table>
<thead>
<tr>
<th>Model notation</th>
<th>Biological significance</th>
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<tbody>
<tr>
<td>$\phi_{0}$</td>
<td>Survival diminish linearly with age from 1 yr of age</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival diminish linearly with age from 1 to 10 yr old, and is age-specific over 10 yr of age</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival is constant from 1 to 7 yr and decreases linearly with age over 7 yr</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival is constant from 1 to 7 yr and age-specific over 7 yr of age</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Carle扅-like model: survival is constant among 3 age classes below 3 yr, prime age (3-7 yr) and senescence (over 8 yr)</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival diminish between the period “before 1973” and “after 1973”</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival differs between deer born at low density red deer born at high density (L and H individual classes)</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Survival is constant over time</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Age-dependent survival</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Additive effects between age (Carleolvency-like model) and time on survival</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Interactive effects between age (Carleolvency-like model) and time on survival</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Additive effects between age (Carleolvency-like model) and density on survival</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Interactive effects between age (Carleolvency-like model) and density on survival</td>
</tr>
<tr>
<td>$\phi_{0.0} \times \theta_{0.0}$</td>
<td>Additive effects of long- and short-term density effects</td>
</tr>
</tbody>
</table>

$\chi^2 = 0.12$, DF = 1, $p = 0.73$, $\phi_{0.0} \times \theta_{0.0} \times \phi = 6.66$, DF = 1, $p = 0.01$, Table 3.

Discussion

Absence of climatic effects on body mass

Climatic factors might affect individual performance through direct energy costs (thermoregulation, movement), and/or through food availability and quality (Clutton-Brock and Albon 1989). The climatic influence on snow cover and the timing of snowmelt determine plant phenology which in turn affects the length of growth season in spring when plant quality is at its highest. Summer drought can also account for mortality in ungulates (Gilford et al. 1975) by prematurely leading plants to senescent stage with very low energetic value for herbivores (high C:N ratio). The climate regimes of the PPNR through our study period did not include any high and long winter snowfalls or summer droughts. Such mild climatic conditions in northeastern France along with the low level of density maintained by hunting pressure may account for the observed pattern, i.e., no correlation between climatic variables and body mass in all classes of age and sex.

Negative effects of density on individual performance

As expected from our first null model predictions, red deer living at high density in the PPNR population were lighter than those living at low density, the between-density difference being larger in young age classes and males. Such a reduction in performance in response to increasing density is in agreement with what is usually observed for large mammals (Fowler 1987). Previous works on ungulates have reported similar consequences of density on individual growth rate (Choquenot 1991, Lelong and Smith 1993) and body condition (red deer: Clutton-Brock et al. 1982, Loxton and Langwka 1998, feral donkeys: Choquenot 1991, reindeer: Skoglund 1983) that presumably involve food limitation (Carleolvency 1970).

In large mammals, the influence of density on survival mainly concerns juveniles (Gilford et al. 2000), although density-dependence has been expected in adult female survival for island populations of red deer (Albon et al. 2000) and tory sheep (Milner et al. 1999 but see Crozes et al. 2001). In red deer on Rum, an increase in the birth population from 30 to 150 led to a decrease in survival of male calve by 0.98 to 0.63 and 0.92 to 0.84 for adult males (Clutton-Brock and Loeschke 1994). However, density did not influence breed survival at the PPNR, despite a decrease in

Table 2. Modeling outcome probability for known-age red deer marked as adult (male or female) and adult red deer (marked at 2 yr of age or more for both sexes). Values correspond in different forms (ABC) between the considered model and the best model; “N” is the sample size and “V” the number of capture occasions. See Table 3 for biological significance of models (Frankot et al. 1992).

<table>
<thead>
<tr>
<th>Model</th>
<th>Female adults</th>
<th>Male adults</th>
<th>Knarne-age females</th>
<th>Knarne-age males</th>
</tr>
</thead>
<tbody>
<tr>
<td>N = 50</td>
<td>N = 53</td>
<td>N = 20</td>
<td>N = 99</td>
<td>N = 21</td>
</tr>
<tr>
<td>$\phi_{0}$</td>
<td>40, 4</td>
<td>45, 95</td>
<td>41, 23</td>
<td>94, 4</td>
</tr>
<tr>
<td>$\phi_{0} \times \theta_{0}$</td>
<td>50, 95</td>
<td>50, 65</td>
<td>60, 29</td>
<td>109, 45</td>
</tr>
<tr>
<td>$\phi_{0} \times \theta_{0}$</td>
<td>2, 49</td>
<td>2, 83</td>
<td>2, 72</td>
<td>4, 49</td>
</tr>
<tr>
<td>$\phi_{0} \times \theta_{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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Table 3. Modeling variation in survival rates for female and male red deer from capture-marking data. Values correspond to different AIC between the best model and the considered model. "N" is the sample size and "1" the number of capture occasions. The selected model occurs in bold type.

