Empirical Evidence of Density-Dependence in Populations of Large Herbivores

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Density-dependence is a key concept in population dynamics. Here, we review how body mass and demographic parameters vary with population density in large herbivores. The demographic parameters we consider are age- and sex-specific reproduction, survival and dispersal. As population density increases, the body mass of large herbivores typically declines, affecting individual performance traits such as age of first reproduction and juvenile survival. We documented density-dependent variations in reproductive rates for many species from the Arctic to subtropical zones, both with and without predation. At high density, a trade-off between growth and reproduction delays the age of primiparity and often increases the costs of reproduction, decreasing both survival and future reproductive success of adult females. Density-dependent preweaning juvenile survival occurs more often in polytocous than monotocous species, while the effects of density on post-weaning juvenile survival are independent of litter size. Responses of adult survival to density are much less marked than for juvenile survival, and may be exaggerated by density-dependent changes in age structure. The role of density-dependent dispersal in population dynamics remains uncertain, because very few studies have examined it. For sexually dimorphic species, we found little support for higher sensitivity to increasing density in the life history traits of males compared to females, except for young age classes. It remains unclear whether males of dimorphic species are sensitive to male density, female density or a combination of both. Eberhardt’s model predicting a sequential effect of density on demographic parameters (from juvenile survival to adult survival) was supported by 9 of 10 case studies. In addition, population density at birth can also lead to cohort effects, including a direct effect on juvenile survival and long-term effects on average cohort performance as adults. Density effects typically interact with weather, increasing in strength in years of harsh weather. For some species, the synchronization between plant phenology and reproductive cycle is a key process in population dynamics. The timing of late gestation as a function of plant phenology determines whether density-dependence influences juvenile survival or adult female reproduction. The detection of density-dependence can be made difficult by non-linear relationships with density, high sampling variability, lagged responses to density changes, changes in population age structure, and temporal variation in the main factors limiting population growth. The negative feedbacks of population size on individual performance, and hence on life history traits, are thus only expected in particular ecological contexts and are most often restricted to certain age-specific demographic traits.
I. INTRODUCTION

Density-dependence is one of the most hotly debated concepts in population biology (den Boer and Reddingius, 1996; Sinclair, 1989). A debate about the contribution of density-dependence to population dynamics started in the 1950s following papers by Nicholson (1933) arguing that population fluctuations were almost entirely due to density-dependent processes. Andrewartha and Birch (1954) championed the contrary view that density-independent processes were dominant. Empirical support from laboratory populations of blowflies led the majority of ecologists to accept Nicholson (1933) density-dependent arguments. The discovery by May (1974, 1976) that simple models could generate dynamics that qualitatively resembled fluctuations in wild populations lent further support to the density-dependent school. However, a general failure is to parameterize existing models in order to capture quantitatively observed dynamics. This led many researchers to reevaluate the simple density-dependent/density-independent dichotomy. During the 1990s, mounting evidence suggested that the dynamics of populations were the result of both density-dependent and density-independent processes which could interact (Coulson et al., 2004b; Fowler, 1987; Messier, 1991; Sinclair, 1989; Turchin, 1995, 1999).

Most ecologists now agree that both density-dependent and density-independent processes are important, and the primary research objective has shifted towards the identification of the pathways via which density-dependence affects population dynamics rather than simply describing its existence. Two approaches have traditionally been used to detect density-dependent responses (Krebs, 1995, 2002; White, 2004): the density paradigm or pattern-oriented approach and the mechanistic paradigm or process-oriented approach (Coulson et al., 2000; Stenseth et al., 1996). Two reviews based on more than 1000 species (Brook and Bradshaw, 2006; Sibly et al., 2005) have shown the near ubiquity of density-dependence assessed from time series (pattern oriented approach). However, analyses of univariate time series of population counts provide only limited insight on the modus operandi of density-dependence on the demographic rates it affects, especially in age-structured populations (Coulson et al., 2001).

Lack (1966) was among the first to suggest different responses of demographic rates to density-dependent and stochastic factors. Relying on bird studies, he proposed that in sufficiently variable environments, populations would be limited by density-independent fecundity and regulated via density-dependent mortality. Fowler (1981, 1987) reviewed the responses of demographic rates (including juvenile and adult survivals, reproductive rate, age at first reproduction and dispersal) and phenotypic traits (body growth and body mass) to variation in density in large mammals (mainly ungulates, pinnipeds, and large carnivores). Fowler (1987) concluded that (1) food shortage is the main factor generating density-dependent responses of

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demographic rates in large mammals, even though predation or parasitism could also be density-dependent, (2) reproductive rates and juvenile survival exhibit the strongest density-dependent responses, and (3) density-dependent responses of demographic rates are most often nonlinear, being stronger at high density than at low density. It is only recently that such propositions can be adequately tested with data (Coulson et al., 2000, 2001).

Taking advantage of the recent accumulation of long-term data on age- and sex-specific demographic parameters of large herbivores, here we assess the relative strength and prevalence of density-dependence on birth, death, and dispersal. We test Lack’s hypothesis in addition to quantifying for the first time the patterns reported by Fowler (1987). We then test whether large herbivores fit the general model of Eberhardt (1977, 2002) which predicts a sequential response of demographic rates to rising density (Box 1, p. 327). According to this model based on female traits only, the first parameter expected to be affected by an increase in density is recruitment through a decrease in juvenile survival, followed by an increase in age at first reproduction, a decline in reproductive rates, and finally a decrease in the survival of prime-aged adults (Figure 1).

![Figure 1](image_url)

**Figure 1** A theoretically increasing population of ungulates that reaches $K$, the carrying capacity (dashed line), assuming a generalised logistic function ($r_o = 0.25$, $K = 1$, and $\theta = 3.55$). Points on the line illustrate the sequence of density-dependent responses for an age-structured population of large mammals expected from Eberhardt’s (1977, 2002) model. Locations of points are arbitrarily and should be interpreted as such.
II. METHODS AND PROBLEMS

A. Assessing Density-Dependence

The most common method to assess density-dependence is to regress a demographic rate against a measure of density or population size (e.g., Fowler, 1987). Measuring the strength of density dependence requires determining the appropriate density-dependent model (see May and Oster, 1976, for the different existing models). Up to now, most studies focusing on the shape of density-dependence have been performed on either population size or growth rate (e.g., Owen-Smith, 2006). When testing for evidence of density dependence on demographic rates only a few models are commonly used (linear: Albon et al., 2000; logistic: Festa-Bianchet et al., 2003; Maynard Smith/Slatkin: Nilsen et al., 2005; Getz: Wilmers et al., 2007). Moreover, a lack of statistical correlation between demographic rates and population size does not necessarily imply density-independent dynamics as small changes in population size are likely to prevent statistical detection of density-dependence. We define a density-dependent process as any response (linear or not), in whole or in part, between population density and a demographic rate, as long as it generates a decrease in mean population growth rate. We, therefore, excluded studies of Allee effects (e.g., Courchamp et al., 1999) from our review. We see density-dependent factors as a particular case of limiting factors that are linked with population density (Sinclair, 1989).

B. Measuring Population Density and Demographic Parameters

A plethora of methods are designed to estimate population size (see Buckland et al., 2000; Seber, 1986; Schwarz and Seber, 1999, for reviews), but accurate estimation of the number of individuals in a population is remarkably difficult. Raw counts of unmarked populations of large herbivores have a very low precision and accuracy. Low precision is reflected by counts that typically have coefficients of variation greater than 20% in mammalian populations (Caughley, 1977), and low accuracy by underestimates of population size by 50% or more (Gaillard et al., 2003a; Strandgaard, 1972). Given that natural variation of populations of large mammals from 1 year to another seldom exceed 25% ($\lambda < 1.35$, Gaillard et al., 2000a), such high sampling variation means that the detection of density-dependence will require either substantial variation in population size during the course of a study (Lambin et al., 1999) or study of a population close to ecological carrying capacity, where density-dependence is likely to be strongest.
Likewise, high sampling variance in demographic parameters can prevent the detection of density-dependence (Bulmer, 1975; Freckelton et al., 2006). The results presented here are thus likely to be conservative with regards to the prevalence of density-dependence.

C. Literature Survey of Case Studies

We reviewed empirical evidence for density-dependence in different demographic parameters in studies where large herbivore density was measured with estimates of population size per se or some proxy of population size such as aerial or terrestrial counts (Lancia et al., 1996; Williams et al., 2002). We focused on literature since 1986 because there were few reliable individual-based studies before then. Studies in our database lasted in average 15 ± 8 years. We reviewed studies on 27 species of large herbivores belonging to the Cervidae, Bovidae, Camelidae, Rhinocerotidae, and Equidae families. We considered any study reporting variation in density caused by natural processes, experimental manipulations or hunting (sensu Sinclair, 1989, 1997).

