

Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic

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Summary

1. Age-specific survival of 215 males and 117 females of the highly sexually dimorphic Alpine ibex *Capra ibex* (L.) was assessed from a 21-year capture–mark–recapture (CMR) programme (1983–2004). The study covered two contrasted periods of population performance (high performance from 1983 to 1997 vs. low performance from 1998 onwards).

2. Based on current life-history theories for sexually dimorphic species, we expected that survival should decrease with age in both sexes, female survival should be buffered against environmental variations, male survival should decrease during the low performance period, and adult survival should be lower in males than females during the low performance period.

3. Survival of both sexes was strongly affected by age, with the four age classes (yearling, prime-aged adults of 2–8 years of age, old adults of 8–13 years of age, and senescent adults from 13 years of age onwards) generally reported for large herbivores.

4. Survival of females at all ages, and of yearling and prime-aged males, was buffered against environmental variations and was the same during periods of high and low population performance. The survival of old males decreased in years of low population performance.

5. All marked yearlings (32 females, 56 males) survived to age 2. Survival of prime-aged females (0.996 ± 0.011) was higher than for other large herbivores, but similarly to other large herbivore species, it declined slowly and regularly with increasing age afterwards. Male survival was 5–15% higher each year than that of males of other large herbivores. Males enjoyed very high survival when prime-aged (0.981 ± 0.009) and as old adults (high-performance period: 0.965 ± 0.028 , low-performance period: 0.847 ± 0.032).

6. The very high survival of males, coupled with their prolonged mass gain, suggests a highly conservative reproductive tactic. Male ibex differ from similar-sized herbivores by showing a nearly indeterminate growth in horn size and body mass. By surviving to an advanced age, males may enjoy high reproductive success because of their large size.

Key-words: actuarial senescence, environmental conditions, mountain ungulate, sexual dimorphism, sexual selection.

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Introduction

Adult survival patterns play a major role in shaping both the life-history strategies and the population dynamics of large vertebrates (Partridge & Harvey 1988; Gaillard *et al.* 1989; Promislow & Harvey 1990; Gaillard &

Yoccoz 2003), because their population growth rate is much more sensitive to adult survival than to any other demographic rate (Gaillard *et al.* 2000; Coulson, Gaillard & Festa-Bianchet 2005). Assessing yearly variation in survival and identifying the causes of that variation is therefore of great interest for both fundamental and applied viewpoints. Previous studies of large mammals reported that changes in sex and age structure account for most temporal variation in adult survival within a population (Ricklefs 1998; Festa-Bianchet, Gaillard & Côté 2003).

Actuarial senescence (the increase of mortality rate with age; McDonald, Fitzpatrick & Woolfenden 1996) results from the decline in physiological functions with ageing, and is expected in any age-structured population because selective pressures should decline as age increases (Hamilton 1966). Several empirical studies have recently provided evidence of actuarial senescence in free-ranging large mammals (Gaillard *et al.* 2003) and birds (Bennett & Owens 2002). Three main age-specific stages are commonly recognized in mammalian survival (Caughley 1966): a juvenile stage with low and variable survival, a prime-age adult stage when survival peaks and is resilient to environmental conditions, and a senescent stage when survival decreases (see Gaillard *et al.* 2000 for large herbivores). Recently, theoretical models supposing a continuous decrease of survival with age have found support in empirical studies (Ricklefs & Scheuerlein 2001; Gaillard *et al.* 2004). Among them, the Gompertz model has received most attention and support (Gaillard *et al.* 2004 for large herbivores).

