Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest

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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.

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Regulation of mammal populations, through density dependent responses of life history traits (sensu Messier 1991) plays a central role in modern ecological theory (Caughley 1977, Fowler and Smith 1981). Recent studies have highlighted the difficulty in distinguishing clearly between density dependence and density inde-

pendence (Loison 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 (Gaillard et al. 2000b). Fowler (1987) and then Saether

(1997) reviewed empirical evidence of density dependence in several life history traits of large mammals. In ungulates, negative effects of density have been reported for body mass (feral donkeys *Equus asinus* Gray: Choquenot 1991; reindeer *Rangifer tarandus* Hamilton-Smith: Klein 1968; roe deer *Capreolus capreolus* Gray: Gaillard et al. 1996), age at first reproduction (red deer *Cervus elaphus* Linnaeus: Albon et al. 1983, 1987; roe deer: Gaillard et al. 1992; reindeer: Skogland 1985; bighorn sheep *Ovis canadensis* Linnaeus: Jorgenson et al. 1993) and adult survival (soay sheep *Ovis aries* Linnaeus: Milner et al. 1999; African buffalo *Syncerus caffer* Hodgson: Sinclair 1974). However, the effects of density can differ within a given species depending on environmental conditions (Gaillard et al. 1996, Coulson et al. 1997, Portier et al. 1998).

Actually, it is also established that large mammal populations respond to density independent factors including local climatic variations (Picton 1984, Albon and Clutton-Brock 1988, Saether and Heim 1993, Loison and Langvatn 1998, Post and Stenseth 1999, Coulson et al. 2000). More recently, several studies reported an influence of large-scale climatic trends like the North Atlantic Oscillation (Hurrell 1995) on ungulate individual life history traits (Post et al. 1997, Post and Stenseth 1998, Forchhammer et al. 1998, Loison et al. 1999c, Milner et al. 1999). However, life history traits responses induced by climate are often associated with extreme conditions like high density, particularly harsh weather or populations living 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 variation in density on sex and age-specific body mass, pregnancy rates and survival from a red deer population inhabiting a temperate forest. More particularly, we aimed to test the following six predictions.

Because of the widespread occurrence of density dependence in ungulate populations (see above), we expected 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 variation in adult life history traits (Doney and Gunn 1981, Clutton-Brock et al. 1982, Birgersson and Ekvall 1997, Festa-Bianchet et al. 2000). Therefore, environmental conditions during the early stage may have long-term effects on fitness components (Albon et al. 1987, Lindström 1999). Such cohort effects have been reported for red deer (Albon et al. 1992, Rose et al. 1998), roe deer (Gaillard et al. 1997), and ibex *Capra ibex* Linnaeus (Toïgo 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 Petite Pierre National Reserve (PPNR) population lives at low density under moderate climatic conditions. In ungulate populations snow accumulation and duration have been reported as the main proximate cause of mortality in winter (Mech et al. 1987, Albon and Clutton-Brock 1988, Goodson et al. 1991, Post and Stenseth 1998, Loison et al. 1999c) and annual variation 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 then expected that 3) body mass would not be affected either by the NAO or by the local weather.

Eberhardt (1977) suggested that density dependent effects are predictable, sequential and additive. Because small animals are less competitive than large ones during food shortage (Begon 1984), juveniles, who are also subject to growth constraints (Stearns 1992), 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, 4) juvenile survival would vary the most and adult survival the least, and 5) pregnancy rates of primiparous females would vary to a greater degree than those of adult females (Gaillard et al. 2000b).

Red deer are highly polygynous and dimorphic in size (Clutton-Brock et al. 1982). Thus, because of both allometric constraints (Peters 1983) and sexual selection (Flook 1970, Clutton-Brock et al. 1982), males are expected to have greater energy requirements than females and are therefore more sensitive to food shortage (Glucksman 1974, Clutton-Brock et al. 1985a, Leberg and Smith 1993, Loison et al. 1999b). 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. 1985b; greater kudu *Tragelaphus strepsiceros* De Blainville: Owen-Smith 1993; bighorn sheep: Jorgenson et al. 1997; reindeer: Skogland 1985). We thus expected that 6) density variation would influence male traits more than female traits.