III. STRENGTH AND PREVALENCE OF DENSITY-DEPENDENCE IN DEMOGRAPHIC PARAMETERS

A. Reproductive Parameters

Density-dependent variation in reproductive rates has been recorded from multiple species from the high Arctic to the tropics (Table 1). North American and European conspecifics such as reindeer (Rangifer tarandus), moose (Alces alces), and red deer (Cervus elaphus) exhibit very similar patterns of density-dependence even though predation risk is generally higher in North America than in Europe. Density-dependence has been reported in components of reproduction from ovule production to weaning success. Overall, increases in density lead to a reduction in components of reproduction which can be reflected in a decrease in population growth. The general pattern of density-dependent effects on reproduction varies markedly with maternal age, with young females reacting at a lower density and to a greater extent than females in their prime (Figure 2A).

Ovule production, usually estimated from examination of the corpora lutea or corpora rubra (Langvatn, 1992), is lower at high density in many cervids with similar results found for pregnancy rates (Table 1). In polytocous species that typically weigh less than 100 kg as adults—the notable exception being moose (≥300 kg)—litter size decreases with increasing density (e.g., roe
<table>
<thead>
<tr>
<th>Species</th>
<th>Reproduction component</th>
<th>Location</th>
<th>Predator?</th>
<th>References</th>
</tr>
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<tbody>
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<td></td>
<td>Fecundity</td>
<td>Sweden</td>
<td>Yes</td>
<td>Sand (1996)</td>
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<tr>
<td></td>
<td>Age of primiparity</td>
<td>Newfoundland (Canada)</td>
<td>?</td>
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<td></td>
<td>Fecundity</td>
<td>Alaska (USA)</td>
<td>Yes</td>
<td>Gasaway <em>et al.</em> (1992)</td>
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<td></td>
<td>Age of primiparity</td>
<td>Ontario (Canada)</td>
<td>Yes</td>
<td>Ferguson (2002)</td>
</tr>
<tr>
<td></td>
<td>Twinning rate</td>
<td>Storfosna (Norway)</td>
<td>No</td>
<td>Andersen and Linnell (2000)</td>
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<td><em>Capreolus</em></td>
<td>Number of offspring/females</td>
<td>Dourdan (France)</td>
<td>No</td>
<td>Vincent <em>et al.</em> (1995)</td>
</tr>
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<td>capreolus</td>
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<td>Tredozio (Italy)</td>
<td>Yes</td>
<td>Focardi <em>et al.</em> (2002)</td>
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<td></td>
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<td>Trois-Fontaines and Chizé (France)</td>
<td>No</td>
<td>Gaillard <em>et al.</em> (1992)</td>
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<td></td>
<td>Fertility</td>
<td>Multisite (England)</td>
<td>No</td>
<td>Hewison (1996)</td>
</tr>
<tr>
<td></td>
<td>Fecundity</td>
<td>Yellowstone (USA)</td>
<td>Yes</td>
<td>Gogan and Taper (2002)</td>
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<td><em>Cervus</em></td>
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<td>Coulson <em>et al.</em> (2004a)</td>
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<td>canadensis</td>
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<td></td>
<td>Conradt <em>et al.</em> (1999)</td>
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<td></td>
<td>Lifetime breeding success</td>
<td>Norway (whole country)</td>
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<td>Langvatn <em>et al.</em> (2004)</td>
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<td></td>
<td>Fecundity</td>
<td>La Petite Pierre (France)</td>
<td>No</td>
<td>Bonenfant <em>et al.</em> (2002)</td>
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<td><em>Cervus elaphus</em></td>
<td>Young:female ratio</td>
<td>Nakanoshima Island (Japan)</td>
<td>No</td>
<td>Kaji <em>et al.</em> (1988)</td>
</tr>
<tr>
<td></td>
<td>Fecundity (≥4 years-old females)</td>
<td>Norway (whole country)</td>
<td></td>
<td></td>
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<td></td>
<td>Pregnancy</td>
<td>La Petite Pierre (France)</td>
<td>No</td>
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<td><em>Cervus nippon</em></td>
<td>Age of primiparity</td>
<td>Nakanoshima Island (Japan)</td>
<td>No</td>
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</tr>
<tr>
<td>Species</td>
<td>Reproduction component</td>
<td>Location</td>
<td>Predator?</td>
<td>References</td>
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<tr>
<td><em>Connochaetes taurinus</em></td>
<td>Young:female ratio</td>
<td>Serengeti-Mara (Tanzania, Kenya)</td>
<td>Yes</td>
<td>Mduma et al. (1999)</td>
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<td><em>Dama dama</em></td>
<td>Young:female ratio</td>
<td>Doñana National Park (Spain)</td>
<td>Yes</td>
<td>Braza et al. (1990)</td>
</tr>
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<td><em>Diceros bicornis</em></td>
<td>Age of primiparity</td>
<td>Pilanesberg national</td>
<td>Yes</td>
<td>Hrabar and du Toit (2005)</td>
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<td><em>Equus asinus</em></td>
<td>Age of primiparity</td>
<td>Park (South Africa)</td>
<td>No</td>
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<td></td>
<td>Breeding proportion</td>
<td>The Victoria river Region (Australia)</td>
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<td></td>
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<tr>
<td></td>
<td>(Over 0.085 animals km(^{-2}))</td>
<td></td>
<td></td>
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<td></td>
<td>Age of primiparity</td>
<td>Nevada Wild Horse Range (USA)</td>
<td>?</td>
<td>Garrott et al. (1991)</td>
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<td><em>Kobus kob kob</em></td>
<td>Pregnancy</td>
<td>Comoé National Park (West Africa)</td>
<td>Yes</td>
<td>Fischer and Linsenmair (2002)</td>
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<td><em>Oreamnos americanus</em></td>
<td>Young: female ratio</td>
<td>Colorado (USA)</td>
<td>Yes</td>
<td>Bailey (1991)</td>
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<td></td>
<td>Age of primiparity</td>
<td>Olympic National Park, Washington (USA)</td>
<td>No</td>
<td>Houston and Stevens (1988)</td>
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<td></td>
<td>Proportion of lactating female</td>
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<td></td>
<td>Twinning rate</td>
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<td><em>Ovis aries</em></td>
<td>Fecundity</td>
<td>St Kilda Archipelago (Scotland)</td>
<td>No</td>
<td>Coulson et al. (2001)</td>
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<td></td>
<td>Twinning rate</td>
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<td>Age of primiparity</td>
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<td></td>
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<td><em>Ovis canadensis</em></td>
<td>Number of offspring/females</td>
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<td>Ovis gmelini</td>
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<td>Hungary</td>
<td>Náhlik and Takačs (1996)</td>
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<td>Odocoileus virginianus</td>
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<td>Lower Yellowstone River (USA)</td>
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<td>Pregnancy</td>
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<td>Verme (1991)</td>
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<td>Young:female ratio</td>
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<td>Indiana (USA)</td>
<td>Swihart et al. (1998)</td>
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<td>Odocoileus hemionus</td>
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<td>Rangifer tarandus</td>
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<td></td>
<td>Age of primiparity</td>
<td>Hardangervidda (Norway)</td>
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<td></td>
<td>Young:female ratio</td>
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<td>Solberg et al. (2001)</td>
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<td>Young:female ratio</td>
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<td>Young:female ratio</td>
<td>Lapland (Finland)</td>
<td>Helle and Kojola (1994)</td>
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<td>Saiga tatarica</td>
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<td>Betpak-Dala (Kazakhstan)</td>
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<td></td>
<td>Twinning rate</td>
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<td>Tragelaphus strepsiceros</td>
<td>Young:female ratio</td>
<td>Kruger National Park (South Africa)</td>
<td>Owen-Smith (1990)</td>
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The column labeled “Predator?” reports whether predators both for young and adults are known to occur in the study area.
Figure 2  Relative responses of demographic rates to changes in density in large herbivore species. The presented variable is the change of a trait (percentage) divided by the corresponding change in density (percentage). In (A), the boxplot (vertical bar: median; box: range between first and third quartile; horizontal bars: range between the 5th and 95th percentile) presents the age-specific pattern \((n = 137)\). **Key:** Ad_Rep = adult female reproduction; Ad_Sur = adult survival (both sexes combined); Juv_Rep = juvenile female reproduction (encompasses age at first reproduction and reproductive rates); Juv_Sur = juvenile survival (both sexes combined);
deer (Capreolus capreolus): Focardi et al. (2002); Hewison (1996); Hewison and Gaillard (2001); saiga antelope (Saiga tatarica): Coulson et al. (2000); Soay sheep (Ovis aries): Clutton-Brock et al. (1991); moose: Boer (1992); see Table 1). For example, as density of mountain goats (Oreamnos americanus) increased from 0.87 to 3.3 individuals · km$^{-2}$ twinning rates decreased from 0.40 to 0.07 (Houston and Stevens, 1988). In addition to depressed fecundity rates at high densities, the fitness costs of raising offspring can also increase with density, which in turn can influence future reproductive success (bighorn sheep (Ovis canadensis): Bérubé et al. (1996); red deer: Clutton-Brock et al. (1983); ibex (Capra ibex): Toigo et al. (2002)). For example, most red deer hinds on the Isle of Rum, Scotland, only breed successfully once every 2 years at high population density, but reproduce every year at lower densities (Clutton-Brock et al., 1982). This delay is thought to be a result of females taking longer to regain peak condition following reproduction at high density compared to low density (Clutton-Brock and Coulson, 2002).