In large iteroparous and sexually dimorphic species, males and females show contrasted life-history tactics, and male survival is typically lower than female survival at all ages (Clutton-Brock, Guinness & Albon 1982 on red deer *Cervus elaphus* L.; Jorgenson *et al.* 1997 on bighorn sheep *Ovis canadensis* Shaw; Modafferi and Becker 1997 on moose *Alces alces* L.). Sex differences in survival are usually attributed to male–male competition during the rut and to higher susceptibility of males to nutritional stress and predation, often linked to the energetic requirements of large body size (Darwin 1871; Clutton-Brock *et al.* 1982). A comparative analysis of adult survival rates in large herbivores, however, showed that males survive less than females only under poor environmental conditions (Toïgo & Gaillard 2003). Females may restrain their reproductive effort in a given year to favour their own survival (Gaillard & Yoccoz 2003; see Festa-Bianchet & Jorgenson 1998 for empirical evidence on bighorn sheep). Consequently, female prime-age survival and senescence rate should remain constant over a range of environmental conditions, and most evidence supports this expectation (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000). On the contrary, males of polygynous species should allocate much of their resources to mating attempts even when food availability is low (Clutton-Brock *et al.* 1982; Hogg & Forbes

1997). The prime-age survival of males should thus decrease, and the senescence rate increase, when environmental conditions deteriorate (Coulson *et al.* 2001 on Soay sheep *Ovis aries* L.; Bonenfant *et al.* 2002 on red deer).

We assessed survival patterns of Alpine ibex *Capra ibex* L. over two contrasted periods of population performance through long-term monitoring of marked individuals, using capture–mark–recapture (CMR) methods. In the first period, the ibex population increased exponentially following its reintroduction to unoccupied habitat, and experienced very good environmental conditions (Toïgo, Gaillard & Michallet 1996; Toïgo *et al.* 2002). In the second period, environmental conditions deteriorated, most likely in response to increased population size, leading to a decrease of ibex performance in several life-history traits (Michallet & Toïgo 2004).

We tested the following predictions:

1. Senescence in survival should occur in both sexes.
2. Actuarial senescence should be better described by the Gompertz model than by a discontinuous age class model in both sexes.
3. According to current theories of life-history variation in highly sexually dimorphic species (Toïgo & Gaillard 2003) (a) survival of prime-age males and females should be similar under good environmental conditions, whereas prime-age survival should be higher for females than for males under harsh conditions, and (b) the age-specific survival of males should be lower in harsh than in good conditions, whereas in females age-specific survival should be independent of environmental conditions.

Material and methods

Alpine ibex survival was monitored for 21 years (1983–2004) in the Belledonne-7-Laux Reserve (Isère, France) managed by the Office National de la Chasse et de la Faune Sauvage. The population was founded in 1983 with 20 ibex from Mont-Pleureur (Switzerland). Ibex were captured and ear-tagged each spring, using tele-anaesthesia, cage traps or leg-hold snares, all methods approved by the French Environment Ministry. Age at capture could be easily determined by counting horn annuli, that form every year and are readily visible (Michallet, Grand & Bonardi 1988).

The population was intensively monitored each year between May and August, when the study area was regularly surveyed on foot, with an effort to identify marked individuals. We used re-sightings to estimate adult survival using CMR methods. Between 1983 and 2004, 117 females (aged 1–13 years at capture) and 215 males (aged 1–12 years at capture) were marked and monitored (see Appendix S1, Supplementary material).

From 1983 to 1994 demographic rates were typical of colonizing populations. The natural rate of increase (λ) of 1.28 (Toïgo *et al.* 1996) was near the maximum expected for monotocous species (Gaillard *et al.* 2000).

Females showed neither a reproductive cost nor individual heterogeneity in reproductive success (Toïgo *et al.* 2002). Primiparity was at 2 years and most females reproduced every year (Toïgo 1998). Such a covariation of life-history traits is typical of high-performance individuals in good environmental conditions.

