

Empirical Evidence of Density-Dependence in Populations of Large Herbivores

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SUMMARY

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 nonlinear 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 -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 -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

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).

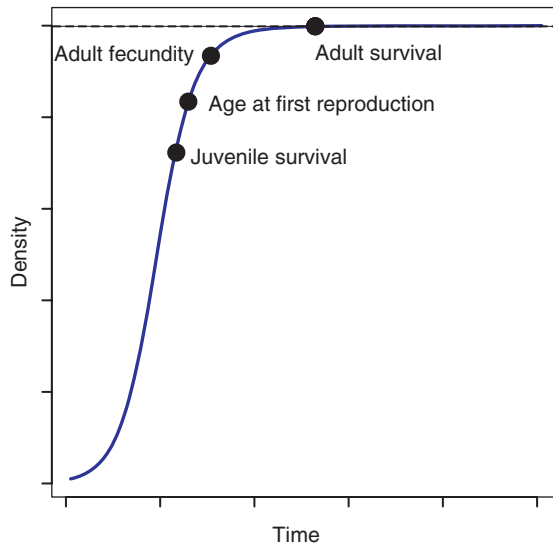


Figure 1 A theoretically increasing population of ungulates that reaches K , the carrying capacity (dashed line), assuming a generalised logistic function ($r_0 = 0.25$, $K = 1$, and $\theta = 3.55$). Points on the line illustrate the sequence of density-dependent responses for an age-structured population 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 1 Studies reporting density-dependent responses in reproduction of large herbivores

Species	Reproduction component	Location	Predator?	References
<i>Alces alces</i>	Young:female ratio	Vefsn (Norway)	No	Solberg <i>et al.</i> (1999)
	Fecundity	Sweden	Yes	Sand (1996)
	Age of primiparity	Newfoundland (Canada)	?	Boer (1992)
	Fecundity			
	Age of primiparity	Alaska (USA)	Yes	Gasaway <i>et al.</i> (1992)
	Twinning rate			
<i>Capreolus capreolus</i>	Age of primiparity	Ontario (Canada)	Yes	Ferguson (2002)
	Number of offspring/females	Storfosna (Norway)	No	Andersen and Linnell (2000)
	Age of primiparity			
	Number of offspring/females	Dourdan (France)	No	Vincent <i>et al.</i> (1995)
	Fertility	Tredozio (Italy)	Yes	Focardi <i>et al.</i> (2002)
	Litter size			
<i>Cervus canadensis</i>	Pregnancy	Trois-Fontaines and Chizé (France)	No	Gaillard <i>et al.</i> (1992)
	Fecundity	Multisite (England)	No	Hewison (1996)
	Fecundity	Yellowstone (USA)	Yes	Gogan and Taper (2002)
<i>Cervus elaphus</i>	Number of offspring/females	Rum Island (Scotland)	No	Coulson <i>et al.</i> (2004a)
	Fecundity (≥ 4 years-old females)			
	Lifetime breeding success			Conrad <i>et al.</i> (1999)
	Fecundity	Norway (whole country)		Langvatn <i>et al.</i> (2004)
	Pregnancy	La Petite Pierre (France)	No	Bonenfant <i>et al.</i> (2002)
<i>Cervus nippon</i>	Age of primiparity			
	Young:female ratio	Nakanoshima Island (Japan)	No	Kaji <i>et al.</i> (1988)

(continued)

Table 1 (continued)