Although the mean values of components of reproduction are depressed at elevated densities, density-related costs of reproduction can vary substantially among females (Gaillard et al., 2001; MacNamara and Houston, 1996). In high-density bighorn sheep populations, the costs of reproduction decrease as female mass increases (Festa-Bianchet et al., 1998). Higher somatic costs of reproduction with increasing density can also influence energy budgets: female bighorn sheep reduce the amount of energy allocated to reproduction as density increases, with the greatest proportional reduction reported among lightweight females (Festa-Bianchet and Jorgenson, 1998). Similarly, in red deer on Rum and Soay sheep on the Island of Hirta in the St. Kilda archipelago, Scotland, the fitness costs of reproduction are greater in lightweight and subordinate females than in those that are heavier and more dominant (Clutton-Brock et al., 1996; Kruuk et al., 1999a; Tavecchia et al., 2005). Within a population, females with little costs of reproduction will reproduce at any density while females incurring higher costs of reproduction will fail to reproduce successfully at high population density thereby increasing interindividual variance in reproductive performance as density increases (Toigo et al., 2002). Such a pattern was predicted by Łomnicki’s (1978) model (Box 1).

Yr_Sur = yearling survival (both sexes combined); Ratio = number young per females (derived from count statistics); Sc_Sur = survival of senescent individual (both sexes combined); Yr_Sur = yearling survival (both sexes combined). In (B), the sex-specific pattern ($n = 45$). Key: Ad_Mal_Sur = adult male survival; Ad_Fem_Sur = adult female survival; Jul_Mal_Sur = male juvenile survival; Juv_Fem_Sur = female juvenile survival; Sc_Male_Survival = senescent male survival; Sc_Fem_Sur = senescent female survival; Yr_Mal_Sur = yearling male survival; Yr_Fem_Sur = yearling female survival.
<table>
<thead>
<tr>
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<th>Predator?</th>
<th>References</th>
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<td><em>Aepyceros melampus</em></td>
<td>Juvenile survival</td>
<td>Kruger park, (South Africa)</td>
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<td>Adult survival</td>
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<td>Survival of all age classes</td>
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<td>Andersen and Linnell (1998)</td>
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<tr>
<td><em>Capreolus capreolus</em></td>
<td>Summer juvenile survival</td>
<td>Tredozio (Italy)</td>
<td>Yes</td>
<td>Focardi <em>et al.</em> (2002)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td>Trois-Fontaines and Chizé (France)</td>
<td>No</td>
<td>Gaillard <em>et al.</em> (1993)</td>
</tr>
<tr>
<td><em>Cervus canadensis</em></td>
<td>Adult survival</td>
<td>Yellowstone (USA)</td>
<td>Yes</td>
<td>Gogan and Taper (2002)</td>
</tr>
<tr>
<td></td>
<td>Summer juvenile survival</td>
<td>Yellowstone (USA)</td>
<td>Yes</td>
<td>Coughenour and Singer (1996)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td>Rocky mountain National Park (USA)</td>
<td>Yes</td>
<td>Lubow <em>et al.</em> (2002)</td>
</tr>
<tr>
<td></td>
<td>Juvenile survival</td>
<td>Rum and Inner Hebrides (Scotland)</td>
<td>No</td>
<td>Kruuk <em>et al.</em> (1999a)</td>
</tr>
<tr>
<td><em>Cervus elaphus</em></td>
<td>Juvenile survival (male)</td>
<td>La Petite Pierre (France)</td>
<td>No</td>
<td>Bonenfant <em>et al.</em> (2002)</td>
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<tr>
<td></td>
<td>Juvenile survival (female)</td>
<td>Rum Island (Scotland)</td>
<td>No</td>
<td>Coulson <em>et al.</em> (2004)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival (male)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival (female)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yearling survival (male)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Connochaetes taurinus</em></td>
<td>Dry season juvenile survival</td>
<td>Serengeti (Tanzania, Kenya)</td>
<td>Yes</td>
<td>Mduma <em>et al.</em> (1999)</td>
</tr>
<tr>
<td></td>
<td>Yearling survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult survival</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Equus asinus</em></td>
<td>Summer juvenile survival</td>
<td>The Victoria river region (Australia)</td>
<td>No</td>
<td>Choquenot (1991)</td>
</tr>
<tr>
<td><em>Equus burchelli</em></td>
<td>Juvenile survival</td>
<td>Kruger Park</td>
<td>Yes</td>
<td>Owen-Smith <em>et al.</em> (2005)</td>
</tr>
<tr>
<td>Species</td>
<td>Survival Phase</td>
<td>Location</td>
<td>Status</td>
<td>Reference</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------------------------</td>
<td>-----------------------------------------------</td>
<td>----------</td>
<td>----------------------------------</td>
</tr>
<tr>
<td><em>Giraffa camelopardalis</em></td>
<td>Adult survival</td>
<td>South Africa</td>
<td>Yes</td>
<td>Owen-Smith <em>et al.</em> (2005)</td>
</tr>
<tr>
<td></td>
<td>Juvenile survival</td>
<td>Kruger Park, South Africa</td>
<td>Yes</td>
<td>Fischer and Linsenmair (2002)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Kobus kob kob</em></td>
<td>Adult survival</td>
<td>South Africa</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yearling males survival</td>
<td>Comoé National Park, West Africa</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile survival</td>
<td>Torres del Paine National Park, Chile</td>
<td>Yes</td>
<td>Sarno <em>et al.</em> (1999)</td>
</tr>
<tr>
<td></td>
<td>(inverse relationship)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Odocoileus hemionus</em></td>
<td>Winter juvenile survival</td>
<td>Piceance Basin, USA</td>
<td>Yes</td>
<td>White and Bartmann (1998)</td>
</tr>
<tr>
<td></td>
<td>Juvenile survival</td>
<td>Colorado, USA</td>
<td>?</td>
<td>White and Bartmann (1998)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td>Colorado, USA</td>
<td></td>
<td>Bartmann <em>et al.</em> (1992)</td>
</tr>
<tr>
<td><em>Odocoileus virginianus</em></td>
<td>Summer juvenile survival</td>
<td>Lower Yellowstone River, USA</td>
<td>Yes</td>
<td>Dusek <em>et al.</em> (1989)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Odocoileus virginianus</em></td>
<td>Winter juvenile survival</td>
<td>Bridger mountain, Range, Montana, USA</td>
<td>No</td>
<td>Pac <em>et al.</em> (1991)</td>
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<tr>
<td></td>
<td>Female Adult survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ovis aries</em></td>
<td>Summer juvenile survival</td>
<td>St Hirta Archipelago, Scotland</td>
<td>No</td>
<td>Coulson <em>et al.</em> (2001)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yearling survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile survival (female)</td>
<td>St Hirta Archipelago, Scotland</td>
<td>No</td>
<td>Catchpole <em>et al.</em> (2000)</td>
</tr>
<tr>
<td></td>
<td>Juvenile survival (male)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Survival (senescent female)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ovis canadensis</em></td>
<td>Winter juvenile survival</td>
<td>Ram mountain, Canada</td>
<td>Yes</td>
<td>Portier <em>et al.</em> (1998)</td>
</tr>
<tr>
<td></td>
<td>Adult survival</td>
<td>Ram mountain, Canada</td>
<td>Yes</td>
<td>Jorgenson <em>et al.</em> (1997)</td>
</tr>
<tr>
<td></td>
<td>Juvenile survival</td>
<td>Lake Mead National Recreation area, Nevada</td>
<td>No</td>
<td>Douglas and Leslie (1986)</td>
</tr>
<tr>
<td><em>Rangifer tarandus</em></td>
<td>Winter juvenile survival</td>
<td>Hardangervidda, Norway</td>
<td>No</td>
<td>Skogland (1990)</td>
</tr>
<tr>
<td></td>
<td>Winter juvenile survival</td>
<td>Svalbard, Norway</td>
<td>No</td>
<td>Solberg <em>et al.</em> (2001)</td>
</tr>
</tbody>
</table>