Study area

The Petite Pierre National Reserve (PPNR) is a 2800 ha forest located in northeast France (48.5°N, 7°E) in the Vosges mountain at a mean elevation of 300 m. The climate is continental with oceanic influences (mean January and mean July temperature are 0.6°C and 18.4°C respectively) characterized by mild winters and cool 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),

suggesting relatively poor food availability, and as a consequence, the reserve cannot be considered as favourable habitat for red deer. In addition, roe deer and wild boar *Sus scrofa* Linnaeus occur within the reserve. All the three ungulates are hunted, either based on quotas (deer) or freely (wild boar). During the last 10 yr, an average of 35 red deer, 50 roe 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 managed by the Office National de la Chasse (ONC) and hunted in autumn each year by both professionals and sport hunters. Every deer shot was sexed and aged (N = 996); ONC managers recorded dressed weight and for hinds reproductive status. If the pregnancy was assessed before 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 102 hinds for which we obtained fecundity data. Only singletons were produced. 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 and > 2 yr). 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 yr 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 calf body mass for shooting date using a linear regression and standardizing values to 5 December (mean shooting 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 65 deer were shot in 1981 and 1982 vs an average of 37 deer after 1983) and caused 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 continous variable in the analyses because of its low

accuracy (CV = 29.7%) 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 ($F_{1,21} = 74.33$, 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 "cohort" (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 covariance (ANCOVA) for examining the response of red deer to weather variables, the mean dressed body mass as the dependent variable, the NAO index (available from: ⟨http://www.cdg.ucar.edu/cas/climind⟩), the mean precipitation 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 procedure. We used a logistic regression with pregnancy status as the binary dependent variable, mass as covariate 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 (Searle 1971). A factor was considered significant when p < 0.05. All calculations were performed using S-plus software (Venables and Ripley 1994).

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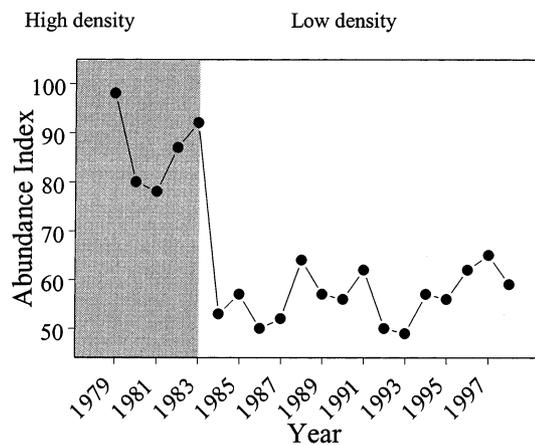

Fig. 1. Yearly variation in the Abundance Index from 1977 to 1999 for the PPNR red deer population (France). The marked change of the index observed in 1983 resulted from an increase in hunting pressure.

population (N = 86 males and N = 109 females); for a given year, between 15 and 20% of the population was individually identified. This allowed us to estimate apparent survival from Capture-Mark-Recapture models (CMR sensu Lebreton et al. 1992). We had only access to apparent survival as the study area was not fenced, permanent emigration 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 (see Lebreton et al. 1992 for general approach and Gaillard et al. 1993, 1997, Loison et al. 1994, Cransac et al. 1997, Jorgenson et al. 1997, Toïgo et al. 1997 for applications to ungulates). As physical recapture data were not available for our study, we used shooting and/or resighting of marked deer during the rutting period or during autumn counts as recapture data. To satisfy the underlying assumptions of the CMR model, we limited the period of resighting to 4 months during which we assumed a mortality rate close to zero. The median date of the sex-specific observations was used as the starting date in the CMR analysis in order to get the narrower confidence interval of the estimates (Lebreton et al. 1992) so the timing of observations differed according to sex: males were mostly seen during rutting activities from July to October whereas females were better seen during winter night-counts from January to April. Furthermore we assumed 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 obtained when using standard Goodness-Of-Fit (GOF) tests by Release (Burnham et al. 1987) revealed sparseness problems. We therefore used the U-Care package (Choquet et al. 2001) that propose robust GOF tests accounting for sparseness, transience and trap dependence for each sex separately. Since the CJS model can be rejected because of the occurrence of between-age differences in survival (e.g., Jorgenson 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 Surge (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 pattern, Gaillard et al. 1993, 2000b, Loison et al. 1999a) 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 8th yr of life). In each case, additive and interactive effects of time were examined. Finally, we used the best age-dependent model to test for additive and interactive effects of density on survival. In this third step model

selection was based on Akaïke Information Criterion (AIC). In addition, we used the Likelihood Ratio Test (LRT) among nested models (Lebreton et al. 1992) to test our predictions. Following Anderson et al. (1994), and Burnham et al. (1995), we applied a correction to the AIC, here denoted AICc, based on the size of the data set. The most parsimonious (i.e. lowest AICc) model was selected as the best model.

