Variable age structure and apparent density dependence in survival of adult ungulates

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Summary

1. Large herbivores have strongly age-structured populations. Because recruitment often decreases as population density increases, in unexploited populations the proportion of older adults may increase with density. Because survival senescence is typical of ungulates, ignoring density-dependent changes in age structure could lead to apparent density-dependence in adult survival.

2. To test for density dependence in adult survival, we used data from three populations that underwent considerable changes in density. Bighorn sheep (*Ovis canadensis*) on Ram Mountain, Alberta, ranged from 94 to 232, mountain goats (*Oreamnos americanus*) on Caw Ridge, Alberta, varied from 81 to 147, and estimates of roe deer (*Capreolus capreolus*) older than 1 year at Chizé, France, ranged from 157 to 569.

3. We used recent developments of capture–mark–recapture modelling to assess the response of adult survival to changes in density when age structure was and was not taken into account.

4. Survival rates were 10–15% higher during the prime-age stage than during the senescent stage for all sex-species combinations. When adults were pooled into a single age class there was an apparent negative effect of density on female survival in bighorns and roe deer, and negative trends for female mountain goats, male roe deer and male bighorn sheep. When age class was taken into account, there were no significant effects of density on adult survival. Except for male mountain goats, the strength of density dependence was lower when age was taken into account.

5. In ungulate populations, age structure is an important determinant of adult survival. Most reports of density dependence in adult survival may have been confounded by changes in age structure.

Key-words: age structure, *Capreolus capreolus*, individual differences, life-history theory, longevity, mark–recapture, *Oreamnos americanus*, *Ovis canadensis*, senescence, survival.

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Introduction

Populations of large herbivorous mammals may include 10–15 reproducing cohorts of females (Gaillard *et al*. 2000a). At high density, most populations show consistent changes in vital rates: primiparity is

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delayed (Jorgenson *et al*. 1993a; Langvatn *et al*. 1996) and juvenile mortality increases (Clutton-Brock *et al*. 1987; Clutton-Brock *et al*. 1996; Gaillard *et al*. 1997; Singer *et al*. 1997; Portier *et al*. 1998). Little is known, however, about the effects of density on adult survival.

Fowler (1987) claimed that nine studies of ungulates reported density dependence in adult female survival. Examination of those studies, however, reveals that they either did not report density dependence specifically for survival of presenescent females (Caughley 1970; Klein & Olson 1960; Grubb 1974; Fowler & Barmore

1979; Hansen 1980; Clutton-Brock, Guinness & Albon 1982; Leader-Williams 1982) or did not account for age or sex differences among adults (Sinclair 1977). Less information is available about changes in adult male survival, but some long-term studies suggest that it may not be strongly density-dependent (Gaillard *et al*. 1993; Clutton-Brock *et al*. 1997a; Jorgenson *et al*. 1997). Clutton-Brock & Lonergan (1994) reported that survival of adult male red deer (*Cervus elaphus* L.) decreased with increasing density, but did not account for possible changes in male age structure.

Whether or not adult ungulates show density-dependent survival is important for two reasons. First, from a theoretical viewpoint, research on ungulate reproductive strategies suggests that females reduce maternal effort when resources are scarce (Albon, Mitchell & Staines 1983; Festa-Bianchet & Jorgenson 1998; Festa-Bianchet, Gaillard & Jorgenson 1998). If adult females allocated resources to maintenance rather than to reproduction when food was scarce, their survival should be density-independent within a certain range of resource availability. Males of dimorphic and polygynous species, on the other hand, adopt a risk-prone reproductive strategy (Clutton-Brock *et al*. 1982; Hogg & Forbes 1997) and may show density dependence in survival, because when resources are scarce they may be unable to recover the energy expended during the rut. Second, from a practical viewpoint, it is important to know whether apparent changes in adult survival at high density (Fowler 1987) are due to density dependence in survival or to changes in age structure. If age structure was mostly responsible for changes in adult survival, increasing density may lower overall 'adult' survival in naturally regulated populations but not in harvested populations, where very few animals reach senescence (Langvatn & Loison 1999). Eberhardt (1985) pointed out that substantial errors in the estimate of 'adult' survival result when senescence is ignored.