After 1997, the lower individual performance of ibex compared with previous years suggested that environmental conditions had deteriorated. We suspect that density-dependent responses occurred in several life-history traits. Primiparity was delayed, and the phenotypic quality of males decreased, as revealed by both chest girth (standardized to age 5: 99.51 cm, SE = 5.95 for males born until 1997; 97.29 cm, SE = 4.44 for males born later, $t = 2.315$, d.f. = 200, $P = 0.022$) and horn length (standardized to age 5: 59.38 cm, SE = 7.09 for males born until 1997; 55.75 cm, SE = 4.60 for males born later, $t = 3.243$, d.f. = 206, $P = 0.001$) (Michallet & Toïgo 2004). Based on marked changes in individual performance of ibex after 1997, we identified two contrasted periods of environmental conditions: a good period between 1983 and 1997, and a harsh period between 1998 and 2004.

To analyse ibex survival patterns, we used CMR modelling implemented in M-SURGE (Choquet *et al.* 2005a). We considered the sexes separately because of the wide sex-specific differences in survival generally reported for large herbivores (Toïgo & Gaillard 2003). We first performed the goodness-of-fit test of the Cormack–Jolly–Seber model (with fully time-dependent survival and re-sighting probabilities) using U-CARE (Choquet *et al.* 2005b). The Cormack–Jolly–Seber model fitted the data well for both females ($\chi^2 = 42.040$, d.f. = 64, $P = 0.985$) and males ($\chi^2 = 99.231$, $P = 0.999$), and we detected no transience in either sex ($Z = -1.333$, $P = 0.909$ for females; $Z = -1.5112$, $P = 0.935$ for males). However, there was a positive trap dependence for both females ($Z = -3.535$, $P = 0.0004$) and males ($Z = -5.794$, $P < 0.0001$): animals seen a given year had higher chances to be seen again the following year than individuals that were not seen. It is likely that some individuals used areas with low visibility, and therefore were often missed during censuses. Following the model of Markovian trap dependence described by Gimenez, Choquet & Lebreton (2003) to account for trap dependence we considered that the re-sighting probability followed a two-state model, with state 1 (seen in a given year), and state 2 (not seen in a given year). The probability of seeing an individual in state 2 is 0. The model thus estimates the probability of being seen in a given year when seen the previous year, the probability of transition from state 1 to state 2, the probability of transition from state 2 to state 1, and survival rates.

From this model, we first tested the time dependence of re-sighting probability and survival. Then, starting from the best model, we fitted a series of models with different effects of age on survival, and for which the

variability of survival according to year (t) or to period (two periods) was tested in interaction with (**), or in addition (+) to age:

- 1 A complete age-dependent model, with a survival estimate at each age, denoted Φ_a .
- 2 A model with four age classes following Gaillard *et al.* (2004): yearlings (survival from 1 to 2 years), prime-aged adults (2–8 years), old adults (8–13 years), and senescent adults (13 years and older). This age class dependent model was denoted Φ_c .

Finally, we fitted two Gompertz models to describe a continuous decrease of survival with age: one from 2 and one from 8 years onwards (assuming constant survival during the prime-age stage). These models, denoted Φ_G and Φ_{GS} , estimated two parameters: initial adult mortality, μ , which represents the instantaneous initial mortality risk at 2 (model Φ_G) and 8 (model Φ_{GS}) years of age; and the senescence rate, σ , which quantifies the increase in mortality with age (the higher σ , the more intense the ageing, see Gaillard *et al.* 2004 for further details). We could not test the variability of survival according to year or periods using these models because of the small sample size of old individuals during the first period.

To avoid estimates > 1 , survival was logit-transformed in the unconstrained models of age dependence (Φ_a and Φ_c). For Gompertz models, we fitted the Log(–log) transformed survival to linear age: $(\text{Log}(-\log(\Phi(a_i))) = \log(\mu_i) + \sigma * a_i$ with $i = 2$ for Φ_G , and $(\text{Log}(-\log(\Phi(a_i))) = \log(\mu_8) + \sigma * a_i$ with $i = 8$ for Φ_{GS}).