Results

Body mass

Mean 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 density (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 56.1 kg at low density for yearlings ($p < 0.0001$) and 72.8 kg at high density vs 80.4 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 ($p = 0.01$), 43.0 kg at high density vs 48.4 kg at low density for yearlings ($p < 0.0001$) and 56.0 kg at high density vs 59.7 kg at low density for adults ($p < 0.0001$). 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 compared to 3.7 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 stags (48.2 kg vs 56.6 kg, $F_{2,111} = 14.6$, $p < 0.0001$) but not adult males (78.8 kg vs 72 kg, $F_{2,72} = 2.83$, $p = 0.15$) but management policies biased the sampling towards young of these latters (Fig. 3b). On the other hand, both yearling (43.2 kg vs 48.8 kg, $F_{2,109} = 14.6$, $p = 0.0001$) and adult (57.1 kg vs 59.7 kg, $F_{2,200} = 5.68$, $p = 0.016$) females were lighter when born in years of high density (Fig. 3).

Whatever the sex and the age of PPNR red deer, neither the NAO index nor the local weather (January–February and May–June average temperature and precipitation) had a significant effect on body mass (Table 5) as expected from the mild climatic conditions of the PPNR.

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
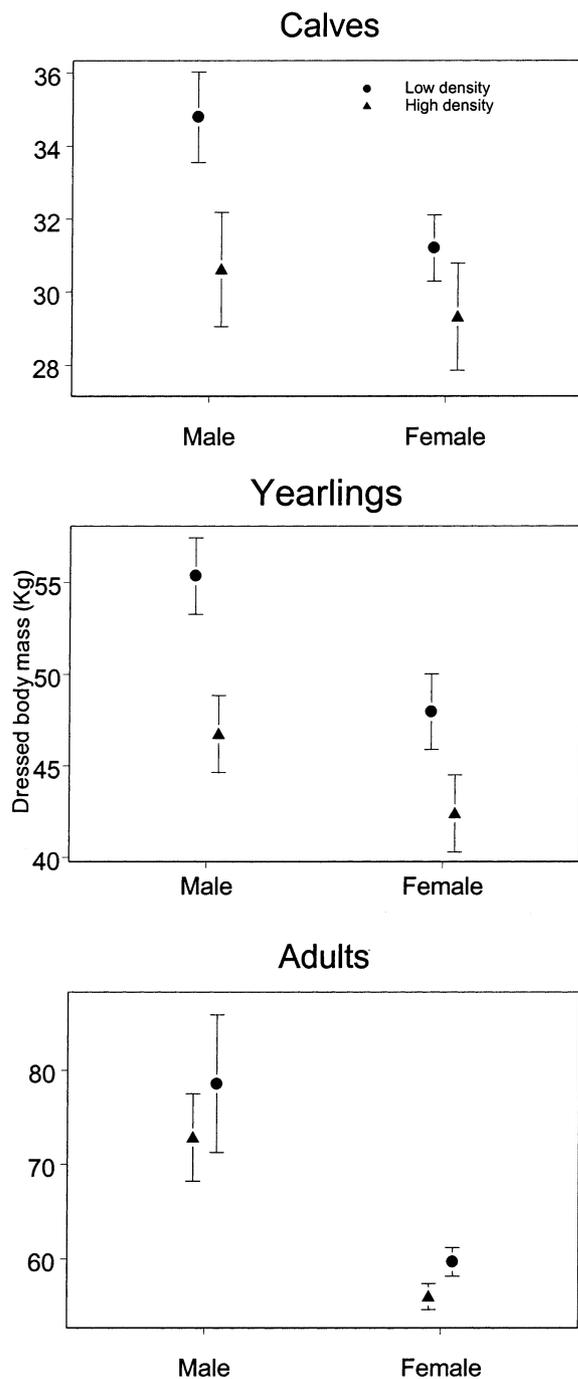
Fig. 2. Short-term density effects on age- and sex-specific dressed body mass (after log-transformation) for the red deer population of PPNR (France). Sample sizes are (N_{low} vs N_{high} density): male calves (120 vs 58), female calves (137 vs 74), male yearlings (73 vs 41), female yearlings (75 vs 37), male adults (42 vs 33) and female adults (109 vs 94).

low density), pregnancy rate of first-breeding hinds (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 hinds was high and quite constant ($\chi^2 = 0.46$, DF = 2, p = 0.79) at 0.85 (± 0.05), irrespective of the level of density during the year of birth.