Species	Reproduction component	Location	Predator?	References
<i>Comchoaetes taurinus</i>	Young:female ratio	Serengeti-Mara (Tanzania, Kenya)	Yes	Mduma <i>et al.</i> (1999)
<i>Dama dama</i>	Young:female ratio	Doñanà National Park (Spain)	Yes	Braza <i>et al.</i> (1990)
<i>Diceros bicornis</i>	Age of primiparity	Pilanesberg national Park (South Africa)	Yes	Hrabar and du Toit (2005)
<i>Equus asinus</i>	Age of primiparity Breeding proportion (Over 0.085 animals km ⁻²)	The Victoria river Region (Australia)	No	Choquenot (1991)
<i>Equus caballus</i>	Pregnancy	Assateague Island and Chincoteague (USA)	?	Kirkpatrick and Turner (1991)
	Age of primiparity	Nevada Wild Horse Range (USA)	?	Garrott <i>et al.</i> (1991)
<i>Kobus kob kob</i>	Pregnancy	Comoé National Park (West Africa)	Yes	Fischer and Linsenmair (2002)
<i>Oreamnos americanus</i>	Young: female ratio	Colorado (USA)	Yes	Bailey (1991)
	Age of primiparity	Olympic National Park, Washington (USA)	No	Houston and Stevens (1988)
<i>Ovis aries</i>	Proportion of lactating female			
	Twinning rate			
	Fecundity	St Kilda Archipelago (Scotland)	No	Coulson <i>et al.</i> (2001)
<i>Ovis canadensis</i>	Twinning rate			
	Age of primiparity			
<i>Ovis canadensis</i>	Number of offspring/females	Ram Mountain (Canada)	Yes	Bérubé <i>et al.</i> (1996)

	Young:female ratio	California (USA)	?	Wehausen <i>et al.</i> (1987)
	Age of primiparity	Sheep River and Ram Mountain (Canada)	Yes	Festa-Bianchet <i>et al.</i> (1995)
	Young:female ratio	Lake Mead National Recreation area Nevada (USA)	No	Douglas and Leslie (1986)
<i>Ovis gmelini</i>	Pregnancy	Hungary	?	Náhlík and Takács (1996)
<i>Odocoileus virginianus</i>	Pregnancy	Lower Yellowstone River (USA)	Yes	Dusek <i>et al.</i> (1989)
	Pregnancy	Michigan (USA)	?	Verme (1991)
	Young:female ratio	Lower Yellowstone River (USA)	Yes	Mackie <i>et al.</i> (1990)
	Fecundity	Indiana (USA)	?	Swihart <i>et al.</i> (1998)
<i>Odocoileus hemionus</i>	Young:female ratio	Missouri River, Montana (USA)	?	Hamlin and Mackie (1989)
<i>Rangifer tarandus</i>	Young:female ratio	Hardangervidda (Norway)	No	Skogland (1990)
	Age of primiparity	Hardangervidda (Norway)	No	Skogland (1989)
	Young:female ratio	Svalbard (Norway)	No	Solberg <i>et al.</i> (2001)
	Fertility	Svalbard (Norway)	No	Milner <i>et al.</i> (2003)
	Young:female ratio	George River (Canada)	Yes	Messier <i>et al.</i> (1988)
	Young:female ratio	Lapland (Finland)	Yes	Helle and Kojola (1994)
<i>Saiga tatarica</i>	Fecundity	Betpak-Dala (Kazakhstan)	Yes	Coulson <i>et al.</i> (2000)
	Twinning rate			
<i>Tragelaphus strepsiceros</i>	Young:female ratio	Kruger National Park (South Africa)	Yes	Owen-Smith (1990)

The column labeled “Predator?” reports whether predators both for young and adults are known to occur in the study area.