(continued)
Table 2 (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Survival component</th>
<th>Location</th>
<th>Predator?</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rupicapra rupicapra</em></td>
<td>Survival of all age classes</td>
<td>Alps (Italy)</td>
<td>Yes</td>
<td>Capurro et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>≥1 year old (2 years delay)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tragelaphus strepsiceros</em></td>
<td>Yearling survival</td>
<td>Kruger Park,</td>
<td>Yes</td>
<td>Owen-Smith et al. (2005)</td>
</tr>
<tr>
<td></td>
<td>Adult survival</td>
<td>(South Africa)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Senescent survival</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Four stages of survival were distinguished when possible: summer and winter juvenile survival, yearling survival and adult survival. The column labeled “Predator?” reports whether predators both for young and adults are known to occur in the study area.
Life history theory predicts that as resources become limiting, individuals should grow more slowly and achieve sexual maturity at a later age (Stearns, 1992, p. 124). Depressed growth rates at high density should consequently delay age at first reproduction. In large herbivores, age at first reproduction is very sensitive to density (Table 1, Figure 2A). Density-dependent delays in first reproduction are typically of 1–2 years in red deer (Bertouille and De Crombrugghe, 2002; Bonenfant et al., 2002; Langvatn et al., 1996), and up to

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**Box 1**

Models of Eberhardt and Łomnicki

In 1977, Eberhardt proposed a model to account for the observed pattern of density-dependence in marine mammals (Eberhardt, 1977). In 2002, Eberhardt generalized his model to most species of large vertebrates (Eberhardt, 2002). Eberhardt’s model is based on empirical observations of sequential changes of demographic parameters as population density increases. First juvenile survival decreases, second, the age at first reproduction increases, then reproductive rates of prime-aged females decline and finally, the survival of prime-aged females decreases (Figure 1). Everything else being equal, a given increase in density should thus lead to differential changes in the four demographic parameters considered, decreasing from juvenile survival to adult survival. Eberhardt’s model therefore predicts that, within or among populations, the observed variability of demographic parameters generated by changes in population density should decrease from juvenile survival to adult survival. Another interesting property of this model is that it allows assessing the status of a population, that is, whether a population is living at a relatively high or low density (Eberhardt, 2002).

Łomnicki’s model is based on the idea that food partitioning among animals is unequal as a result of contest competition for resources (Łomnicki, 1978). Łomnicki’s model suggests that this unequal partitioning of resources among individuals becomes more pronounced as resources become scarce therefore predicting that as density increases individual heterogeneity in life history traits should increase too. One tenet of Łomnicki’s model is that this increase in individual heterogeneity that leads to increased variance in demographic parameters, should participate to the decrease of population growth rate as population density increases. Such a mechanism of regulation has received recent support from theoretical development in demography (Tuljapurkar et al., 2003) but still lacks of empirical support.

Life history theory predicts that as resources become limiting, individuals should grow more slowly and achieve sexual maturity at a later age (Stearns, 1992, p. 124). Depressed growth rates at high density should consequently delay age at first reproduction. In large herbivores, age at first reproduction is very sensitive to density (Table 1, Figure 2A). Density-dependent delays in first reproduction are typically of 1–2 years in red deer (Bertouille and De Crombrugghe, 2002; Bonenfant et al., 2002; Langvatn et al., 1996), and up to
3 years in bighorn sheep (Festa-Bianchet et al., 1995). At Ram Mountain, Alberta, 52% of 2-year-old bighorn females were lactating at a density of 0.79 females·km\(^{-2}\) compared to 0% at 1.30 females·km\(^{-2}\) (Jorgenson et al., 1993). Because of the widespread evidence for a density-dependent increase in age of primiparity and much weaker evidence for an all-age density-dependent depression in parturition rates (see below), we suggest that many of the reported decreases in fecundity at high density in studies that did not account for female age could be due primarily to an increase in the age of first reproduction.

We found twelve studies reporting density-related changes in the young to female ratio based on counts (Table 1). The young to female ratio is a composite measure and the result of several demographic processes such as age-specific survival and fecundity (most particularly age of first reproduction) and the population age-structure that varies with density and stochastic environmental variations. Moreover, at the individual level, the young to female ratio confounds both female fecundity and juvenile survival. The relative strength of density-dependence in the young to adult female ratio is intermediate to that of juvenile survival and adult reproductive rates, and has almost the same variability as the age at first reproduction (Figure 2A). Such a high variability, however, may be inflated by inappropriate sampling designs (Bonenfant et al., 2005).

Across a wide range of species, the form and strength of the density-dependence can vary with life histories and ecology. One prediction is that the greater reproductive potential of polytocous species can generate stronger, and less linear, density-dependence in reproduction compared to monotocous species (Andersen and Linnell, 2000; McCullough, 1997; van Sickle, 1990). As the maximum population growth rate increases with litter size and decreases with body size at the interspecific level (Millar and Zammuto, 1983), carrying capacity can be reached—and potentially exceeded—much more quickly in small polytocous species, generating more variable population dynamics than in larger monotocous species (Nicholson, 1933; Royama, 1977; Sinclair and Pech, 1996; van Sickle, 1990).

A comparison of the population dynamics of red deer and Soay sheep on Scottish islands lends support to this proposition. The medium-sized and slightly polytocous Soay sheep (mean adult female mass of 24 kg) show only weak changes in fecundity rates in response to changes in density, whereas the larger and monotocous red deer (mean adult female body mass of 80 kg) consistently show linear decreases in reproductive output with increasing density (Clutton-Brock et al., 1997). These differences in life history generate different patterns of density-dependence in population growth, and could generate the contrasting population dynamics of the two species (Clutton-Brock and Coulson, 2002).

Life history differences in how density-dependence in components of reproduction manifests itself may be further exacerbated by differences in
behavior between species. For example, depending on the spatial distribution of high-quality grazing, and the degree of sociality exhibited by the species, density-dependent reproduction may result from either scramble or contest competition (Clutton-Brock et al., 1997; Illius and Gordon, 1999) which, in the latter case, may not affect all individuals similarly.

B. Density Effects on Age-Specific Survival Rates

The effect of density-dependence on survival rates of 20 species are radically different according to sex and age class (Table 3). Sex-specific responses to density have seldom been considered and may be complicated by sexual segregation for species exhibiting sexual size dimorphism. Survival during the first year is the demographic rate most frequently reported to be density-dependent. It also shows the largest variation with density among all studied LHT, at least in temperate areas (Figure 2A). One typical example comes from an experimental manipulation of mule deer (Odocoileus hemionus) where a reduction in density by 75% increased fawn survival from 0.40 to 0.77 (White and Bartmann, 1998). In large herbivores, juvenile survival can be divided into two distinct stages: survival from birth to weaning and survival from weaning to 1 year (Clutton-Brock et al., 1982; Gaillard et al., 2000a, although the juvenile period may be extended in megaherbivores). In temperate ecosystems, survival from weaning to 1 year encompasses the first winter of life, while in tropical ecosystems it encompasses the first dry season. Density-dependent responses of survival to weaning have been found in most studies of polytocous species (roe deer, Soay sheep, white-tailed deer (Odocoileus virginianus), mule deer) whereas studies on monotocous species often did not report density-dependence in this demographic parameter (e.g., Clutton-Brock et al., 1987; Portier et al., 1998). Nine of sixteen studies reported density-dependence in post-weaning juvenile survival, including both monotocous and polytocous species. In five populations, density-dependence occurred in both survival to weaning and survival from weaning to 1 year. Yearlings were also prone to density-dependent mortality in Soay sheep, wildebeest (Connochaetes taurinus), kob (Kobus kob kob), and chamois (Rupicapra rupicapra) (Table 3), but to a lesser extent than juveniles (Figure 2A). For example, in greater kudu (Tragelaphus strepsiceros), the increase in juvenile mortality in density was 30% greater than for yearlings (Owen-Smith, 1990).

Survival of adults should differentiate prime-age from senescent individuals (Caughley, 1966). Individuals of prime-age are those reaching the state of peak performance in both reproduction and survival ranging between the end of the growing period and the onset of senescence. The survival of prime-aged females has been claimed to be density-dependent in Soay sheep, red
Table 3  Studies reporting density-dependent responses of body mass in ungulate populations