Survival

To fit the CJS model, we separated the data into two data sets. One data set contained individuals of known age (53 males and 50 females) and the second data set pooled adults (> 2 yr old for which the exact age was not known: 33 males and 59 females). None of the GOF tests rejected the CJS model (denoted $\phi_t p_t$ following Lebreton et al. 1992 notations, see Table 1 for biological significance) with all $p > 0.80$. We used a constant recapture probability for modeling survival
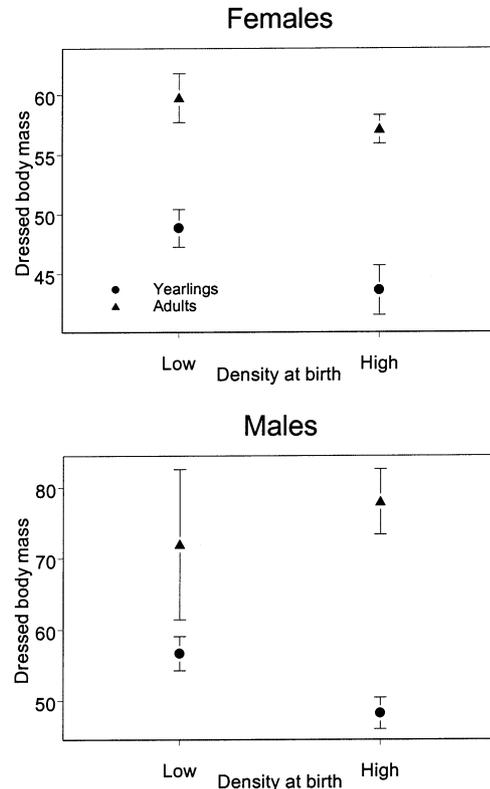
Fig. 3. Long-term density effects on age- and sex-specific dressed body mass (after log-transformation) for the red deer population of PPNR (France). Sample sizes are ($N_{born\ at\ low\ density}$ vs $N_{born\ at\ high\ density}$): female yearlings (64 vs 48), female adults (67 vs 136), male yearlings (64 vs 50), male adults (11 vs 42).

stronger effect in the young class. On the other hand, for a given body mass, while the pregnancy rate of adult hinds did not significantly change in relation to density (0.79 ± 0.09 at high density vs 0.90 ± 0.06 at

Fig. 4. Short-term density effects on pregnancy rates of yearling and adults hinds for the red deer population of PPNR (France). The fitted logistic model (black line) as well as its standard deviation (dashed line) are shown. Circles are proportional to the sample size available for each of the body mass classes indicated by the triangles (respectively for high and low density N = 69 and N = 103 for adults, N = 17 and N = 54 for yearlings).
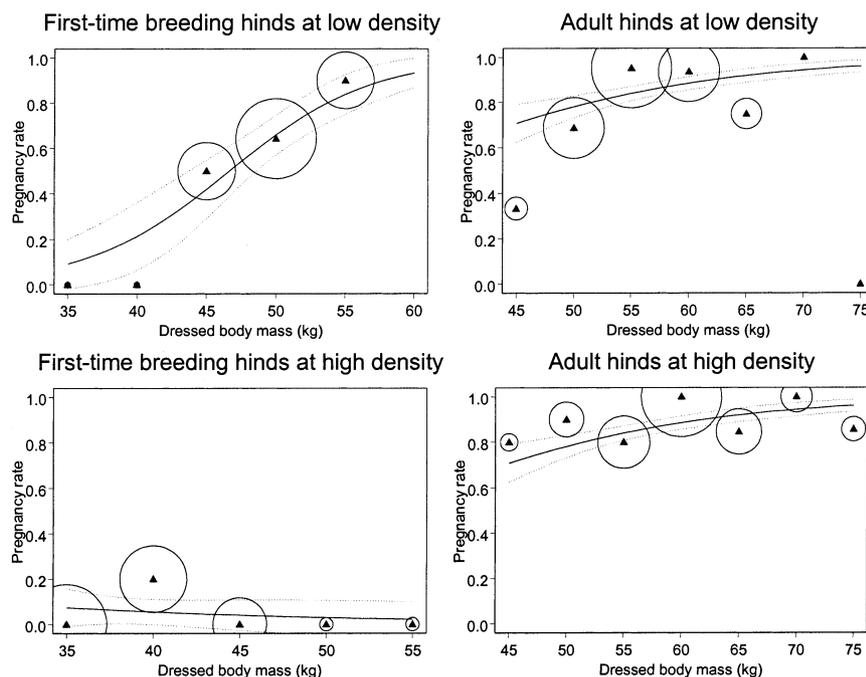
because the model ϕ_t, p had the lowest AICc (p = 0.59 [95% CI: 0.50; 0.67] for females and p = 0.48 [95% CI: 0.35; 0.61] for males, Table 2). Mean survival excluding hunting mortality and irrespective of age differed significantly between the sexes (0.90 [95% CI: 0.84; 0.93] for females vs 0.73 [95% CI: 0.64; 0.81] for males, Wald test [Blondel et al. 1992], W = 3.389, p = 0.026).