Here we analyse capture–mark–recapture (CMR) data for long-term studies of marked roe deer (*Capreolus capreolus* L.) in France and bighorn sheep (*Ovis canadensis* Shaw) and mountain goats (*Oreamnos americanus* de Blainville) in Canada. Bighorns and mountain goats are capital breeders with strong sexual dimorphism (males weigh about 100–110 kg, females 70 kg) (Festa-Bianchet *et al*. 1996; Festa-Bianchet *et al*. 1998; Côté & Festa-Bianchet 2003). Roe deer are income breeders with limited dimorphism (males weigh about 24 kg, females 22 kg) (Andersen *et al*. 2000). Adult roe deer and bighorn sheep have similar age- and sex-specific survival rates (Loison *et al*. 1999) and show positive relationships between individual mass and longevity (Gaillard *et al*. 2000b). In the roe deer and bighorn study populations, density more than doubled during our studies, partly because of experimental changes in management regimes. The mountain goat population almost doubled. We used recent developments of CMR modelling to quantify the potential effects of density
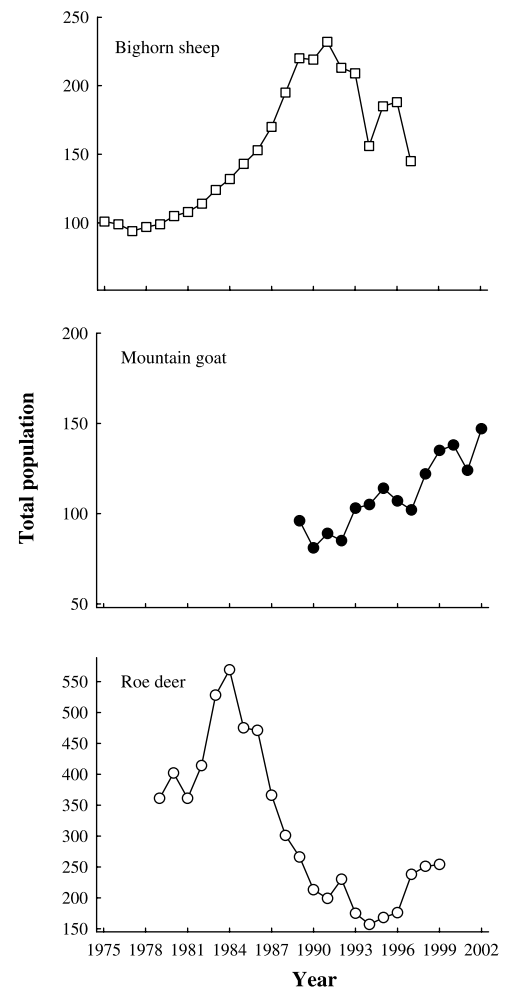
Fig. 1. The total number of bighorn sheep at Ram Mountain, Alberta, and of mountain goats at Caw Ridge, Alberta, and the estimated total population size of roe deer (> 1 years of age in March) at Chizé, France, 1975–2002.

on adult survival when age structure was and was not considered, expecting that density would appear to have a stronger effect if age structure was ignored.

STUDY AREAS AND METHODS

Bighorn sheep survival was monitored at Ram Mountain (52° N, 115° W), Alberta, from 1975 to 1997. We previously used the number of adult ewes to measure population density (see Festa-Bianchet *et al*. 1998). Because most other studies of ungulates report population size as the total number of individuals, however, here we measure density as the total number of sheep in June, after lambing. The number of ewes and the total number of sheep were highly correlated during the 22 years considered here ($r = 0.92$). The number of bighorn sheep in June ranged from 94 to 232 (Fig. 1). All adult ewes were marked, and resighting probability was > 99%. Over 98% of adult rams were marked, and annual resighting probability exceeded 95% (Jorgenson *et al*. 1997). From 1972 to 1980, yearly removals of 12–24% of adult ewes (Jorgenson, Festa-Bianchet & Wishart

1993b) kept the population at 94–105 sheep. After 1980, ewe removals were discontinued and the population increased. Some males aged 4 years and older were shot by hunters (average 2·4 year^{-1}, range 0–6), both during and after the period of ewe removals (Jorgenson *et al.* 1993b). Ages of all individuals were known because they were first captured when 4 years or younger (almost all as lambs or yearlings), when age can be accurately determined from horn annuli (Geist 1966). Potential predators of adult bighorns included cougars (*Puma concolor* L.) and wolves (*Canis lupus* L.). We did not include data collected after 1997 because 11 ewes were removed that year and mortality was affected by a subsequent substantial increase in cougar predation (Ross, Jalkotzy & Festa-Bianchet 1997).

Mountain goats were monitored at Caw Ridge (54° N, 119° W), Alberta, from 1989 to 2002. The number of goats in June, after the annual birth pulse, ranged from 81 to 147. Goats were captured in traps and marked with ear tags or canvas collars. The proportion of marked adults increased from 31% to 94% over the study, and was over 70% after 1990. We knew the exact age of all goats born after 1987. For goats first caught as adults, age was determined by the number of horn annuli, a technique reliable up to about 7 years (Côté, Festa-Bianchet & Smith 1998). Individuals included in analyses were aged 6 years or less when first caught. Resighting probability exceeded 98% in males and 99% in females. Mountain goats were preyed upon by cougars, wolves and grizzly bears (*Ursus arctos* L.) (Festa-Bianchet, Urquhart & Smith 1994).