<table>
<thead>
<tr>
<th>Species</th>
<th>Age class</th>
<th>Location</th>
<th>Predator?</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alces alces</em></td>
<td>Calf body mass</td>
<td>Vefsn (Norway)</td>
<td>No</td>
<td>Solberg <em>et al.</em> (1999)</td>
</tr>
<tr>
<td></td>
<td>Yearling calf</td>
<td>South–Eastern (Norway)</td>
<td>No</td>
<td>Hjeljord and Histøl (1999)</td>
</tr>
<tr>
<td></td>
<td>Yearling calf</td>
<td>Sweden (whole country)</td>
<td>Yes</td>
<td>Sand <em>et al.</em> (1995)</td>
</tr>
<tr>
<td><em>Capreolus capreolus</em></td>
<td>Adult body mass (female)</td>
<td>Britain Kielder (UK)</td>
<td>No</td>
<td>MacIntosh <em>et al.</em> (1995)</td>
</tr>
<tr>
<td></td>
<td>Adult body mass (female)</td>
<td>Storfosna (Norway)</td>
<td>No</td>
<td>Andersen and Linnell (2000)</td>
</tr>
<tr>
<td></td>
<td>Adult body mass (female)</td>
<td>Dourdan (France)</td>
<td>No</td>
<td>Vincent <em>et al.</em> (1995)</td>
</tr>
<tr>
<td></td>
<td>Fawn body mass</td>
<td>Trois-Fontaine and Chizé</td>
<td>No</td>
<td>Gaillard <em>et al.</em> (1996)</td>
</tr>
<tr>
<td></td>
<td>Adult body mass</td>
<td>Dourdan (France)</td>
<td>No</td>
<td>Pettorelli <em>et al.</em> (2001)</td>
</tr>
<tr>
<td><em>Cervus elaphus</em></td>
<td>Adult body mass</td>
<td>Western Norway</td>
<td>No</td>
<td>Mysterud <em>et al.</em> (2002b)</td>
</tr>
<tr>
<td></td>
<td>Body mass at birth</td>
<td>Rum Island (Scotland)</td>
<td>No</td>
<td>Albon <em>et al.</em> (2000)</td>
</tr>
<tr>
<td></td>
<td>Calf body mass</td>
<td>La Petite Pierre (France)</td>
<td>No</td>
<td>Bonenfant <em>et al.</em> (2002)</td>
</tr>
<tr>
<td><em>Dama dama</em></td>
<td>All age classes</td>
<td>Waterleidingduinen (The Netherlands)</td>
<td>No</td>
<td>Pélabon and van Breukelen (1998)</td>
</tr>
<tr>
<td><em>Odocoileus hemionus</em></td>
<td>Fawn body mass</td>
<td>Piceance Basin (USA)</td>
<td>?</td>
<td>White and Bartmann (1998)</td>
</tr>
<tr>
<td></td>
<td>Fetus body mass</td>
<td>Buttermilk Winter Range (USA)</td>
<td>?</td>
<td>Kucera (1997)</td>
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<tr>
<td></td>
<td>Adult body mass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Odocoileus virginianus</em></td>
<td>Body mass of fawns, yearlings and adult males and females</td>
<td>Ontario (Canada)</td>
<td>?</td>
<td>Ashley <em>et al.</em> (1998)</td>
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<tr>
<td><em>Ovis canadensis</em></td>
<td>Lamb body mass</td>
<td>Ram Mountain (Canada)</td>
<td>Yes</td>
<td>Leblanc <em>et al.</em> (2001)</td>
</tr>
<tr>
<td></td>
<td>Adult body mass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ovis aries</em></td>
<td>Body mass at birth</td>
<td>St Kilda Archipelago (Scotland)</td>
<td>No</td>
<td>Forchhammer <em>et al.</em> (2001)</td>
</tr>
<tr>
<td><em>Rangifer tarandus</em></td>
<td>Adult female carcass weight</td>
<td>Baffin Island (Canada)</td>
<td>Yes</td>
<td>Ferguson and Messier (2000)</td>
</tr>
<tr>
<td></td>
<td>Body mass at birth</td>
<td>Harddangervidda (Norway)</td>
<td>No</td>
<td>Skogland (1990)</td>
</tr>
</tbody>
</table>

The column labeled “Predator?” reports whether predators both for young and adults are known to occur in the study area.
deer, chamois, elk (*Cervus canadensis*), wildebeest, greater kudu, impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), white-tailed deer and zebra (*Equus burchelli*), but many of these results must be interpreted with caution (Table 3). Two studies estimated mortality through carcass recoveries (chamois: Capurro et al. (1997); wildebeest: Mduma et al. (1999))—which assumes the population is at the equilibrium age-structure (see Caughley, 1977)—and tested for density-dependence using key-factor analysis—an approach that can produce spurious results (Manly, 1977; Royama, 1996). Results from several African species (kudu, impala, giraffe, and zebra) rely on count-ratios (but see Bonenfant et al., 2005), which also assume a constant age-structure. That assumption is unlikely to be supported as average female age typically increases with population density (Festa-Bianchet et al., 2003). An explicit example of density-dependence in the survival of prime-age females comes from feral donkeys (*Equus asinus*): a difference in density between 1.65 and 3.25 individuals $\cdot$ km$^{-2}$ led to a 51% and 12% decrease in juvenile and senescent survival rate respectively; adult female survival was lowered by only 5% (Choquenot, 1991). A density-dependent decrease in adult female survival has been documented in red deer on Rum Island (Albon et al., 2000) but mainly affected the oldest females (>9 years, Catchpole et al., 2004). Two additional suggestions of a higher mortality at high density for prime-aged females were discarded by further investigation that separated survival of prime-aged individuals and senescent individuals (Soay sheep: Milner et al. (1999) vs. Catchpole et al. (2000); Bighorn sheep: Bérubé et al. (1999) vs. Festa-Bianchet et al. (2003)). Overall, the evidence for density-dependence in the survival of adult females in their prime is limited (Gaillard and Yoccoz, 2003, Figures 2A and B), restricted to extremely high densities and with a weak effect size compared to other demographic rates. Consequently, the detection of density-dependence response in adult female survival would require long time series of data and high population density.

Few studies have examined how population density may affect adult survival in males compared to females. Male survival has been shown to be density-dependent for juveniles and adults in two highly dimorphic species, red deer (for males >9 years) and Soay sheep (Catchpole et al., 2000, 2004). In Soay sheep, there was a tendency for male lambs to exhibit relatively larger increases in mortality rates than female lambs with increasing population size (male and female survival were 0.30 and 0.35 respectively at high density but were equivalent at 0.81 and 0.82 at low density; Coulson et al. (2001)). In red deer, the slope of the relationship between survival and population size was steeper on the logit scale for male calves compared to female calves (0.86 vs. 0.43). Among yearlings, male survival was affected by an increase in density to a greater extent than female survival (approximate decrease in survival of 0.6% and 2.2% per increase of 10 individuals for males...
and females respectively, Catchpole et al. (2004)). Males, however, are not always the most sensitive sex to changes in density. In the dimorphic mule deer, female survival dropped from 0.87 to 0.65 when density increased from 3.73 deer km\(^{-2}\) to 6.72 deer km\(^{-2}\) while no effects were reported for males (Pac et al., 1991).

Density-dependence has seldom been investigated in senescent animals (Catchpole et al., 2000, 2004; Festa-Bianchet et al., 2003; Solberg et al., 2001), probably because old individuals are scarce. The resulting low sample size and limited statistical power make the detection of density-dependent senescence a rather difficult task. This problem is particularly acute in species where adults cannot be reliably aged, so that exact age is known only for animals first marked when aged 2 years or less (Hamlin et al., 2000). Population monitoring must last at least 10–12 years before data are obtained on senescent individuals of known age. Although variation in senescent survival has been only rarely investigated, the absence of density-dependence in senescent survival has been explicitly reported for three species [roe deer, bighorn sheep, and mountain goat: Festa-Bianchet et al. (2003)].

Most increases in mortality rates associated with high density were attributed primarily to increased competition for food. Predation and parasitism can act as additive sources of mortality to competition; however, care has to be taken in the direction of causality here, as reduced food availability may increase susceptibility to predators (Sih, 1980; Sinclair and Arcese, 1995) and parasites. Among large herbivores, predators prey more heavily upon juveniles than other age classes (up to 98% on pronghorn (Antilocapra americana); Byers (1997); see Linnell et al. (1995) for a review) which could limit our ability to detect density-dependence in juvenile survival (see Saro et al., 1999). Interestingly, a regulatory role of internal parasites on female survival or body mass of all age categories has been reported at high density in Svalbard reindeer (Albon et al., 2002; Stien et al., 2002), Soay sheep (Gulland, 1992; Wilson et al., 2004) and roe deer (Segonds-Pichon et al., 1998).

C. Dispersal Rate and Density

Although seldom considered in the context of population regulation of large mammals (but see Strandgaard, 1972), dispersal can be a dominant regulating agent through population expansion or colonization of empty areas (Clobert et al., 2001) and is particularly important for metapopulation dynamics (Hanski, 1998; Hanski and Gilpin, 1997). In most mammals, dispersal rates differ between males and females, with males typically being the dispersing sex (Dobson, 1982; Greenwood, 1980). However, in white-tailed deer (Hamlin and Mackie, 1989; Nelson and Mech, 1992) and reed-buck (Redunca arundinum: Howard, 1986), females have been reported to disperse more often than
males. In roe deer (Gaillard et al., 2008), guanaco (Lama guanicoe; Sarno et al. (2003)) and feral horses (Equus caballus; Berger (1986)), dispersal rates do not differ between the sexes and vary a lot among populations (between 20% and 70% for roe deer, Gaillard et al., 2008). The contribution of density-dependent dispersal to population dynamics is unclear as studies relating density to dispersal are too scarce to draw general conclusions (see Matthysen, 2005; Travis and French, 2000, for reviews). Among large herbivores, increasing dispersal rates with increasing density have been documented in both sexes of white rhinoceros (Ceratotherium simum), where males are more likely to disperse than females (Owen-Smith, 1988). Similar results have been reported for red deer (Catchpole et al., 2004; Clutton-Brock et al., 2002) on Rum (male dispersal rates increased from 8% to 21% as density increased from 8 to 20 deer km\(^{-2}\)) and mule deer (Bunnell and Harestad, 1983). Young moose are prone to disperse (Ballard et al., 1991), and there is anecdotal evidence that dispersal is related to population density (Labonte et al., 1998). In contrast, Loison et al. (1999a) and Gaillard et al. (2008) found no evidence of density influencing dispersal in chamois and roe deer respectively.