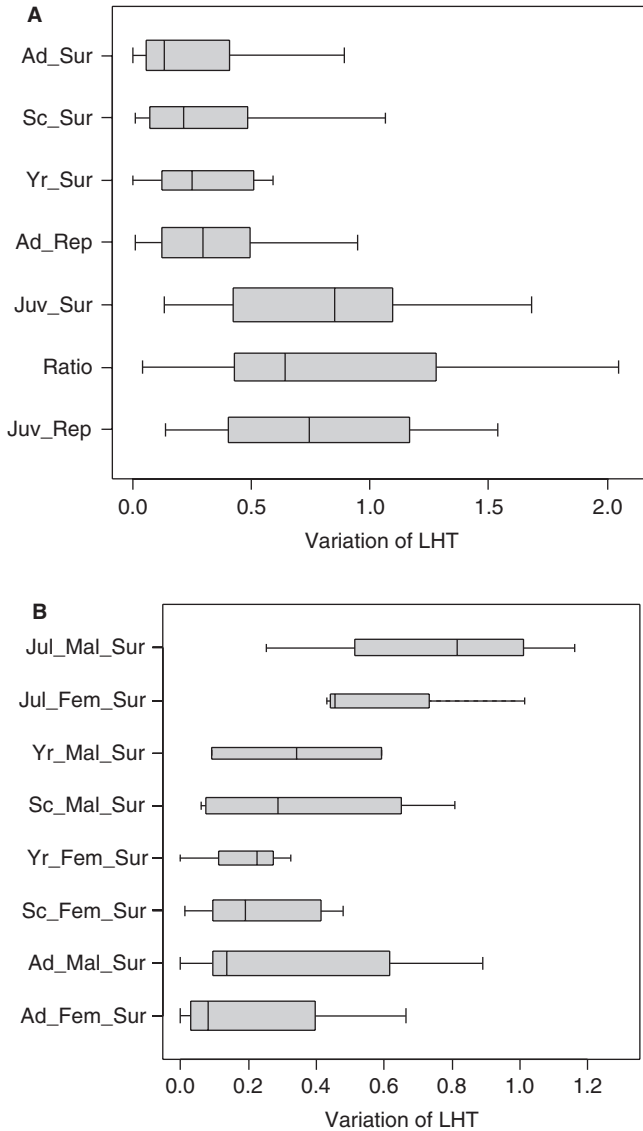


Figure 2 Relative responses of demographic rates to changes in density in large herbivore species. The presented variable is the change of a trait (percentage) divided by the corresponding change in density (percentage). In (A), the boxplot (vertical bar: median; box: range between first and third quartile; 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); saïga 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*): Toïgo *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 (Toïgo *et al.*, 2002). Such a pattern was predicted by Lomnicki'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 2 Studies reporting density-dependent responses of survival in ungulate populations

Species	Survival component	Location	Predator?	References
<i>Aepyceros melampus</i>	Juvenile survival Adult survival	Kruger park, (South Africa)	Yes	Owen-Smith <i>et al.</i> (2005)
<i>Alces alces</i>	Adult survival	Yukon territories (Canada)	Yes	Gasaway <i>et al.</i> (1992)
<i>Antilocapra americana</i>		National Bison Range (USA)	Yes	Byers (1997)
<i>Bos taurus</i>	Survival of all age classes	Chillingham (England)	No	Hall and Hall (1988)
<i>Capreolus capreolus</i>	Summer juvenile survival	Storfosna (Norway)	No	Andersen and Linnell (1998)
<i>Capreolus capreolus</i>	Summer juvenile survival	Tredozio (Italy)	Yes	Focardi <i>et al.</i> (2002)
	Summer juvenile survival	Trois-Fontaines and	No	Gaillard <i>et al.</i> (1993)
	Winter juvenile survival	Chizé (France)		
<i>Cervus canadensis</i>	Adult survival	Yellowstone (USA)	Yes	Gogan and Taper (2002)
	Summer juvenile survival	Yellowstone (USA)	Yes	Coughenour and Singer (1996)
	Winter juvenile survival		Yes	
	Juvenile survival	Rocky mountain National Park (USA)	Yes	Lubow <i>et al.</i> (2002)
<i>Cervus elaphus</i>	Juvenile survival (male)	Rum and Inner	No	Kruuk <i>et al.</i> (1999a)
	Juvenile survival (female)	Hebrides (Scotland)		
	Juvenile survival (male)	La Petite Pierre (France)	No	Bonenfant <i>et al.</i> (2002)
	Winter juvenile survival (female)	Rum Island (Scotland)	No	Coulson <i>et al.</i> (2004)
	Winter juvenile survival (male)			
	Yearling survival (male)			
	Adult survival (female)			
	Adult survival (male)			
<i>Connochaetes taurinus</i>	Dry season juvenile survival	Serengeti	Yes	Mduma <i>et al.</i> (1999)
	Yearling survival	(Tanzania, Kenya)		
	Adult survival			
<i>Equus asinus</i>	Summer juvenile survival	The Victoria river region (Australia)	No	Choquenot (1991)
<i>Equus burchelli</i>	Juvenile survival	Kruger Park	Yes	Owen-Smith <i>et al.</i> (2005)