We used the Akaike Information Criterion to select the best model (Burnham & Anderson 1998). When the difference in the AICs of two competing models was less than 2, we selected the most parsimonious model. We compared age-specific survival between sexes and between periods using Wald tests.

Results

MALES (TABLE 1)

The model with a time-dependent re-sighting probability (Φ_t, P_t) fitted the data better than the model with a constant re-sighting probability (Φ_t, P). Re-sighting probabilities of individuals seen the previous year varied from 0.661 (± 0.104) in 1992 to 1 in 5 years. Given that an ibex was alive, its probability to be missed in year 2 if it was missed in year 1 averaged 0.607. On the other hand, the probability to be missed in year 2 for ibex seen in year 1 averaged 0.080. A model with year-dependent survival was better than a model with constant survival (Φ, P_t vs. Φ_t, P_t). We thus started from the Cormack–Jolly–Seber model to further investigate the effects of age and time on survival.

Age proved to strongly structure survival, with the model including additive effects of age and year (Φ_{a+t}, P_t) providing much better fit than the model with no age effect (Φ_t, P_t). No male in our data set survived past 16 years.

Table 1. Number of parameters (Np) and difference in AICs between each tested model and the best model (Δ AIC) for the effects of year and age on survival probability of Alpine ibex in the Belledonne population. Model notations are explained in the text. The best models appear in bold: the Gompertz model with senescence from 2 years onwards for males (deviance of 1447.201 and AIC of 1499.201); and the Gompertz model with senescence from 8 years onwards for females (deviance of 704.830 and AIC of 758.830)

Model	Males		Females	
	Np	Δ AIC	Np	Δ AIC
Φ, P_t	24	79.514	24	35.906
Φ_{i^*}, P	24	103.088	24	88.231
$\Phi_{(1)-G2}, P_t$	26	0	26	14.787
$\Phi_{(1)-(2-7)-G8}, P_t$	27	4.390	27	0
Φ_{c^*}, P_t	27	7.044	27	2.616
Φ_{c+2per^*}, P_t	28	8.690	28	1.552
$\Phi_{(1)-(3c+2per)^*}, P_t$	30	4.931	30	3.859
$\Phi_{c^*2per^*}, P_t$	31	6.931	31	5.859
Φ_{a^*}, P_t	39	21.163	43	16.409
Φ_{a+2per^*}, P_t	40	13.737	44	20.774
Φ_{i^*}, P_t	43	74.594	43	53.888
Φ_{c+i^*}, P_t	47	9.021	47	17.735
Φ_{a+2per^*}, P_t	54	27.571	62	80.281
Φ_{a+i^*}, P_t	60	8.260	63	24.234
Φ_{c+i^*}, P_t	89	63.849	84	103.314
Φ_{a+i^*}, P_t	276	337.674	230	297.724

The four age class model described reasonably well, but not accurately, age variation in survival (models Φ_{a+t} and Φ_{c+t} had similar AICs). The two periods accounted satisfactorily for yearly variation in survival (model Φ_{c+2per} had lower AIC than model Φ_{c+t}). The model with interactive effects of age class and period estimated yearling survival as 1 in both periods. Inspection of the data set confirmed that all 56 marked yearling males were sighted when 2 years of age or older. The best model with four age classes therefore included a constant yearling survival and an interaction of period and age class on adult survival ($\Phi_{(1)-(3c+2per)^*}, P_t$).

This model outperformed all the general models including age and time effects on survival. As expected, survival of old adults was higher during the good condition period than during the poor condition period, decreasing from 0.965 to 0.847. Contrary to our expectations, however, survival did not differ between periods for either prime-age or senescent males (Table 2a). This latter result may be explained because we only monitored 13 males older than 12 years during the good condition period (vs. 76 afterwards).