IV. LINKING DENSITY-DEPENDENCE WITH OTHER MAJOR SOURCES OF VARIATION IN DEMOGRAPHIC PARAMETERS

A. The Confounding Effects of Age

Fluctuations in population age-structure have long been recognized as an important component of the population dynamics of vertebrates (Caughley, 1966; Charlesworth, 1980). Increasing and decreasing populations have predictably different age structures (Caswell, 2001), implying marked changes in age structure with changing density. Age structure can also render the detection of density-dependence from time series data or non-age-structured demographic data difficult (Festa-Bianchet et al., 2003; Zabel and Levin, 2002). However, until recently (Coulson et al., 2004a) there were few empirical data on the effects of changes in age structure on population dynamics, because accurate ageing of cervids is difficult (see e.g., Hamlin et al., 2000). When changes in age structure are ignored, spurious conclusions about density-dependent responses may arise when the strength of density-dependent effects on demographic rates varies with age. Either the age-structure of the population is not strongly correlated with population size (Coulson et al., 2001) and then temporal fluctuations in the age-structure can mask density-dependent responses or a positive correlation occurs and then a spurious density-dependent responses of survival is found because the
proportion of senescent individuals—that have a lower survival—increases with density (Festa-Bianchet et al., 2003). The higher proportion of senescent individuals at high compared to low density is the direct consequence of the differential response of density-dependence that affect juvenile survival and female reproduction more strongly and at a lower densities than adult survival. Decreases in fecundity rates at high density reported by studies not based on individuals of known age could theoretically be due to an increase in age of first reproduction. Perhaps this effect explains why delayed age at first reproduction and reductions in adult reproductive rates are reported equally frequently in the studies of unmarked individuals (Table 1).

B. On the Importance of Sex

The sex structure was not included in Eberhardt’s (1977, 2002) model, likely because males of large herbivores generally are polygynous, and do not allocate energy to offspring. Hence, the contribution of males to changes in population growth has traditionally been overlooked (but see Gaillard et al., 2003b; Komers et al., 1994; Noyes et al., 1996). Only recently has it been suggested that males may play a substantial role in the population dynamics of large herbivores (Mysterud et al., 2002a) and that their contribution may deserve more attention. In moose (Solberg et al., 2002) and reindeer (Holand et al., 2003), male age-structure affects female pregnancy rates and fetal sex ratio—two parameters that can directly influence population growth rate. In sexually dimorphic species males are expected to be more sensitive to food shortage and weather harshness than females (Clutton-Brock et al., 1982, 1985; Flook, 1970). Depending on mating system, males may be unable to replenish the energy expended during the rut and hence might survive less than females, especially at high density (Byers, 1997; Hogg and Forbes, 1997; Toigo and Gaillard, 2003). However, males may modulate the costs of secondary sexual traits by adjusting the energy allocation to reproduction according to the level of density (bighorn sheep: Festa-Bianchet et al. (2003); Leblanc et al. (2001); red deer: Yoccoz et al. (2002) fallow deer (Dama dama): McElligott et al. (2003)). Hence, predicting the density-dependent responses of male life history traits is not straightforward. Within the framework of population dynamics, the main consequence of the greater energy requirements of males compared to females is that they often have lower survival than females (red deer: Catchpole et al. (2004); kudu: Owen-Smith (1993); bighorn sheep: Jorgenson et al. (1997); reindeer: Skogland (1985); roe deer: Gaillard et al. (1993); see Toigo and Gaillard (2003) and Clutton-Brock and Isvaran (2007) for reviews). Besides, because of marked sexual segregation in dimorphic species (Ruckstuhl and Neuhaus, 2005), the survival, growth, and reproduction of males and females may not be affected by the same population components. Consequently, total population
counts may have different values as predictors of density-dependent dynamics between the sexes.

In several size dimorphic species, survival rates may differ between the sexes in utero. A higher abortion rate of male fetuses compared to females is often suggested as the mechanism explaining the increasing skew in fetal sex ratios with increasing environmental harshness (red deer: Mysterud et al. (2000); reindeer: Weladji et al. (2003); tahr (Hemitragus jemlahicus): Forsyth et al. (2004)). Between-sex differences in mortality rates persist after birth, and for a given increase in population density, both preweaning and postweaning juvenile survival generally decrease more for males than for females (Table 3). The picture is less clear for adults. Catchpole et al. (2004) showed that male survival in red deer decreased more strongly than female survival with increasing population size. A similar trend was found in bighorn sheep and roe deer (Festa-Bianchet et al., 2003). In four studies, adult male mortality was significantly dependent on density after accounting for age effects (red deer: Bonenfant et al. (2002); Catchpole et al. (2004); Soay sheep: Milner et al. (1999); mule deer: Hamlin and Mackie (1989)) while only one study demonstrated density-dependent mortality of adult females older than 9 years of age (Catchpole et al., 2004). Whether males are mostly sensitive to male density, female density, or both, remains unclear (Mysterud et al., 2002a). One study on red deer showed that males were unaffected by male density at all ages, but responded to female density (Clutton-Brock et al., 1985). However, the increased density in that study mainly resulted from changes in female numbers, presumably reducing the amount of vegetation available to both sexes. Very few studies have investigated male reproductive performance within and among populations of large herbivores, because they usually require genetic assessment of paternity (Hughes, 1998; Pemberton et al., 1992). Coltman et al. (1999) reported that Soay sheep males born at low density had higher lifetime breeding success than did those born at high density. Likewise, young feral donkey males produce less sperm when density increases, leading to a density-dependent age at first reproduction (Choquenot, 1991). The proportion of mature 2.5-year-old male donkeys increased from 42% to 100% as density decreased from 3.25 to 1.65 animals ha$^{-1}$ (Choquenot, 1991). To expand Eberhardt’s (1977, 2002) model to encompass the male segment (Figure 1), further long-term studies are urgently required.

C. Cohort Effects

Environmental conditions experienced by juveniles in late gestation and early postnatal life when most growth occurs (Sadleir, 1969) can generate cohort effects, that is, persistent effects that vary among animals born in different
years (Albon et al., 1987). Cohort effects have two main consequences for population dynamics (Gaillard et al., 1997, 2003b): (1) a direct and short-term numerical effect on recruitment through changes in juvenile mortality, and (2) an indirect and long-lasting effect on individual performance, often correlated with cohort-specific changes of adult body mass. The magnitude of both effects varies negatively with population productivity (Albon et al., 1992; Gaillard et al., 1998). Cohort effects are pervasive in large vertebrates (Beckerman et al., 2002, 2003; Gaillard et al., 2003b), and affect several demographic parameters and phenotypic traits (body growth, body mass, survival, fertility, litter size).

Numerical effects are often generated by density-dependent juvenile survival. Long-term cohort effects related to density in the year of birth have been detected in several species. In red deer (Bonenfant et al., 2002; Mysterud et al., 2002b), moose (Solberg et al., 2004; Vucetich et al., 2005) and roe deer (Pettorelli et al., 2002), adult males born at high density are lighter than those born at low density. Given the relationship between body mass and reproductive success in males of polygynous species (Clutton-Brock, 1988), males born during periods of high density are expected to be of lower phenotypic quality, and to have lower reproductive success than those born at lower density. This prediction was confirmed for Soay sheep (Coltman et al., 1999), and was suggested for red deer on Rum where male lifetime reproductive success is lower for light-born than heavy-born males (Kruuk et al., 1999b). The pattern of long-term consequences of high density at birth on females is similar. Females born at high density experienced lower survivorship between 2 and 4 years of age in Soay sheep (Forchhammer et al., 2001) and a decreased lifetime reproductive success in red deer (Kruuk et al., 1999b) than those born at low population density (primarily due to a reduction in fecundity rather than in longevity: Albon et al. (1992)). In roe deer, 40% of variability in female adult body mass was accounted for by population size at birth (Pettorelli et al., 2002) with among-cohort differences in average body mass of up to 20%. Both short- and long-term cohort effects are consistently found in all populations of large herbivores studied. However, such a pattern is based on only 3% of the extant species and further studies are needed to confirm its generality.

D. Interaction Between Climate and Density

Weather has well documented effects on demographic rates of large herbivores and on vertebrates in general (Mysterud et al., 2003; Sæther, 1997; Weladji et al., 2002). Large-scale climatic variation like the North Atlantic Oscillation and the El Niño Southern Oscillation account for substantial
amounts of variation in population growth (Forchhammer et al., 1998; Post and Stenseth, 1998; Stenseth et al., 2002). Typically, the effects of climate are modulated by variation in population density (Boyce et al., 2006; Sæther, 1997) yet the relative impacts of density and weather variables are difficult to assess because they are seldom expressed in comparable units.