Roe deer were studied at Chizé (46° N, 0° E), France, from 1978 to 1999. The population is in a 26-km^2 enclosure and about 70% of the adults are marked. Each year, about 50% of adults are captured with drive nets and some unmarked deer are removed for release elsewhere in France (Gaillard *et al.* 1993). Ages of almost all marked roe deer born since 1978 were known because they were caught as fawns, but in the first few years of the study several deer were marked as adults and their exact age was not known. Changes in the number of deer removed led to population estimates varying from 157 to 569 deer older than 1 year in March (excluding fawns born the previous year) (Gaillard *et al.* 1993). There were no predators of adult roe deer.

Because roe deer can accurately be aged only if first caught as fawns, we had no known-age deer older than 6 in 1984, when density peaked (Fig. 1). To test for density dependence without accounting for age structure (see below) we therefore examined the survival of all adult roe deer captured during the first 3 years of monitoring (1978–80).

Based on earlier results (Loison *et al.* 1999), we considered three age classes for roe deer and bighorn sheep: yearling (survival from 1 to 2 years), prime-aged (2–7 years), and senescent adults (8 years and older). For mountain goats, we considered a separate class of animals aged 2 and 3 years, the age of all known emigrants. No 2-year-old and only 4% of 3-year-old females produced kids (Coté & Festa-Bianchet 2001). We considered goats aged 4–9 years as 'prime-aged', so that 'prime-age' lasted 6 years for all species. In addition, for female goats survival senescence appeared to begin about 2 years later than for the other species. Senescent mountain goats were therefore aged 10 years and older. Similarly to our previous work, the sexes were analysed separately for each species.

We analysed our data with recent developments of capture–mark–recapture techniques. We first fitted a time-dependent model, the so-called Cormack–Jolly Seber (CJS) model (Lebreton *et al.* 1992). To test whether our data sets met all the assumptions of the CJS model, we used the program U-CARE (Choquet *et al.* 2001), which examines homogeneity of recapture probabilities independent of capture order, and looks for possible differences in recapture probabilities independent of survival.

All animals that died because of hunting or accidents, or were removed, were excluded from our sample in the year of their death or removal. Emigration was impossible at Chizé because of the perimeter fence, and extremely rare at Ram Mountain (Jorgenson *et al.* 1997; Loison *et al.* 1999). Some young goats of both sexes emigrated from Caw Ridge (Coté & Festa-Bianchet 2003). To assess how age structure of bighorn and mountain goat females varied according to density, we compared the proportion of prime-aged females to total population size each year using logistic regression.

Model notations and biological meanings are summarized in Table 1. To model the effects of density

Table 1. Notations used for models tested to describe the survival of adult bighorn sheep at Ram Mountain, Alberta, mountain goats at Caw Ridge, Alberta, and roe deer at Chizé, France, and their biological meaning

Model notation	Explanation and biological meaning
DD	Density dependence: linear relationship between survival on a logit scale and population size each year
Age	Two age classes taken into account for adult survival (prime-age and senescent)
No age	All adults (2 years and older for both bighorns and roe deer, 4 years and older for mountain goats) pooled into a single class
Sa	Adult survival (2 years and older for bighorn and roe deer, 4 years and older for mountain goats)
Sy	Yearling survival
Spa	Survival of prime-aged adults (2–7 years for bighorn and roe deer, 4–9 years for mountain goats)
SS	Survival of senescent adults (bighorns and roe deer aged 8 and older, mountain goats aged 10 and older)
S23	Survival of mountain goats aged 2 or 3 years

dependence and age structure on survival we first did not account for age structure and fitted a simple model with constant survival. Then, we investigated density dependence by fitting a linear relationship between the survival estimate for each year for all adults combined and population density on a logit scale. For the roe deer analysis, this first step included only adults marked between 1978 and 1980, whose exact age was unknown. In a second step, we took into account two adult age classes, estimated survival separately for each age class, then looked for density dependence in each class. The second step included all years of monitoring but excluded animals first caught as adults (and therefore of unknown age) at the beginning of the study. Recapture probabilities for bighorns and mountain goats were very high (> 0·95) and did not vary among years. For roe deer, recapture probabilities varied during two phases of the study, and therefore two levels of capture probabilities were included as parameters in all models (see Gaillard *et al.* 1993 and Loison *et al.* 1999 for further details).