The Gompertz model fitted from 2 years onwards best described the relationship between survival and age: model $\Phi_{(1)-G2}, P_t$ had a lower AIC than model $\Phi_{(1)-(2-7)-G8}, P_t$ and out-competed all previous models. Our selected model (Fig. 1a) included a very low initial mortality at 2 years ($\mu = 0.003$, SE = 0.002), and a high senescence rate ($\sigma = 0.387$, SE = 0.061).

FEMALES (TABLE 1)

Similarly to the results for males, a model with year-dependent re-sighting probability (Φ_{i^*}, P_t) provided a better fit to female survival than one with constant re-sighting probability (Φ_{i^*}, P). We thus considered a year-dependent re-sighting probability in the following analyses. Re-sighting probability of females seen the previous year varied from 0.521 (± 0.069) in 2002–1 in 11 years. Given that a female was alive, the probability to be missed in year 2 when it was missed in year 1 averaged 0.674. On the other hand, the probability to be missed in year 2 when it was seen in year 1 was only 0.061.

Female survival was constant over the years (model Φ, P_t had a lower AIC than model Φ_{i^*}, P_t), but highly dependent on age. The model (Φ_{a^*}, P_t) had a much lower AIC than the model (Φ, P_t). Including time effects did not improve the fit regardless of what time-dependent model we considered ($\Phi_{a+i^*}, P_t; \Phi_{a+2per^*}, P_t; \Phi_{a+2per^*}, P_t$). No female survived beyond 20 years of age. The models with additive (Φ_{c+2per^*}, P_t) or interactive ($\Phi_{(1)-(3c+2per)^*}, P_t$) effects of age class and two periods

Table 2. Survival estimates, standard errors ($\Phi \pm$ SE), and results of Wald tests comparing survival across two periods of population performance for each age class for (a) male and (b) female Alpine ibex in the Belledonne population

Age class	Performance period		Wald test	
	Good	Low	<i>W</i>	<i>P</i>
	$\Phi \pm$ SE	$\Phi \pm$ SE		
(a)				
Prime-aged (2–8 years)	0.986 \pm 0.012	0.980 \pm 0.013	0.353	0.375
Old adults (8–13 years)	0.965 \pm 0.028	0.847 \pm 0.032	2.764	0.009
Senescent adults (≥ 13 years)	0.257 \pm 0.156	0.506 \pm 0.112	1.301	0.171
(b)				
Prime-aged (2–8 years)	0.999 \pm 0.012	0.992 \pm 0.014	0.648	0.352
Old adults (8–13 years)	0.888 \pm 0.043	0.863 \pm 0.041	0.663	0.337
Senescent adults (≥ 13 years)	0.693 \pm 0.116	0.851 \pm 0.066	0.882	0.118

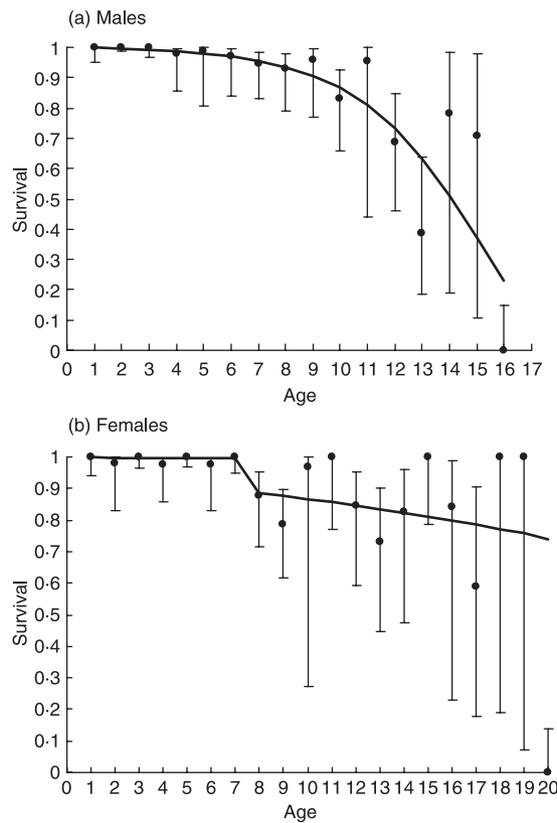


Fig. 1. Age-specific survival of Alpine ibex, with 95% confidence intervals for the Belledonne population (France). The values of the Gompertz model are represented by the solid line for (a) males, from 2 years of age onwards and (b) females, from 8 years of age onwards. For the estimates equal to 0 or 1, the profile likelihood confidence intervals are provided (following the procedure described in Gimenez *et al.* 2005).