Female survivorship (Table 3): the Caughley-like model [model ϕ_c] was the most parsimonious descriptor of the survival pattern for females, with a maximal survival for prime-age deer (0.84 [95% CI: 0.68; 0.95] for calf, 0.92 [95% CI: 0.89; 0.94] for prime-age and 0.80 [95% CI: 0.58; 0.92] for senescent stage). In spite of its low AICc, model $\phi_1\phi_{al}$ (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 (-0.17 [95% CI: -0.62; 0.14]).

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 procedure, the common model that provided an accurate description of survivorship for both sexes was the Caughley-like model. Using this latter, apparent survival estimates were 0.88 [95% CI: 0.41; 0.98] for calf, 0.67 [95% CI: 0.54; 0.78] for prime-age and 0.82 [95% CI: 0.36; 0.97] for senescent deer.

Contrary to our first prediction, population density did not influence significantly female survival of any age class: calves: 0.90 [95% CI: 0.23; 0.99] vs 0.83 [95% CI: 0.22; 0.98]; prime-age adults: 0.96 [95% CI: 0.47; 0.99] vs 0.93 [95% CI: 0.47; 0.99]; old adults: 0.85 [95% CI: 0.36; 0.98] vs 0.75 [95% CI: 0.49; 0.9] for high vs

low density respectively (ϕ_c vs ϕ_{c+d}: $\chi^2 = 0.306$, DF = 1, p = 0.58; $\phi_{c \times d}$ vs ϕ_{c+d}: $\chi^2 = 0.187$, DF = 2, p = 0.91; Table 3, Fig. 5). In contrast, survival of red deer stags varied according to density (Fig. 5) in support to our first prediction. The model including an interaction between density and age effects fitted the data better than any other model ($\phi_{c \times d}$ vs ϕ_{c+d}: $\chi^2 = 5.488$, DF = 2, p = 0.032, one-side test, Table 3). Calf survival increased markedly from 0.54 at high density to 0.99 at low density. Likewise, the survival of old adults increased with decreasing density (from 0.45 to 0.58). 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 of 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 [CI 95%: 0.88; 0.96] vs 0.89 [CI 95%: 0.79; 0.94], ϕ_{co+d} vs ϕ_d: $\chi^2 = 1.283$, DF = 1, p = 0.25; ϕ_{co} vs ϕ: $\chi^2 = 1.435$, DF = 1, p = 0.23, Table 3). Hinds > 2 yr had a constant survival over time (0.92 [95% CI: 0.88; 0.95], ϕ_t vs ϕ: $\chi^2 = 15.331$, DF = 19, p = 0.7) irrespective of density. Male survival followed the same patterns as, when accounting for immediate density effects, the long-term cohort effect was not significant (ϕ_{co+d} vs

Table 1. Notation and biological significance of models fitted to assess the sources of variation in survival and capture probabilities of red deer in PPNR (France).

Model notation	Biological significance
$\phi_1\phi_{al}$	Survival decreases linearly with age from 1 yr of age.
$\phi_{al1-10}\phi_{a>10}$	Survival decreases linearly with age from 1 to 10 yr old, and is age-dependent over 10 yr of age.
$\phi_{1-7}\phi_{al>7}$	Survival is constant from 1 to 7 yr and decreases linearly with age over 7 yr.
$\phi_{1-7}\phi_{>7}$	Survival is constant from 1 to 7 yr and age-specific over 7 yr of age.
ϕ_c	Caughley-like model: survival is constant among 3 age classes [calves (0–1 yr), prime age (2–7 yr) and senescent (over 8 yr)].
ϕ_d	Survival differs between the period "before 1983" and "after 1983".
ϕ_{co}	Survival differs between deer born at low density and deer born at high density (L and H individual classes).
$\phi.$	Survival is constant over time.
ϕ_t	Time-dependent survival.
ϕ_{ag}	Age-dependent survival.
ϕ_{c+t}	Additive effects between age (Caughley-like model) and time on survival.
$\phi_{c\times t}$	Interactive effects between age (Caughley-like model) and time on survival.
ϕ_{c+d}	Additive effects between age (Caughley-like model) and density on survival.
$\phi_{c\times d}$	Interactive effects between age (Caughley-like model) and density on survival.
ϕ_{co+d}	Additive effects of long- and short-term density effects.