<table>
<thead>
<tr>
<th>Model</th>
<th>Known-age males</th>
<th>Known-age females</th>
<th>Males</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N = 33</td>
<td>N = 50</td>
<td>N = 33</td>
<td>N = 50</td>
</tr>
<tr>
<td></td>
<td>t = 21</td>
<td>t = 25</td>
<td>t = 21</td>
<td>t = 20</td>
</tr>
<tr>
<td>Φ</td>
<td>36.66</td>
<td>30.61</td>
<td>43.12</td>
<td>27.16</td>
</tr>
<tr>
<td>Ψ</td>
<td>0</td>
<td>1.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ0</td>
<td>0</td>
<td>38.4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ0,θ</td>
<td>2.7</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ0,θ,ν</td>
<td>29.09</td>
<td>23.73</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ1</td>
<td>0.33</td>
<td>1.46</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ2</td>
<td>1.17</td>
<td>1.56</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ3</td>
<td>2.55</td>
<td>1.35</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ4</td>
<td>144.45</td>
<td>29.97</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ5</td>
<td>1.47</td>
<td>3.24</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ψ6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.24</td>
</tr>
<tr>
<td>Ψ7</td>
<td>-</td>
<td>-</td>
<td>1.26</td>
<td>0.82</td>
</tr>
<tr>
<td>Ψ8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.54</td>
</tr>
<tr>
<td>Ψ9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Sequential responses of life history traits to density changes

In females, change in population density mainly influenced the pregnancy rate of yearlings, supporting the hypothesis of higher sensitivity of young females to limiting conditions compared to adults. The observed sequence, however, did not fit closely Bitterlich's predictions, because female calf survival did not vary in relation to density. These hypotheses might account for such a result.

1) Gaillard et al. (2009) argued that Bitterlich's model fits the population data of small to medium-sized

Long-term effects of density on red deer

Body mass at high density but did so at same level, contradicting only partially our first prediction. Similar differences between age- and sex-classes in sensitivity of body mass and survival to density have been observed for Norwegian red deer population (Loison and Langvatn 1998). The relationship between mass and survival might not be linear over a wide range of density (Fowler 1981) and might be different according to sex and age-classes. This suggests that, in ungulates, body mass responds more quickly than survival to environmental changes or that body mass does not affect adult survival (Festa-Bianchet et al. 1997).

Table 4: Generalized linear model (using a logit link) of pregnancy rates. The analysis of deviance table gives the effects of age (low level factor: yearlings and adults), density (a two-level factor: high and low), body mass (continuous) and their interactions on pregnancy rates in the Petite Pietra National Reserve. Parameter values with their standard errors are given for the minimal model (including non-significant terms). DF, degree of freedom and SE, standard error.

<table>
<thead>
<tr>
<th>Pregnancy rate</th>
<th>Term</th>
<th>Deviance</th>
<th>DF</th>
<th>p (χ²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age,Body mass</td>
<td>2.235</td>
<td>1</td>
<td>0.136</td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>3.664</td>
<td>1</td>
<td>0.017</td>
<td></td>
</tr>
<tr>
<td>Age,Density</td>
<td>6.135</td>
<td>1</td>
<td>0.041</td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>14.512</td>
<td>1</td>
<td>0.0004</td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>17.697</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>16.952</td>
<td>1</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Minimal model

<table>
<thead>
<tr>
<th>Term</th>
<th>Average effect</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age,Body mass</td>
<td>0.180</td>
<td>0.079</td>
</tr>
<tr>
<td>Age,Density</td>
<td>14.483</td>
<td>9.512</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.205</td>
<td>0.066</td>
</tr>
<tr>
<td>Density</td>
<td>-9.809</td>
<td>1.735</td>
</tr>
<tr>
<td>Age</td>
<td>-10.161</td>
<td>4.008</td>
</tr>
</tbody>
</table>

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Table 5. Regression of mean squared body mass corrected for density of calf, yearling and adult red deer in the Putorino-Mainland Reserve (Fennoscandes) on several climatic factors (NAO, May and June temperature and January and February average precipitation and temperature). The R², the parameter estimates of the regression slope and its associated probability are given in the table for each model.