(poor and good conditions) had AICs close to the model with no period effect (Φ_c, P_t). However, estimates from the additive model provided survival rates that tended to be higher during poor than during good conditions, and survival estimates from the interactive model were not significantly different between periods whatever the age class (Table 2b). Therefore, a model with four age classes and no year or period effects (Φ_c, P_t) best described the effect of age on survival: yearlings ($\Phi = 1$, with all 32 marked female yearlings re-sighted when 2 years or older), prime-age adults from 2 to 8 years of age ($\Phi = 0.995$, 95% CI [0.785, 1]), old adults from 8 to 13 years of age ($\Phi = 0.875$, 95% CI [0.804, 0.922]), and senescent females ($\Phi = 0.800$, 95% CI [0.663, 0.889]). When modelling senescence as a continuous function of age, the Gompertz model with senescence from 8 years onwards best described the data (Fig. 1b). Based on this model, ibex females had an initial mortality (at 8 years) of 0.061 (SE = 0.055) and a low senescence rate of 0.077 (SE = 0.069). A Gompertz model beginning at 2 years showed a very low initial mortality ($\mu = 0.009$, SE = 0.005 at 2 years of age), and a higher senescence rate of 0.220 (SE = 0.041).

COMPARING MALE AND FEMALE SURVIVAL

We documented no yearling mortality for either sex during this study. Prime-aged adults of both sexes had similar survival rates in both periods (Table 2, comparing male and female survival during the good period: $W = 0.761$, $P = 0.223$; poor period: $W = 0.630$, $P = 0.264$). Beyond 13 years of age, male survival was lower than female survival in both periods (Table 2, good period: $W = 2.242$, $P = 0.012$; poor period: $W = 2.653$, $P = 0.004$). Between 8 and 13 years of age, male survival appeared slightly higher than female survival in the good period (Table 2, $W = 1.506$, $P = 0.066$), but survival rates of both sexes were similar during the poor period (Table 2, $W = 0.310$, $P = 0.378$).

Discussion

As expected, actuarial senescence occurred in both sexes. Age-specific female survival was buffered against environmental variations, whereas survival of old males decreased under harsh environmental conditions. Contrary to expectation, however, males survived as well as females up to 13 years of age, even under harsh environmental conditions. Under good conditions, prime-aged males had very high survival as previously reported (Toigo, Gaillard & Michallet 1997). Lastly, the Gompertz model from 2 years of age onwards in males, and from 8 years onwards in females, provided the best fit to the pattern of Alpine ibex survival in relation to age.

Age strongly structured survival of both sexes, as reported for other large herbivores (Gaillard *et al.* 2000; Coulson *et al.* 2001; Festa-Bianchet *et al.* 2003; Catchpole *et al.* 2004). The decreasing survival with increasing age observed for both sexes is a common feature of large herbivores (see Gaillard *et al.* 2003 for a review). Ibex, however, exhibit particularly high survival rates before senescence. Although estimates of female survival in large herbivores are usually very high (> 0.95) (Gaillard *et al.* 2000), the 99% yearly survival of prime-aged ibex females is higher than reported for any other species. Similarly, the very high survival of yearling ibex (all 88 marked yearlings were re-sighted at age 2 or later) is surprising. In all other large herbivores studied so far, yearlings of both sexes had lower survival than prime-aged adults, especially yearling males of polygynous ungulates (see e.g. Jorgenson *et al.* 1997 on bighorn sheep; Coulson *et al.* 2001 on Soay sheep; Coulson *et al.* 2004 on red deer). Because fully grown ibex are highly sexually dimorphic, and probably highly polygynous, one may expect higher mortality of young males than of young females if young males adopted a riskier growth tactic, devoting fewer resources to fat storage and more to skeletal growth compared with females (Clutton-Brock, Albon & Guinness 1985). The very high survival of yearling ibex could be part of a conservative life-history tactic adopted by both sexes. Ibex have very slow body and horn growth, reaching