ϕ_d: $\chi^2 = 0.112$, DF $= 1$, p $= 0.73$; ϕ_{co+d} vs ϕ_{co}: $\chi^2 = 6.66$, 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, movements), and/or through food availability and quality (Clutton-Brock and Albon 1989). The duration of the 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 (Langvatn et al. 1996, Post and Stenseth 1999). Summer drought can also account for mortality in ungulates (Gaillard et al. 1997) by prematurely leading plants to senescent stage with very low energetic value for herbivores (high C/N ratio). The climate regimes of the PPRN through our study period did not include any high and long winter snowfalls nor summer droughts. Such mild climatic conditions in northeast 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 and third predictions, red deer living at high density in the PPNR population were lighter than those living at low density, the between-density differences 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, Leberg and Smith 1993) and body condition (red deer: Clutton-Brock et al. 1982, Loison and Langvatn 1998; feral donkeys: Choquenot 1991; reindeer: Skogland 1983) that presumably involve food limitation (Caughley 1970).

In large mammals, the influence of density on survival mainly concerns juveniles (Gaillard et al. 2000b), although density-dependence has been reported in adult female survival for island populations of red deer (Albon et al. 2000) and soay sheep (Milner et al. 1999 but see Coulson et al. 2001). In red deer on Rum, an increase in the hind population from 50 to 150 led to a decrease in survival of male calves from 0.98 to 0.63 and from 0.92 to 0.84 for adult males (Clutton-Brock and Lonergan 1994). However, density did not influence hind survival at the PPNR, despite a decrease in

Table 2. Modeling recapture probability for known-aged red deer (marked as calves or yearlings) and adult red deer (marked at 2 yr of age or more for both sexes). Values correspond to differences in AICc between the considered model and the best model, "N" is the sample size and "t" the number of capture occasions. See Table 1 for biological significance of models (Lebreton et al. 1992).

Model	Female adults N = 50 t = 20	Male adults N = 53 t = 21	Known-age females N = 59 t = 20	Known-age males N = 33 t = 21
$\phi_t p_t$	40, 4	45, 95	41, 23	94, 42
$\phi_t p_a$	55, 95	55, 61	61, 39	109, 43
$\phi_t p_{ca}$	2, 49	2, 83	2, 72	4, 49
$\phi_t p$	0	0	0	0

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

Model	Known-age males N = 33 t = 21	Known-age females N = 59 t = 20	Males N = 53 t = 21	Females N = 50 t = 20
ϕ_t	36, 66	30, 61	43, 12	27, 16
$\phi_.$	0	1, 43	–	–
ϕ_a	55, 74	38, 6	–	–
$\phi_1\phi_{al}$	2, 1	0	–	–
$\phi_{al1-10}, \phi_{a>10}$	29, 09	21, 73	–	–
$\phi_{1-7}\phi_{al>7}$	0, 33	1, 08	–	–
$\phi_{1-7}\phi_{>7}$	1, 97	1, 56	–	–
ϕ_c	**2, 02**	**1, 25**	–	–
$\phi_{c \times t}$	367, 25	144, 85	–	–
ϕ_{c+t}	43, 65	29, 67	–	–
ϕ_{c+d}	1, 87	3, 24	–	–
$\phi_{c \times d}$	1, 01	7, 48	–	–
$\phi_.$	–	–	7, 2	0
ϕ_{co}	–	–	6, 55	0, 12
ϕ_d	–	–	0	0, 62
ϕ_{co+d}	–	–	2, 14	1, 43

body mass at high density but did so for males, 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).

Long-term effects of density on red deer

Being born at high density had negative effects on body mass for both sexes but did not influence survival or pregnancy rates. Thus our second prediction was only partially supported. Such cohort effects on survival (Albon et al. 1987, 1992, Rose et al. 1998) and fecundity (Albon et al. 1992) have been reported for red deer on Rum, which experienced worse environmental conditions than those of our study population. Cohort effects might be generated by adverse environmental conditions and/or by lower maternal care during unfavorable conditions. Here we detected effects of density on mass but not on fitness components that both depend on mass. This may be due to differential sensitivity of traits to changes in density and may indicate threshold relationships between body mass and fitness components. Accordingly above a certain mass threshold, density may not have any negative effect on fitness. As body mass is density dependent, the level of density encountered by PPNR deer could be too low to generate such long-term effects.

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 Eberhardt's predictions, because female calf survival did not vary in relation to density. Three hypotheses might account for such a result.