<table>
<thead>
<tr>
<th>Test variable</th>
<th>Calf</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NAO</td>
<td></td>
<td>0.319 ± 0.383</td>
<td>0.03</td>
<td>0.32</td>
<td>1.110 ± 0.819</td>
<td>0.19</td>
<td>0.20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun-Feb temp.</td>
<td></td>
<td>0.034 ± 0.213</td>
<td>0.37</td>
<td>0.45</td>
<td>0.850 ± 0.728</td>
<td>0.75</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan-Jun precip.</td>
<td></td>
<td>-0.033 ± 0.023</td>
<td>0.55</td>
<td>0.53</td>
<td>-0.006 ± 0.033</td>
<td>0.86</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May-Jun temp.</td>
<td></td>
<td>0.046 ± 0.302</td>
<td>0.46</td>
<td>0.30</td>
<td>0.006 ± 0.411</td>
<td>0.97</td>
<td>0.07</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>May-Jun precip.</td>
<td></td>
<td>-0.006 ± 0.012</td>
<td>0.97</td>
<td>0.43</td>
<td>-0.014 ± 0.007</td>
<td>0.42</td>
<td>0.12</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test variable</th>
<th>Yearling</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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<td></td>
<td></td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NAO</td>
<td></td>
<td>0.036 ± 0.277</td>
<td>0.45</td>
<td>0.43</td>
<td>1.216 ± 1.377</td>
<td>0.35</td>
<td>0.30</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Jun-Feb temp.</td>
<td></td>
<td>-0.216 ± 0.475</td>
<td>0.67</td>
<td>0.40</td>
<td>0.632 ± 0.453</td>
<td>0.51</td>
<td>0.22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan-Jun precip.</td>
<td></td>
<td>-0.033 ± 0.054</td>
<td>0.32</td>
<td>0.43</td>
<td>-0.034 ± 0.034</td>
<td>0.74</td>
<td>0.22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May-Jun temp.</td>
<td></td>
<td>0.115 ± 0.087</td>
<td>0.73</td>
<td>0.42</td>
<td>0.712 ± 0.083</td>
<td>0.34</td>
<td>0.49</td>
<td></td>
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</tr>
<tr>
<td>May-Jun precip.</td>
<td></td>
<td>-0.016 ± 0.026</td>
<td>0.19</td>
<td>0.46</td>
<td>-0.037 ± 0.026</td>
<td>0.16</td>
<td>0.35</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Test variable</th>
<th>Adult</th>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td>β estimates</td>
<td>p</td>
<td>R²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NAO</td>
<td></td>
<td>0.127 ± 0.368</td>
<td>0.59</td>
<td>0.09</td>
<td>0.125 ± 0.590</td>
<td>0.88</td>
<td>0.20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun-Feb temp.</td>
<td></td>
<td>0.069 ± 0.225</td>
<td>0.41</td>
<td>0.12</td>
<td>0.237 ± 0.290</td>
<td>0.42</td>
<td>0.21</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan-Jun precip.</td>
<td></td>
<td>0.087 ± 0.138</td>
<td>0.34</td>
<td>0.08</td>
<td>-0.077 ± 0.052</td>
<td>0.13</td>
<td>0.35</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May-Jun temp.</td>
<td></td>
<td>0.736 ± 0.796</td>
<td>0.35</td>
<td>0.13</td>
<td>0.004 ± 0.426</td>
<td>0.91</td>
<td>0.23</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May-Jun precip.</td>
<td></td>
<td>-0.087 ± 0.067</td>
<td>0.90</td>
<td>0.35</td>
<td>0.088 ± 0.017</td>
<td>0.33</td>
<td>0.22</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Up to now, models describing sequential responses of life history traits to changes in density focused mostly on the female component of the population (Galliard et al. 2000b). In dimorphic species, males show temporal variations in body mass or survival to a greater extent than females do (red deer: Firok 1970; Chotton-Brock et al. 1982; greater kudu: Owen-Smith 1993; fallow deer Dama doux Frisch: Pfieborn et al. 1995; thus: Telgri et al. 1999). Indeed, in the red deer population we studied, male calf survival reached first, then pregnancy rates of first time breeders, then adult male survival, then female calf survival, and lastly pregnancy rates and survival of adult females. By incorporating sex-specific effects of density on survival, we could improve the accuracy of population dynamic and management models for dimorphic ungulates.