We used the Akaike Information Criterion (AIC) to select the most parsimonious model (Burnham & Anderson 1992) at each stage of the analysis. Because both steps of the analysis involved the same data set for bighorn sheep and mountain goats but not for roe deer, we could select a general model for the entire analysis only for the first two species. The AIC is calculated as the deviance (–2 Ln(L) where L is the likelihood function) plus twice the number of free parameters in the model. The selected models are those with the lowest AIC. Because all models had less than eight parameters, we had a high information : parameter ratio (> 40). We therefore used AIC instead of AICc (Burnham & Anderson 1998). Models that differ in AIC by less than 2 units cannot be clearly distinguished, therefore in that case we selected the simplest model, as recommended by Burnham & Anderson (1998). To test specific hypotheses among nested models, we also used classical Likelihood-Ratio-Tests. For CMR modelling we used the program SURGE (Lebreton *et al.* 1992; see http://www.phidot.org/software/surge/guide/html for details about the most recent version). It is important to note that regressions were fitted within the procedure of estimation, and not *a posteriori* on CMR estimates. Thus we fitted a series of CMR models in which survival was consistently logit-transformed (to avoid possible estimates over 1, as recommended by Lebreton *et al.* 1992) and was either constant, age-dependent, or constrained to a logistic linear relationship with population density (Clobert & Lebreton 1985).

Results

BIGHORN SHEEP

The Cormack–Jolly Seber model satisfactorily fitted the survival–recapture data of bighorn sheep of both sexes ($\chi^2 = 21\cdot92$, d.f. = 38, $P = 0\cdot98$ for males; $\chi^2 = 24\cdot08$, d.f. = 22, $P = 0\cdot34$ for females). The proportion of 'prime-aged' ewes decreased from 84·5% of all adult ewes when the population included 100 sheep to 70·4% when it doubled to 200 sheep (Logistic regression, $2\cdot53 - 0\cdot00832$(N sheep), $\chi^2 = 31\cdot58$, d.f. = 1, $P < 0\cdot0001$, $r^2 = 0\cdot65$) (Fig. 2a).

When all ewes 2 years of age and older were pooled, mean adult survival was 0·91, with a negative effect of density (models 1 vs. 2, $\chi^2 = 4\cdot49$, d.f. = 1, $P = 0\cdot034$, Table 1 and Fig. 3). When age structure was accounted for, however, the trend for density dependence in survival was negative and not significant for prime-aged ewes (models 3 vs. 4: $\chi^2 = 2\cdot28$, d.f. = 1, $P = 0\cdot13$) and positive and not significant for senescent ewes (models 3 vs. 5: $\chi^2 = 0\cdot94$, d.f. = 1, $P = 0\cdot33$, Table 2).

The mean adult survival of adult rams was 0·85. When age differences were ignored, ram survival tended to decline with increasing density (models 1 vs. 2: $\chi^2 = 2\cdot18$, d.f. = 1, $P = 0\cdot14$, Table 3). When age classes were taken into consideration, the negative trend remained but it was not significant for either prime-aged males (models 3 vs. 4: $\chi^2 = 1\cdot67$, d.f. = 1, $P = 0\cdot20$, Table 3) or senescent males (models 3 vs. 5: $\chi^2 = 0\cdot73$, d.f. = 1, $P = 0\cdot39$, Table 3.

MOUNTAIN GOATS

The Cormack-Jolly Seber model satisfactorily fitted the survival-recapture data of mountain goats of both sexes ($\chi^2 = 8\cdot42$, d.f. = 14, $P = 0\cdot87$ for males; $\chi^2 = 12\cdot32$, d.f. = 14, $P = 0\cdot58$ for females). The mean survival of females aged 4 years and older was 0·92 (Table 4). There was no effect of density on adult female survival, whether age structure was accounted for (models 3 vs. 4: $\chi^2 = 0\cdot04$, d.f. = 1, $P = 0\cdot85$ for prime-age, models 3 vs. 5: $\chi^2 = 0\cdot06$, d.f. = 1, $P = 0\cdot81$ for senescents) or not (models 1 vs. 2: $\chi^2 = 0\cdot96$, d.f. = 1, $P = 0\cdot33$) (Table 4). The non-significant trend for density dependence, however, was stronger when age structure was ignored (Table 4).

Mean survival of mountain goat males was 0·86 and appeared independent of density (Table 5). When age structure was ignored, there was a very weak non-significant trend for positive density dependence (Table 5: models 1 vs. 2: $\chi^2 = 0\cdot10$, d.f. = 1, $P = 0\cdot75$) and when we recognized two adult age classes the non-significant density-dependent trend was negative (models 3 vs. 4: $\chi^2 = 0\cdot04$, d.f. = 1, $P = 0\cdot85$ for prime age, models 3 vs. 5: $\chi^2 = 0\cdot16$, d.f. = 1, $P = 0\cdot69$ for senescents, Table 5.