<i>Giraffa camelopardalis</i>	Adult survival	(South Africa)		
	Juvenile survival	Kruger Park,	Yes	Owen-Smith <i>et al.</i> (2005)
	Adult survival	(South Africa)		
<i>Kobus kob kob</i>	Juvenile survival	Comoé National Park	Yes	Fischer and Linsenmair (2002)
	Yearling males survival	(West Africa)		
<i>Lama guanicoe</i>	Juvenile survival (inverse relationship)	Torres del Paine National Park (Chile)	Yes	Sarno <i>et al.</i> (1999)
<i>Odocoileus hemionus</i>	Winter juvenile survival	Piceance Basin (USA)	Yes	White and Bartmann (1998)
	Juvenile survival	Colorado (USA)	?	White and Bartmann (1998)
	Winter juvenile survival	Colorado (USA)		Bartmann <i>et al.</i> (1992)
<i>Odocoileus virginianus</i>	Summer juvenile survival	Lower Yellowstone River	Yes	Dusek <i>et al.</i> (1989)
	Winter juvenile survival	(USA)		
	Adult survival			
<i>Odocoileus virginianus</i>	Winter juvenile survival Female Adult survival	Bridger mountain Range, Montana (USA)	No	Pac <i>et al.</i> (1991)
<i>Ovis aries</i>	Summer juvenile survival	St Hirta Archipelago	No	Coulson <i>et al.</i> (2001)
	Winter juvenile survival	(Scotland)		
	Yearling survival			
	Adult survival			
	Juvenile survival (female)	St Hirta Archipelago (Scotland)	No	Catchpole <i>et al.</i> (2000)
<i>Ovis canadensis</i>	Juvenile survival (male)			
	Survival (senescent female)			
	Winter juvenile survival	Ram mountain (Canada)	Yes	Portier <i>et al.</i> (1998)
	Adult survival	Ram mountain (Canada)	Yes	Jorgenson <i>et al.</i> (1997)
<i>Rangifer tarandus</i>	Juvenile survival	Lake Mead National Recreation area (Nevada)	No	Douglas and Leslie (1986)
	Winter juvenile survival	Hardangervidda (Norway)	No	Skogland (1990)
	Winter juvenile survival (female)	Svalbard (Norway)	No	Solberg <i>et al.</i> (2001)

(continued)

Table 2 (continued)

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

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.

Box 1**Models of Eberhardt and Lomnicki**

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).

Lomnicki's model is based on the idea that food partitioning among animals is unequal as a result of contest competition for resources (Lomnicki, 1978). Lomnicki'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 Lomnicki'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 Crombrughe, 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 \cdot km⁻² compared to 0% at 1.30 females \cdot 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

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

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 [Sarno *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 (Labonté *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 (Myserud *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; Toïgo 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 Toïgo 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), saïga 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

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)

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

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 owing to a too small sample size.

^dContradictory findings.

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.

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 Crombrughe, 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 (Jorgenson *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 (Bérubé *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

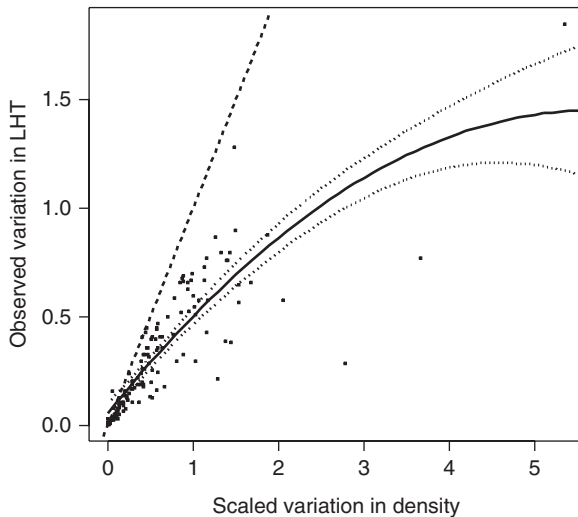


Figure 3 Change in value of life history trait plotted against the change in density for populations of large herbivores ($n = 137$). The scatter plot shows how much demographic parameters are expected to vary (percentage of variation) for a given change of density (percentage of variation). Relative 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: $LHT = 0.330 + 2.724 \times \text{dens} + 0.675 \times \text{dens}^2 + 1.055 \times \text{dens}^3$; $R^2 = 0.821$). 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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