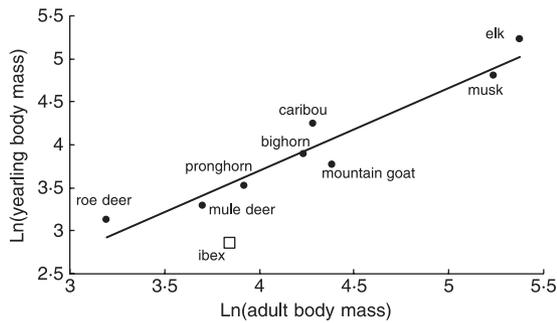


Fig. 2. Allometric relationship between yearling and adult body mass of females in nine species of large herbivores. Compared with other species, ibex yearling have a much lower body mass than expected from their adult size. Bighorn: *Ovis canadensis* Shaw (Festa-Bianchet *et al.* 1996); caribou: *Rangifer tarandus* L. (Ouellet *et al.* 1997); elk: *Cervus elaphus nelsoni* L. (Boyce 1989); ibex: *Capra ibex* L. (Toïgo 1998); mountain goat: *Oreamnos americanus* Blainville (Festa-Bianchet & Côté, unpubl. data); mule deer: *Odocoileus hemionus* Rafinesque (Kie, Burton & Menke 1984); muskox: *Ovibos moschatus* Zimmermann (Latour 1987); pronghorn: *Antilocapra americana* Ord (Mitchell 1980); roe deer: *Capreolus capreolus* L. (Office National de la Chasse et de la Faune Sauvage, unpubl. data).

adult size late; male ibex may have indeterminate growth (Toïgo, Gaillard & Michallet 1999), and their horns grow throughout life (von Hardenberg *et al.* 2004). When compared with similar-sized large herbivores, yearling ibex indeed reach a much lower proportion of asymptotic mass (Fig. 2): they weigh 17 kg, or nearly 50% less than the 33 kg predicted by the interspecific regression. A low energy allocation to growth during early development could allow ibex to divert more energy to maintenance, and thereby lead to high survival.

Male ibex exhibited a unique survival pattern compared with males of other large herbivores. The most striking difference was their very high yearly survival up to about 13 years, 5–20% higher than that of males in other large herbivores, including those in other populations without large predators (Gaillard *et al.* 2000). Whereas males of isard *Rupicapra pyrenaica* Bonaparte, roe deer *Capreolus capreolus* L., bighorn sheep (Loison *et al.* 1999), red deer (Catchpole *et al.* 2004) or Soay sheep (Catchpole *et al.* 2000) all show a marked decrease of survival beyond 8 years, male ibex enjoy very high survival until 13 years. Only from 13 years of age onwards did male mortality increase steeply (Fig. 1a). The survival pattern of ibex males, best described by the two-parameter Gompertz model, was thus characterized by very low initial mortality at 2 years (on average 0.003 over the study) and very high senescence rate (0.387) compared with for instance bighorn sheep (respectively 0.121 and 0.105) or roe deer (respectively 0.064 and 0.171) (Gaillard *et al.* 2004). On the other hand, the pattern of female survival according to age mirrored the classical pattern reported for other large herbivores, with a slow and regular decline (Loison *et al.* 1999; Gaillard *et al.* 2004). If the initial mortality at 2 years (0.009) of female ibex was lower,