Similarly to what we found for bighorn ewes, the proportion of 'prime-aged' female goats (aged 4–9 years) decreased with increasing density, from 79% of all adult females when the population included 85 goats to 59% when it increased to 140 (Logistic regression, $2\cdot75 - 0\cdot017$ (N goats), $\chi^2 = 5\cdot07$, d.f. = 1, $P = 0\cdot024$, $r^2 = 0\cdot31$) (Fig. 1b). Years before 1992 were not included because the proportion of marked females was less than 85%.
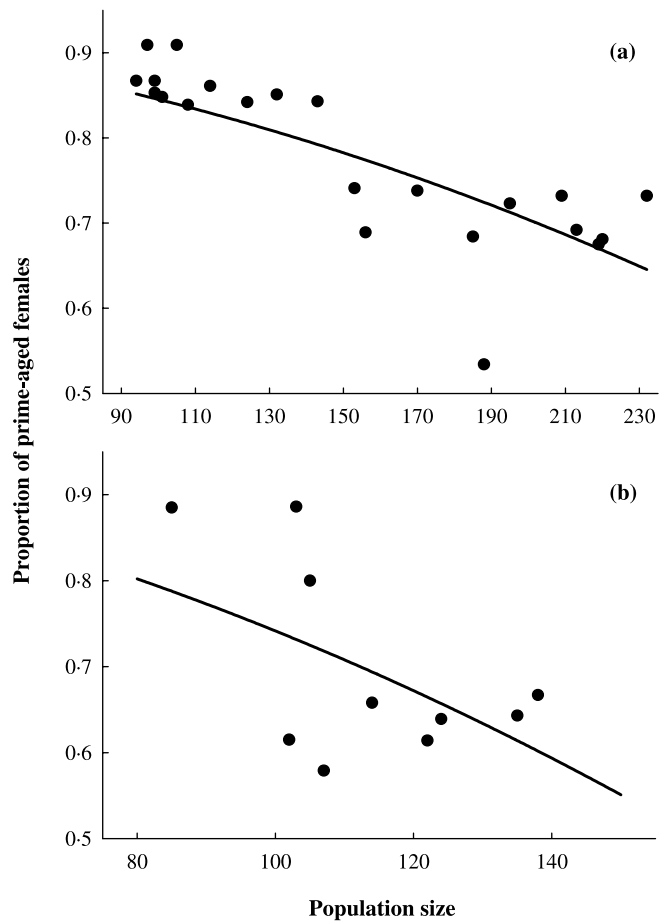
Fig. 2. (a) The proportion of bighorn ewes aged 2–7 years compared to the total population size at Ram Mountain, Alberta. (b) The proportion of female mountain goats aged 4–9 years compared to the total population size at Caw Ridge, Alberta. Line indicates the fitted logistic regressions.
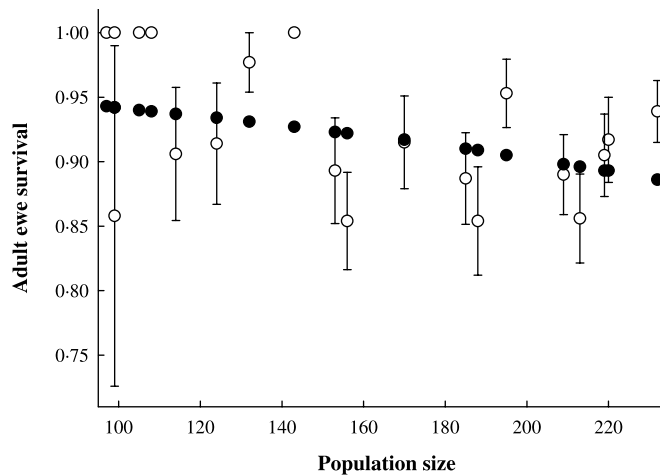

Fig. 3. Survival (± SE) of adult bighorn ewes (all ages pooled) at Ram Mountain, Alberta, compared with the total number of adult ewes in the population in June each year, 1975–97. Open circles (○) indicate actual survival, closed circles (●) the survival predicted by a model assuming linear density dependence of ewe survival. The yearly sample of adult ewes ranged from 30 to 103, and averaged 60.

ROE DEER

The Cormack–Jolly Seber model fitted satisfactorily the CMR data of roe deer marked as adults, both males ($\chi^2 = 15\cdot19$, d.f. = 14, $P = 0\cdot36$) and females ($\chi^2 = 33\cdot12$, d.f. = 31, $P = 0\cdot32$). The same model also provided an adequate fit for the CMR data for males of known age ($\chi^2 = 81\cdot97$, d.f. = 76, $P = 0\cdot30$). The data for female roe deer of known age, however, were poorly fitted by this model ($\chi^2 = 99\cdot65$, d.f. = 76, $P = 0\cdot036$).