Age-specific density dependence in pregnancy rates

In support to our fourth prediction, pregnancy rates of yearlings were negatively influenced by population density. Likewise, yearling females lost mass at high den-
Density dependence and sexual selection in red deer

As expected from sexual selection theory concerning polygynous species (P縺y, 1992, Clinton and Lebont 1993) and in support to our fish prediction, male survival was both lower and more sensitive to changes in density than female survival. Calf, yearling and adult male body mass of males increased by 11.9, 15.7 and 9.4% respectively when density decreased, while the changes in female body mass were only 6.2, 11.2 and 6.1% respectively. Likewise, long-term cohort effects were stronger among stags than hinds (Kraus et al. 1999): comparing deer born at high and low density, mean body mass of yearlings changed by 16.5% in males but by only 11.7% for females. Although the between-density difference in weight of adult males was the largest in absolute terms, we failed to detect significant effect of density on adult males, likely because of both a low sample size and a management rule that favored the shooting of young individuals. Lastly, we found negative effects of density on young and senescing male survival whereas female survival did not respond to changes in density.

Low survival in males compared to females has been previously reported in several studies on moose and red deer (Reek 1960, Sauve and Boyce 1983, Clinton-Bruck et al. 1958, 1998, Coughenour and Singer 1996 but see Leison and Langvatn 1998) as well as in other endomorphic ungulates (greater kudu: Owen-Smith 1993, bighorn: Jorgenson et al. 1997, reindeer: Skogland 1993, noro sheep: Clinton-Bruck et al. 1992, but not: Tolja et al. 1997; red deer: Leison and Langvatn 1998). Both intraspecific competition for mating (Clinton-Bruck et al. 1982) and high energetic requirements due to a large body size (Demment and Van Scyoc 1985) may jeopardize male survival. The absence of between-density differences in survival have been found mainly in favorable environments that allow males to cope with the additional costs of high growth and energy storage (Cran sac et al. 1997, Toljo et al. 1997, Leison and Langvatn 1998). The highly sex-skewed survival at high density in favour of female calves may also be accounted for by marked sexual selection in red deer. Indeed, male calves are a greater part of energy to growth than females to improve their fitness and, having less body reserves than females, are more likely to die from starvation (Clinton-Bruck et al. 1983). That most pim-e-age stages

![Graph](image)

Fig. 5. Short term density effects on female and male survival rate (log-log) for the red deer population of PPNR (France). N = 33 and N = 36 for males and females respectively.

( < 7 yr) did not participate in the rut (for stages in Scotland, the age at which animals experienced the rut was not mentioned. In some cases, it ranged from 7 to 12 yr old with a maximum at 9 yr. Chilton-Brack et al. 1988, Chilton-Brack and Albion 1989) and showed opposite changes in survival with density suggested the hypothesis of costs of breeding in terms of survival in red deer stages. However, an alternative hypothesis involves dispersal patterns. Because the PNNR population is not fragmented, the methodology we used to estimate survival rates cannot distinguish between survival and dispersal. Negative effects of density on body mass reported here indicate that these were on average heavier at low density. We should test the higher survival at low density (see Guillaumet et al. 2000a for a positive relationship between body mass and longevity at the individual level). On the contrary, we found a lower apparent survival of prime- age deer at low density. Such a result might be accounted for by an increase in male dispersal rate at low density as previously found in roe deer (Wahlström 1994). Thus, although repartition effects of dispersal has been rejected for roe deer for an island population (Chilton-Brack et al. 1992), dispersal of prime-age males could be involved in population regulation of red deer in PNNR, in an invariantly density dependent way. Even if we could not demonstrate that the heaviest stages effectively disperse more at low than high density, we suggested here that although most often neglected, dispersion may play a role in dynamics of sparsely open ungulate populations.

Acknowledgments — We thank the Other National de Bocage for organizing the fieldwork that allowed the collection of deer data. We are grateful to Steve Albon, Marco Ferras-Buckler, Mark Hewison and Jean-Dis- simone Labbe for helpful suggestions on earlier drafts of this paper.

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