Complex interactions between density and climate have been reported in red deer (Loison and Langvatn, 1998), Soay sheep (Coulson et al., 2001), saiga antelope (Coulson et al., 2000), zebra (Equus quagga) (Georgiadis et al., 2003), bighorn sheep (Portier et al., 1998), moose (Crête and Courtois, 1997; Mech et al., 1987), reindeer (Solberg et al., 2001), roe deer (Gaillard et al., 1997), and white-tailed deer (Patterson and Power, 2002). Density typically has a stronger effect on population growth rate in harsh than in favorable conditions so that few, if any, weather variables really act in a purely “density-independent” manner (Andrewartha and Birch, 1954, p. 18–19) and the ability to detect density-dependence is often a function of the climatic regime. For example, the rate of increase of the Tule elk (Cervus elaphus nannodes) population of Point Reyes, California, is density-dependent only in years of poor productivity (Brooks et al., 2002). Theoretically, depending on climate, populations of large herbivores may never experience density-dependence and remain at low density because of stochastic climatic events. This could be the case for herbivores such as kangaroos (Macropus sp.) living in highly variable environments (Caughley, 1977), muskoxen (Ovibos moschatus) and reindeer living in highly seasonal environments (Caughley and Gunn, 1993; Gunn, 1992) or populations facing high predation pressures (McLoughlin et al., 2003; Sinclair et al., 2003; Wittmer et al., 2005). Alternatively populations experiencing highly variable environments may also experience density-dependence, which we would actually fail to detect because of low statistical power (as well demonstrated by works dealing with the variability generated by measurement errors, Bulmer, 1975; Freckelton et al., 2006).

V. THE EVOLUTIONARY CONTEXT OF DENSITY-DEPENDENCE

A. Linking Density-Dependent Patterns to Environmental Canalization

Many detailed study cases suggest that density-dependence affects reproductive rates and juvenile survival to a much greater extent than adult female survival, as suggested by Fowler (1987). Therefore, contrary to
Lack’s (1966) prediction that variation in reproduction is predominantly a result of density-independent processes, our survey demonstrates substantial evidence for density-dependent reproduction in large herbivores. In fact, the sequence of changes in demographic rates to variation in population density is the same as the one observed for stochastic variation (see Gaillard et al., 2000a,b, for reviews). In both cases, survival and reproduction of prime-aged adults are less sensitive to changes in density than juvenile survival (Figure 2A). Therefore, the sequence of responses of demographic rates does not depend on the type of environmental factors, supporting the concept of an overall role of environmental variation. The high resilience of adult survival to any source of environmental variation (Coulson et al., 2004a; Gaillard et al., 2000a,b), possibly at the cost of reduced offspring production and care (Festa-Bianchet and Jorgenson, 1998), supports the concept of environmental canalization (Gaillard and Yoccoz, 2003). From this viewpoint we can recast Eberhardt’s (1977, 2002) pioneering work into the framework of environmental canalization. Indeed, Eberhardt’s model can be interpreted as a continuum opposing weakly canalized demographic parameters (i.e., that quickly respond to density and other sources of environmental variations) to strongly canalized rates such as adult survival.

### Table 4

Long-term studies showing the sequence of density-dependent effects on demographic parameters as predicted by Eberhardt (1977, 2002) (abbreviations in parentheses refer to study areas)

<table>
<thead>
<tr>
<th>Species</th>
<th>JS</th>
<th>AFR</th>
<th>FEC</th>
<th>YS</th>
<th>SA</th>
<th>ΔD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pronghorn (NBR)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7–142</td>
</tr>
<tr>
<td>Mountain goat (CR)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>81–147</td>
</tr>
<tr>
<td>Roe deer (TF)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>125–304</td>
</tr>
<tr>
<td>Bighorn (SR)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>99–153</td>
</tr>
<tr>
<td>Bighorn (RM)</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>94–232^a</td>
</tr>
<tr>
<td>Red deer (LPP)</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>49–98^b</td>
</tr>
<tr>
<td>Roe deer (CH)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>157–569</td>
</tr>
<tr>
<td>Roe deer (STO)</td>
<td>+</td>
<td>+</td>
<td>+^c</td>
<td>0</td>
<td>0</td>
<td>81–276</td>
</tr>
<tr>
<td>Soay sheep (KIL)</td>
<td>+</td>
<td>+</td>
<td>+^d</td>
<td>+^d</td>
<td>+^d</td>
<td>200–595</td>
</tr>
<tr>
<td>Red deer (RUM)</td>
<td>+</td>
<td>+</td>
<td>+^d</td>
<td>+^d</td>
<td>+^d</td>
<td>76–196^a</td>
</tr>
</tbody>
</table>

A “+” indicates a decrease in the observed life history trait with density; a “0” means no density-dependence detected. JS: Juvenile survival; AFR: Age at first reproduction; YS: Yearling survival; FEC: Adult female reproduction; SA: Adult female survival; ΔD is the recorded range in population size.

^aPopulation size refers here to the total population size.

^bEstimate from spotlight counts, given in number of deer per 100 km.

^cNonsignificant result owning to a too small sample size.

^dContradictory findings.
B. Testing the Eberhardt’s Model

We found 10 long-term studies of six species that reported the sequence of density-dependent effects on demographic rates (Table 4). In all cases but one, the observed sequences were in accordance with Eberhardt’s expectation. The exception was a population of red deer in France (LPP, Table 4) where the age of primiparity responded to a rise in density earlier than juvenile survival (Bonenfant et al., 2002). Note, however, that another population of red deer followed Eberhardt’s predicted sequence. Gaillard et al. (2000a,b) argued that juvenile survival may respond to an increase in density before the age at first reproduction in large species because of allometric constraints in seasonal environments. According to the concept of biological time (Calder, 1984), individuals of large species will live at a slower pace than individuals of small species (fast–slow continuum, Stearns, 1992). For example, 90% of adult body size is completed within 3.5 years in 80 kg female red deer (Clutton-Brock and Albon, 1989) and about 2 years in 25 kg roe deer (Gaillard et al., 2000a,b). To ovulate, young females must reach a threshold body mass of about 80% (Sadleir, 1987). For a given level of seasonality, females of fast species will enjoy a relatively longer favorable period, and will thereby be able to grow and reproduce to a higher extent than females of slow species (Calder, 1984). Large species like red deer may therefore experience stronger constraints on body growth and thus display higher sensitivity to density than smaller ones. Whether the Eberhardt’s model is size-dependent or not deserves further investigation as large species may experience a stronger trade-off between growth and reproduction than small ones.

C. The Role of Species-Specific Energy Allocation to Reproduction

Survival from birth to weaning and survival from weaning to 1 year of age may respond differently to an increase in density according to the species-specific amount of energy allocated to reproduction (monotocous vs. polytocous species: Gaillard et al., 1997). In polytocous species, females contribute more reproductive effort than females in monotocous species (Robbins and Robbins, 1979). We have already reported (section “Density effects on age-specific survival rates”) that density-dependence in summer survival was more prevalent in polytocous species, whereas young of monotocous species exhibited density-dependent winter survival (Table 3). Such a pattern strongly suggests that density-dependent juvenile survival before weaning is closely linked to species-specific reproductive tactics, being more frequent in species that allocate a lot of energy to each reproductive event (Gaillard et al., 1997).
D. On the Importance of Timing of Birth

The synchronization between plant phenology and life cycles of large herbivores appears to be a key process in population dynamics (Clutton-Brock et al., 1997; Sinclair et al., 2000). Indeed, both the availability and the quality of forage fluctuate throughout the year either in a predictable (seasonal) or an unpredictable (stochastic) way. Therefore, density-dependent effects on juvenile survival and reproduction may or may not emerge according to the temporal match between late gestation, lactation, and plant phenology (Clutton-Brock and Coulson, 2002). As an illustration, we can use Clutton-Brock and Coulson’s (2002) comparison of red deer and Soay sheep. Red deer on Rum experience late gestation in April–May when the vegetation flushes and neonatal survival is density independent. Calf birth mass could thus be more affected by variations in plant quality and quantity determined by spring weather than by density. In contrast, Soay sheep experience late gestation in February–March, well before the period of highest spring food abundance; and are consequently very sensitive to food shortage induced by high density (Clutton-Brock and Coulson, 2002). Compared to red deer hinds, prime age Soay sheep females do not exhibit density-dependent fecundity because of the possible lower costs of reproduction to ovid females as compared to cervid females (Clutton-Brock et al., 1996; Festa-Bianchet, 1998; Tavecchia et al., 2005). Female sheep also benefit from an earlier weaning of their offspring, allowing them to fully replenish their body reserves before the next reproductive attempt (Clutton-Brock and Pemberton, 2004). In contrast, at high density, pregnancy rates of female red deer decreased from 89% to 40% because individuals could not regain condition after weaning a calf sufficiently fast to conceive in the following rut. Consequently, at high density female red deer typically reproduce only every other year on Rum (Clutton-Brock et al., 1983). These differences in timing of reproduction and gestation lead to the typical unstable dynamics of the Soay sheep population (Clutton-Brock et al., 1991, 1997). Further comparisons are needed to assess the general validity of such a density-dependent process in large herbivores.