Table 2. Model selection for survival of adult bighorn ewes at Ram Mountain, Alberta. The selected model is shown in bold. Symbols are explained in Table 1. 95% CI: 95% confidence intervals of slope and survival estimates

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	3	995·03		Sy = 0·813 (0·760, 0·857) Sa = 0·911 (0·893, 0·926)
2 No age, DD	4	992·54	−0·00554 (−0·011, −0·00029)	Sa from 0·944 to 0·886
3 Age, no DD	**4**	**964·88**		**Sy = 0·813 (0·760, 0·857) Spa = 0·940 (0·922, 0·954) SS = 0·821 (0·771, 0·862)**
4 Spa DD	5	964·61	−0·00508 (−0·012, 0·0016)	Spa from 0·960 to 0·922
5 SS DD	5	965·95	+0·00547 (−0·0055, 0·016)	SS from 0·748 to 0·850
6 Spa & SS DD	6	965·67		

Table 3. Model selection for survival of adult bighorn rams at Ram Mountain, Alberta. The selected model is shown in bold. Symbols are explained in Tables 1 and 2

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	**3**	**1003·53**		Sy = 0·837 (0·781, 0·881) Sa = 0·846 (0·816, 0·871)
2 No age, DD	4	1003·35	−0·0037 (−0·0087, 0·0013)	Sa from 0·882 to 0·818
3 Age, no DD	4	1003·84		Sy = 0·837 (0·781, 0·881) Spa = 0·850 (0·820, 0·876) SS = 0·752 (0·561, 0·878)
4 Spa DD	5	1004·17	−0·0033 (−0·0084, 0·0018)	Spa from 0·882 to 0·826
5 SS DD	5	1005·11	−0·0156 (−0·0534, 0·0222)	SS from 0·913 to 0·623
6 Spa & SS DD	6	1005·46		

Table 4. Model selection for survival of adult mountain goat females at Caw Ridge, Alberta. The selected model is shown in bold. Symbols are explained in Tables 1 and 2

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	4	358·82		Sy = 0·844 (0·739, 0·911) S23 = 0·913 (0·850, 0·952) Sa = 0·923 (0·889, 0·946)
2 No age, DD	5	359·86	−0·0118 (−0·0357, 0·0121)	Sa from 0·947 to 0·901
3 Age, no DD	**5**	**348·06**		Sy = 0·844 (0·739, 0·911) S23 = 0·913 (0·850, 0·952) Spa = 0·952 (0·919, 0·972) SS = 0·816 (0·713, 0·888)
4 Spa DD	6	350·02	−0·0031 (−0·0357, 0·0295)	Spa from 0·956 to 0·948
5 SS DD	6	350·00	+0·0057 (−0·0394, 0·0507)	SS from 0·799 to 0·830
6 Spa & SS DD	7	351·96		

Table 5. Model selection for survival of adult mountain goat males at Caw Ridge, Alberta. The selected model is shown in bold. Symbols are explained in Tables 1 and 2

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	**4**	**311·61**		Sy = 0·745 (0·621, 0·838) S23 = 0·753 (0·659, 0·828) Sa = 0·858 (0·784, 0·910)
2 No age, DD	5	313·51	+0·0046 (−0·0336, 0·0243)	Sa from 0·843 to 0·875
3 Age, no DD	5	313·31		Sy = 0·745 (0·621, 0·838) S23 = 0·753 (0·659, 0·828) Spa = 0·864 (0·786, 0·916) SS = 0·797 (0·454, 0·949)
4 Spa DD	6	315·28	−0·0025 (−0·0327, 0·0276)	Spa from 0·873 to 0·856
5 SS DD	6	315·15	−0·0275 (−0·165, 0·111)	SS from 0·867 to 0·707
6 Spa & SS DD	7	317·13		

Table 6. Model selection for the survival of adult roe deer does at Chizé, France. The selected models are shown in bold. Models 1 and 2 include only adults marked in the first 3 years of the study whose exact age was unknown, and cannot be compared with models 3–10 that are based on known-age animals (see text for more details). Symbols are explained in Tables 1 and 2

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	3	400·60		Sa = 0·866 (0·816, 0·904)
2 No age, DD	**4**	**390·98**	−0·0087 (−0·0159, −0·00154)	Sa from 0·983 to 0·607
3 Age, no DD	**5**	**1979·99**		Sy = 0·798 (0·726, 0·854)
				Spa = 0·954 (0·929, 0·971)
				SS = 0·861 (0·813, 0·899)
4 Spa DD	6	1981·31	+0·0016 (−0·0023, 0·0054)	Spa from 0·941 to 0·968
5 SS DD	6	1981·99	−0·00022 (−0·0065, 0·0061)	SS from 0·863 to 0·855
6 Spa & SS DD	7	1983·25		

Table 7. Model selection for the survival of adult roe deer bucks at Chizé, France. The selected models are shown in bold. Models 1 and 2 include only adults marked in the first 3 years of the study whose exact age was unknown, and cannot be compared with models 3–10 that are based on known-age animals (see text for more details). Symbols are explained in Tables 1 and 2