1) Gaillard et al. (2000b) argued that Eberhardt's model fits the population data of small to medium-sized

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

Pregnancy rate Term	Deviance	DF	p (χ^2)
Age.Density.Body mass	2.235	1	0.126
Age.Body mass	3.664	1	0.055
Age.Density	4.155	1	0.041
Body mass	14.636	1	0.0001
Density	17.672	1	<0.0001
Age	31.952	1	<0.00001

Minimal model	Average effect	SE
Age.Body mass	0.183	0.079
Age.Density	14.483	9.512
Body mass	0.205	0.068
Density	−9.080	8.775
Age	−10.261	4.088

Table 5. Regression of mean dressed body mass corrected for density of calf, yearling and adult red deer in the Petite Pierre National Reserve (France) on several climatic factors (NAO, May and June temperature and January and February average precipitation and temperature). The R^2, the parameter estimates of the regression slope and its associated probability are given in the table for each model.

| Tested variable | Calves | | | | | |
| | Males | | | Females | | |
	β estimates	p	R^2	β estimates	p	R^2
NAO	0.279 ± 0.583	0.63	0.52	1.110 ± 0.819	0.19	0.20
Jan–Feb temperature	0.034 ± 0.215	0.87	0.45	0.297 ± 0.298	0.33	0.11
Jan–Feb precipitation	-0.023 ± 0.023	0.33	0.53	-0.006 ± 0.035	0.86	0.08
May–Jun temperature	0.456 ± 0.302	0.14	0.50	0.806 ± 0.411	0.07	0.22
May–Jun precipitation	-0.0004 ± 0.012	0.97	0.45	-0.014 ± 0.017	0.42	0.12

| Tested variable | Yearlings | | | | | |
| | Males | | | Females | | |
	β estimates	p	R^2	β estimates	p	R^2
NAO	1.036 ± 1.337	0.45	0.43	1.275 ± 1.377	0.35	0.30
Jan–Feb temperature	-0.216 ± 0.474	0.65	0.40	0.671 ± 0.453	0.15	0.32
Jan–Feb precipitation	-0.055 ± 0.054	0.31	0.43	-0.007 ± 0.034	0.84	0.19
May–Jun temperature	0.113 ± 0.687	0.87	0.42	0.713 ± 0.683	0.31	0.29
May–Jun precipitation	-0.036 ± 0.026	0.19	0.46	0.037 ± 0.026	0.16	0.35

| Tested variable | Adults | | | | | |
| | Males | | | Females | | |
	β estimates	p	R^2	β estimates	p	R^2
NAO	2.527 ± 3.668	0.50	0.09	0.125 ± 0.850	0.88	0.20
Jan–Feb temperature	0.969 ± 1.125	0.41	0.12	0.237 ± 0.290	0.42	0.21
Jan–Feb precipitation	0.087 ± 0.138	0.54	0.08	-0.077 ± 0.052	0.15	0.35
May–Jun temperature	1.736 ± 1.769	0.35	0.13	0.044 ± 0.426	0.91	0.23
May–Jun precipitation	-0.007 ± 0.060	0.90	0.35	0.016 ± 0.017	0.33	0.22

ungulates more closely than those of herbivores > 50 kg such as red deer. For these large species, fecundity of first time breeders may be affected by population density prior to any change in juvenile survival because of allometric constraints. Our observations support this scenario. Hence because large animals spend more time growing than small ones, they may be more sensitive to environmental constraints (Gaillard et al. 2000b).

2) In the PPRN population first breeding hinds were almost all yearlings (1.5 yr of age) for which the growth period is not completed (Clutton-Brock et al. 1982). We supposed that this could affect the usual growth vs reproduction trade-off observed by amplifying the importance of growth over reproduction to the point that the age at first reproduction becomes the most sensitive life history trait to environmental factors. At the other end, primiparous hinds at 3 or 4 yr of age should not have any density dependent pregnancy rates or at least should react at a lesser extent than juveniles in accordance with Eberhardt's predictions.

3) Lastly, a lack of power of our analysis cannot be excluded. Then, the absence of density dependent response of juvenile female survival could have remained undetected.

Up to now, models describing sequential responses of life history traits to changes in density focused mostly on the female component of the population (Gaillard et al. 2000b). In dimorphic species, males show temporal variations in body mass or survival to a greater extent than females do (red deer: Flook 1970, Clutton-Brock et al. 1982; greater kudu: Owen-Smith 1993; fallow deer Dama dama Frisch: Pélabon et al. 1995; ibex: Toïgo et al. 1999). Indeed, in the red deer population we studied, male calf survival reacted 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-

sity. Both density dependent responses were likely related because of the close link between fertility and body mass in red deer (Clutton-Brock et al. 1983, Albon et al. 1986). For a given dressed body mass (45 kg) we found a similar pregnancy rate as Albon et al. (1986) at Glen Feshie for yearlings (0.46 at PPNR vs 0.5 at Glen Feshie). Reproduction, especially lactation (Sadleir 1984) is energetically costly, so that a female should invest in reproduction only if her physical condition allows her to minimize the risk of mortality during harsh conditions (Stearns 1992). An additional constraint occurs for first-time breeding hinds: they have to grow beyond a threshold mass to reproduce (Sadleir 1969). In PPNR, the effect of density on age at first reproduction was additive to that of body mass, indicating that density influenced first-breeding independently of body mass. It seems therefore that low pregnancy rates observed at high density can be viewed as a way to reduce the risk of mortality engendered by reproduction before growth is completed (Albon et al. 1983, Gaillard et al. 2000b). The absence of negative effects of density on yearling survival supports such an adaptive hypothesis. However, pregnancy rates of adult hind did not change markedly with density whereas hind mass did, illustrating again the existence of a threshold body mass (here 56 kg dressed) above which pregnancy rates does not vary further according to body mass.