E. The Pivotal Role of Body Mass in Density-Dependence

So far we have focused on the associations between density and demographic parameters but have not considered how density-dependence affects those parameters. Presumably, the main pathway is via individual body mass. Individuals in good condition (typically in populations substantially below carrying capacity) have higher fecundity and survival rates, are more likely to reproduce earlier, allocate more resources to offspring, attain adult size and
achieve reproductive maturity at earlier ages than individuals in poor conditions (typically in populations around carrying capacity).

There is much evidence for decreasing body mass with increasing density in large herbivores (Fowler, 1987; Hanks, 1981, Table 2). However, the functional relationship between body mass and demographic parameters has not been reviewed previously. Body mass strongly affects the probability to mature in many species (Sadleir, 1969). Indeed, a critical body mass above which young females may reproduce is frequently reported. For illustration, this threshold body mass is about 57 kg in red deer (Bertouille and De Crombrugghe, 2002; Bonenfant et al., 2002), 19 kg in roe deer (Gaillard et al., 1992), 24 kg in Spanish ibex (Capra pyrenaica) (Fandos, 1989), 17 kg in chamois (Bauer, 1987), 26 kg in bighorn sheep (Jørgensen et al., 1993), 128 kg for moose (Sand, 1996), and 31.5 kg in fallow deer (Langbein and Putman, 1992). Such thresholds can themselves be density-dependent where the required body mass for a young female to reproduce is higher at high density than at low density (Clutton-Brock and Albon, 1989; Heard et al., 1997).

Body mass also affects juvenile survival, with heavier offspring having a lower mortality rate especially at high density (roe deer: Gaillard et al. (1997); bighorn: Festa-Bianchet et al. (1997); mule deer: White and Bartmann (1998)). For instance, in mountain goat (Côté and Festa-Bianchet, 2001), red deer (Catchpole et al., 2004), and bighorn sheep (Festa-Bianchet et al., 1997), the negative relationship between density and juvenile survival was clearly caused by a decrease in body mass, with changes in survival being more marked for the lightest juveniles. In Norwegian red deer calves, a 5 kg change of winter body mass corresponded to a 10% change in winter survival, and male calves had to be 1 kg heavier than female calves to achieve the same survival probability (Loison et al., 1999a). As a general rule, longevity is mass-dependent (Gaillard et al., 2000a), but probably to a lower extent than juvenile survival as observed in bighorn sheep (Berubé et al., 1999; Festa-Bianchet et al., 1997). For large herbivores, any factor that negatively affects body mass such as density or harsh climatic conditions may in turn affect individual performance by lowering survival and/or reproduction (see Garel et al. (2004), for an example on mouflon (Ovis gmelini musimon); see Sæther (1997) for a review).

VI. DETECTION OF DENSITY-DEPENDENCE IN DEMOGRAPHIC PARAMETERS

Weak empirical evidence for density-dependent responses of individual performance is the main argument to refute the current theory of population regulation (Murdoch, 1994; Sinclair, 1989). Because positive results are
easier to publish than negative ones, an assessment of the frequency of density dependence cannot simply rely on a literature search. A more informative alternative is to assess how large a change in density is required to produce a significant change in a demographic rate (Figure 3). Our literature survey shows that regulation processes are widespread in populations of large herbivores (Figure 3) and sheds light on how density effects vary across population segments (Figures 1 and 2). The detection of density-dependent responses remains difficult for biological and technical reasons.

A. Delayed and Non-Linear Effects of Density-Dependence

Response to density is not homogeneous within a population. Eberhardt’s (1977, 2002) model suggests that responses of life history traits to changes in density are sequential and predictable from low density up to the ecological carrying capacity. Consequently, our ability to detect density-dependent responses depends on the sensitivity to population density of the demographic rate under study. Moreover, demographic rates may not react linearly to

Figure 3  Change in value of life history trait plotted against the change in density for populations of large herbivores (n = 137). The scatter plot shows how much demographic parameters are expected to vary (percentage of variation) for a given change of density (percentage of variation). Relative changes in density and demographic parameters were used since both were not always measured at the same scale in every study. The straight dashed line corresponds to a perfect isometric change between demographic parameters and density variations. The solid line represents the best fit to the data: \[ \text{LHT} = 0.330 + 2.724 \times \text{dens} \times 0.675 \times \text{dens}^2 + 1.055 \times \text{dens}^3; R^2 = 0.821 \]. Bounded life history trait values (between 0 and 1 most of the time) account for the lowered relative effect of large variations in density.
changes in density (Gilpin and Ayala, 1973) and nonlinearities are expected to occur for numerous reasons (Fowler, 1981; Stenseth et al., 2002). For instance Houston and Stevens (1988) provided evidence of an accelerating decrease of juvenile survival with increasing density for mountain goats. Some authors proposed that density must exceed a certain threshold, below which density-dependence is not detectable (Getz, 1996, see also Figure 3). In line with Strong’s (1986) suggestion of using flexible fitting procedures, an especially powerful tool to test nonlinearities in density-dependence is offered by Generalized Additive Models (Gimenez et al., 2006; Wood, 2006). Also little attention has been paid to whether density-dependent responses of life history traits are the same when populations are increasing or decreasing in size (Boyce, 1984). The response of demographic rates to changes in density may be more likely to be detected in increasing populations than in decreasing ones. Indeed, the decline of habitat quality and individual performance closely follows an increase in density, whereas the recovery of habitat quality and thereby the improvement of individual performance generally responds with delay to a decrease in density (Caughley, 1977). Since Turchin’s (1990) pioneering work, delayed responses to density changes are systematically examined in pattern-oriented analyses but the interpretation of the results is still a matter of debate (see below). On the other hand, lag effects are often overlooked in process-oriented investigations except in studies investigating long-lasting cohort effects.

B. Pattern-Versus Process-Oriented Approaches

Two dominant methodological approaches have traditionally been used to detect density-dependent responses, especially at the level of population growth (Krebs, 1995, 2002): the density “paradigm” (sensu Krebs, 2002) or pattern-oriented approach and the mechanistic paradigm or process-oriented approach (Coulson et al., 2000; Stenseth et al., 1996). In this review, we primarily concentrated on process-oriented approaches, which seek to identify associations between density and a demographic parameter. The alternative approach is to examine the effects of density through regression analyses of time series of population counts (Royama, 1977; Tong, 1990), before inferring biological processes from the values and patterns of regression coefficients. With this method the relative contributions of direct and lagged density dependence to population dynamics can be identified (Pianka, 1970). This modeling approach has proven popular because a range of population dynamical patterns—including cycles—can be generated (Stenseth et al., 2003). Several authors have reported density-dependent responses through autoregressive time series analyses in populations of large herbivores. The pattern-oriented approach can however generate conclusions that differ substantially from the process-oriented approaches (Hanski, 1990; Lande et al., 2006).
VII. CONCLUSIONS

Most of major developments of density-dependence were conceptualized in terms of unstructured models contrasting with modern developments, which take a more structured demographic approach. Our review generally supported the main predictions of Fowler (1987) and Eberhardt (1977, 2002; Figures 1 and 2) and suggested that density-dependent responses of demographic parameters are widespread among populations of large herbivores but strongly age-dependent. Age is, however, not the only factor structuring density-dependent responses. Instead, we now know that there are important differences in the strength of density-dependence between the sexes and among cohorts. Such variation will generate complex population dynamics. We established, in contrast to Lack’s (1966) hypothesis, that the question is no longer whether a population is regulated or not, but rather what is the relative magnitude of density-dependent responses in generating changes across demographic parameters, compared to other sources of variation (Coulson et al., 2004b; Turchin, 1995; Sæther, 1997). It is also apparent that a general answer to this question will require methodological advances and that other sources of variation in demographic parameters needs to be accounted for in future analyses. Until this is done it will be difficult to conclude that any general pattern of the strength and shape of density-dependent responses to different demographic rates exists (Owen-Smith, 2006). Furthermore, for large herbivores, the negative feedback of population size on individual performance and hence on demography may only be expected in particular ecological contexts (Ray and Hastings, 1996; Sale and Tolimieri, 2000) and most often limited to a few age-specific life history traits, mainly juvenile survival and female reproductive rates. Population regulation is expected to take place in specific situations in time and space. The current challenge for ecologists is to identify when, where and how it is expressed.

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**EMPIRICAL EVIDENCES OF DENSITY-DEPENDENCE 353**