Model	Parameters	AIC	Slope (95% CI)	Survival (95% CI)
1 No age, no DD	**3**	**377·69**		**0·837 (0·816, 0·904)**
2 No age, DD	4	379·55	−0·0014 (−0·0083, 0·0056)	Sa from 0·880 to 0·807
3 Age, no DD	**5**	**1525·87**		**Sy = 0·817 (0·733, 0·879)**
				Spa = 0·880 (0·843, 0·909)
				SS = 0·762 (0·662, 0·840)
4 Spa DD	6	1526·84	−0·0012 (−0·0034, 0·0011)	Spa from 0·898 to 0·845
5 SS DD	6	1527·85	+0·00061 (−0·0097, 0·0109)	SS from 0·755 to 0·788
6 Spa & SS DD	7	1528·76		

The poor fit was due to the test 2.CL ($\chi^2 = 33·61$, d.f. = 18, $P = 0·014$), because all other tests led to an acceptable fit ($\chi^2 = 17·01$, d.f. = 20, $P = 0·65$, $\chi^2 = 28·48$, d.f. = 19, $P = 0·075$, and $\chi^2 = 20·55$, d.f. = 19, $P = 0·36$ for test 3.SR, test 3.Sm and test 2.CT, respectively). A poor fit of test 2.CL indicates a problem with heterogeneity in recapture independent of survival. Because there is currently no simple interpretation of failure of this test to fit the data (Choquet *et al.* 2001), we ignored results from this test in subsequent analyses.

The mean adult survival of roe deer females was 0·87 and declined markedly with increasing density when all age classes were pooled (models 1 vs. 2: $\chi^2 = 11·62$, d.f. = 1, $P = 0·001$, Table 6). All density-dependent relationships disappeared when age structure was accounted for (models 3 vs. 4: $\chi^2 = 0·68$, d.f. = 1, $P = 0·41$ for prime age, models 3 vs. 5: $\chi^2 = 0·01$, d.f. = 1, $P = 0·944$ for senescent does, Table 6).

The mean survival of adult male roe deer was 0·84 and density independent regardless of whether age classes were ignored (models 1 vs. 2 : $\chi^2 = 0·14$, d.f. = 1, $P = 0·71$, Table 7), or taken into account (models 3 vs. 4: $\chi^2 = 1·03$, d.f. = 1, $P = 0·31$ for prime age, models 3 vs. 5: $\chi^2 = 0·02$, d.f. = 1, $P = 0·90$ for senescent, Table 7). The non-significant trend relating survival to density was negative for all ages pooled and for prime-aged males, but positive for senescent males. The negative trend for density dependence in survival of prime-age males was less marked than that found in the survival of all males older than 2 years of age.

Discussion

Our results confirm our prediction that changes in ungulate population density affect age structure and may lead to spurious negative density dependence in survival of adult females. In five of six sex-species combinations, the negative slope relating adult survival to population density was steeper when age structure was ignored than when senescent adults were considered separately from prime-aged ones. Only for mountain goats males (for which we had the smallest sample size, especially for senescent males) we found the reverse trend. For roe deer does and bighorn ewes the apparent negative effect of density on adult survival when age structure was ignored was significant.

Density dependence in age structure was expected because as ungulate populations increase in density they typically show high juvenile mortality and lower fecundity (Gaillard, Festa-Bianchet & Yoccoz 1998a; Gaillard *et al.* 2000a), leading to an increase in the average age of adult females. Cohorts of adult females born at intermediate density may be larger than cohorts born at high density, when juvenile production, juvenile survival and yearling survival decrease (Clutton-Brock *et al.* 1997a; Gaillard *et al.* 1993; Jorgenson *et al.* 1997; Coulson, Milner-Gulland & Clutton-Brock 2000). In our study populations of bighorn sheep and mountain goats, the proportion of senescent females increased with density. Because survival decreases with age for ewes older than 7 years (Loison *et al.* 1999) and female goats older than 9 (this study),

the increasing average age of females led to an increase in pooled 'adult' mortality. The apparent density-dependent increase in adult female mortality (significant for ewes and a negative trend with a slope 3·8 times steeper than when accounting for age structure for female goats) was due to changes in age structure. Age-specific survival was much less dependent on density, approaching significance only for bighorn ewes. Similarly, the survival of prime-age and senescent female roe deer at Chizé was not density-dependent, but adult female survival appeared to be strongly density-dependent if age structure was ignored.

A recent review of ungulate population dynamics suggested that the survival of 'prime-aged' adult females is typically high and varies little from year to year, whereas juvenile survival is highly variable (Gaillard *et al*. 2000a). Our analysis of detailed long-term data on adult female survival in three populations in widely different environments confirms that general pattern.