the senescence rate (0.220) was similar to that reported for bighorn ewes (respectively 0.039 and 0.161) and roe deer females (respectively 0.021 and 0.199) (Gaillard *et al.* 2004). The apparently unique pattern of male ibex survival, which is very high until 13 years and decreases steeply afterwards, may be related to their unusual mating behaviour. During the rut, that appears to involve a tending system similar to that observed in some other large herbivores (Lott 1984 on bison *Bison bison* L.; Hogg 1988 on bighorn sheep), ibex males attempt to defend single oestrous females. Their behaviour may rely mostly on ritualized displays, reducing mating costs compared with species in which violent fights are frequent (Geist 1971, 1986). Observations during three consecutive ruts indicated that ibex males establish a strong hierarchy based on horn and body size (Toïgo 1998), and are then highly reluctant to fight during the rut. As ibex males grow throughout life in both horns and body mass (Toïgo *et al.* 1999), the oldest are also the largest, and probably the most likely to obtain access to oestrus females. Male ibex reproductive schedules could thus be similar to those reported for elephant seals *Mirounga angustirostris* Gill (Clinton & Leboeuf 1993) that also show indeterminate growth (McLaren 1993): a highly conservative life-history tactic to maximize growth and survival until 12–13 years of age, when they gain full access to females. The exceptionally high male survival between 8 and 13 years of age, and the observation that young males apparently do not adopt alternative reproductive tactics (C.T., pers. obs.), which could provide reproductive opportunities while lowering survival (Hogg & Forbes 1997) strongly suggest a conservative reproductive tactic based on maximizing survival to attain large body and horn size at 11–12 years.

Older male ibex, however, were sensitive to changes in environmental conditions, because their survival decreased during harsh conditions. The higher absolute energy requirements of males compared with females, due to their much larger body size (from about 8–9 years of age, males are about twice as heavy as females, Couturier 1962), and to continuous horn and body growth, could make ibex males more susceptible to starvation when food is restricted. Such between-sex differences fit our current knowledge of life-history evolution. Individual fitness of female large herbivores increases with life span (Clutton-Brock 1988). Accordingly, females of long-lived iteroparous species should favour their own survival to the detriment of current reproduction (Gaillard & Yoccoz 2003). Females of large herbivores are thus expected to decrease reproductive effort when food is scarce, and to allocate more energy to maintenance (Festa-Bianchet & Jorgenson 1998). As a consequence, survival of prime-age females is highly resilient to changes in environmental conditions, including changes in density (Festa-Bianchet *et al.* 2003). On the other hand, males should allocate much energy to growth to reach a dominant social position and enhance their lifetime reproductive success.

Because of this constraint and their larger body size, fully grown males have higher absolute energy requirements than females (Demment & Van Soest 1985), and are thus more susceptible to starvation. These results agree with a review on prime-age survival in large herbivores (Toïgo & Gaillard 2003), which pointed out that the survival of males decreased under harsh environmental conditions compared with that of females. The fact that environmental conditions only affected the survival of old males agrees with our suggestion that male ibex adopt a conservative reproductive tactic to maximize survival until they reach very large body and horn size at an advanced age. We suggest that males aged 13 years and older participate actively in the rut, suffering the same negative consequences seen in other male ungulates at a much younger age. While 62% of yearling males survived to 13 years, only 20% of 13 year olds survived to age 15 (Fig. 1a). Data on the reproductive success of male ibex are required to test this hypothesis: if our speculations about their reproductive tactic are correct, in un hunted populations males younger than about 10 years should have very low reproductive success.

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Supplementary material

The following supplementary material is available for this article online.

Appendix S1. M-array (*sensu* Choquet *et al.* 2005a) for male and female CMR data set of Alpine ibex in the Belledone-Sept Laux population.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01254.x>

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