Density dependence and sexual selection in red deer

As expected from sexual selection theory concerning polygynous species (Promislow 1992, Clinton and Leboeuf 1993) and in support to our fifth prediction, male survival was both lower and more sensitive to changes in density than female survival. Calf, yearling and adult body mass of males increased by 11.9, 15.7 and 9.4% respectively when density decreased, while the changes in female mass were only 6.2, 11.2 and 6.1% respectively. Likewise, long-term cohort effects were stronger among stags than hinds (Kruuk 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 11.9% 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 senescent male survival whereas hind survival did not respond to changes in density.

Low survival in males compared to females has been previously reported in several studies on wapiti and red deer (Flook 1970, Sauer and Boyce 1983, Clutton-Brock et al. 1985b, 1988, Coughenour and Singer 1996 but see Loison and Langvatn 1998) as well as in other dimorphic ungulates (greater kudu: Owen-Smith 1993; bighorn: Jorgenson et al. 1997; reindeer: Skogland 1985; soay sheep: Clutton-Brock et al. 1992, but see ibex: Toïgo et al. 1997; red deer: Loison and Langvatn 1998). Both intrasexual competition for mating (Clutton-Brock et al. 1982) and high energetic requirements due to large body size (Demment and Van Soest 1985) may jeopardize male survival. The absence of between-sex 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 (Cransac et al. 1997, Toïgo et al. 1997, Loison 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 allocate 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 (Clutton-Brock et al. 1982). That most prime-age stags
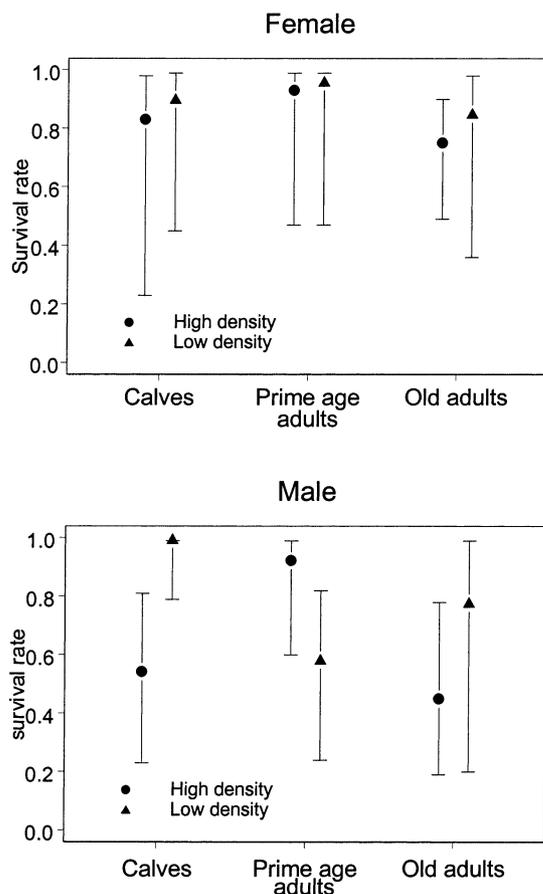

Fig. 5. Short-term density effects on female and male survival rate (± 1 SE) for the red deer population of PPNR (France). $N = 53$ and $N = 50$ for males and females respectively.

(< 7 yr) did not participate to the rut (for stags in Scotland, the age at which annual reproductive success is > 1 ranged from 7 to 12 yr old with a maximum at 9 yr, Clutton-Brock et al. 1988, Clutton-Brock and Albon 1989) and showed opposite change in survival with density supports the hypothesis of costs of breeding in terms of survival in red deer stags. However, an alternative hypothesis involves dispersal patterns.

Because the PPNR population is not fenced, 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 males were on average heavier at low density. We should thus expect higher survival at low density (see Gaillard 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 regulating effects of dispersal has been rejected for red deer for an island population (Clutton-Brock et al. 1982), dispersal of prime-age males could be involved in population regulation of red deer in PPNR, in an inversely density dependent way. Even if we could not demonstrate that the heaviest stags effectively disperse more at low than high density, we suggest here that although most often neglected, dispersal may play a role in dynamics of spatially open ungulate populations.

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