We also found no evidence for density dependence in survival of older adult females. That result is somewhat surprising because senescent females suffer a decrease in the probability of survival. Old bighorn ewes (Bérubé, Festa-Bianchet & Jorgenson 1999) and roe deer does (Gaillard *et al*. 1998b) also experience declines in the ability to reproduce and in body mass. Consequently, we expected that senescent females would be affected by the decrease in resource availability that accompanies high population density. In feral sheep, the survival of older ewes decreased at high density, whereas the survival of prime-aged ewes was density-independent (Coulson *et al*. 2001). Adult females may adjust their acquisition and allocation of resources to their availability, possibly by changing their foraging behaviour (Ruckstuhl & Festa-Bianchet 1998), but more likely by curtailing reproduction when resources are scarce (Festa-Bianchet & Jorgenson 1998). We have no evidence, however, that older females reduce their reproductive effort more than prime-aged females as density increases. In addition, only high-quality individuals survive to old age for both bighorn sheep and roe deer (Bérubé *et al*. 1999; Gaillard *et al*. 2000b). Although they suffer a decrease in survival, older females are phenotypically above-average individuals and may be resistant to resource shortages at high density (Vaupel & Yashin 1985; Carnes & Olshansky 2001).

The age structure of bighorn rams was independent of population density, possibly because hunting continued throughout the study. Rams younger than 4 years do not suffer hunting mortality (Jorgenson, Festa-Bianchet & Wishart 1998). We had expected that the survival of adult males would be density-dependent, but none of the trends we found were significant. Male survival did tend to decrease with increasing density for bighorn sheep and roe deer, both when age structure was ignored and when it was accounted for. Similarly to the patterns observed for females, however, the trend for density dependence of male survival in both species was steeper, although not significant, when age structure was ignored. Adult male survival is density-independent in feral sheep (Coulson *et al*. 2001). In temperate ungulates, adult males are thought to suffer high winter mortality because of energy expenditure during the rut (Geist 1971; Clutton-Brock *et al*. 1982), but there is little evidence directly linking individual reproductive effort to mortality. In fallow deer (*Dama dama* L.) and elephant seals (*Mirounga angustirostris* Gill), male survival is positively correlated with reproductive success, suggesting that breeding males are in very good condition (Clinton & LeBoeuf 1993; McElligott, Altwegg & Hayden 2002). Possibly, males vary their reproductive effort according to resource availability. Yoccoz *et al*. (2002) reported that red deer males decreased their reproductive effort, measured by mass loss during the rut, at high density. In addition, as density increases the adult sex ratio in ungulate populations typically favours females, possibly lowering the level of male-male competition for mates (Clutton-Brock, Rose & Guinness 1997b; Jorgenson *et al*. 1998). Our results do not support a common assumption of wildlife management, that adult male mortality increases markedly with population density (Clutton-Brock & Lonergan 1994).

We found that age-specific adult mortality is mostly independent of population density, but overall 'adult' mortality is sensitive to age structure. Low-density remnant populations with low reproductive rates may include many old animals and therefore show high 'adult' mortality. Changes in population density may have smaller effects on overall adult survival (ignoring age structure) in harvested populations than in natural populations of long-lived, iteroparous animals. Harvested populations include a much smaller proportion of old animals than naturally regulated populations (Langvatn & Loison 1999), and the proportion of senescent animals may not increase with density. Bighorn males were lightly hunted during our study and their age structure did not vary substantially with population density.

Our results and a recent review of the literature suggest that survival of prime-aged ungulates is typically density-independent. Elasticity analyses, however, clearly indicate that any changes in the survival of 'prime-aged' females would have drastic effects on population growth rate (Gaillard *et al*. 2000a). Given that yearly survival of prime-aged female ungulates is typically over 90–95% (Gaillard *et al*. 2000a), it cannot increase much, but it could decline substantially, with a devastating impact on population growth (Schaefer *et al*. 1999). There is now evidence that even after accounting for age structure the survival of adult female red deer on Rum is density-dependent (T. Coulson, pers. comm.) and we found a near-significant effect of density on the survival of prime-aged bighorn ewes. In both cases, doubling or tripling of population density was associated with a decrease in survival of less than 4%. Attempts to test for density effects on the

survival of prime-aged females generally have low statistical power, because of the very high average survival of this age class (Gaillard *et al.* 1998a).

Drastic declines are sometimes reported in some populations of large herbivores, particularly in arid or arctic environments, on islands, or following epizootics of exotic diseases. Those declines are difficult to account for without assuming some changes in the mortality of prime-aged females. Examples may include the 80% overwinter mortality of moose (*Alces alces* L.) in Isle Royale in 1996 (Peterson 1999), or the dramatic climate-induced fluctuations of macropods and possibly high-arctic caribou (*Rangifer tarandus* L.) (Caughley & Gunn 1993). None of those studies, however, monitored marked, known-age individuals. Two of our study areas had full complements of large predators, but predation did not appear to be density-dependent. Density-dependent predation on adults would probably lead to changes in age-specific survival.

Acknowledgements

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