AGE-SPECIFIC SURVIVAL IN FIVE POPULATIONS OF UNGULATES: EVIDENCE OF SENESCENCE

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Abstract. Methodological problems in describing patterns of senescence in wild populations have until recently impeded progress in understanding the evolution of a process that decreases individual fitness. We investigated age- and sex-specific survival in five populations of three species of ungulates (roe deer, *Capreolus capreolus*; bighorn sheep, *Ovis canadensis*; and isard, *Rupicapra pyrenaica*), using recent statistical developments of capture–mark–recapture models and long-term (12 to 22 yr) data on marked individuals. The yearly survival of females aged 2–7 yr was remarkably similar and very high (92–95%) in all five populations. Survival of adult males varied among species and populations. Survival decreased from 8 yr onward for both sexes in all populations, suggesting that senescence was a common phenomenon. Male survival was lower than female survival, and the gender difference increased with age. The extent of sex differences in survival was related neither to sexual dimorphism in mass nor to the level of polygyny, suggesting that species differences in social behavior, particularly mating system and the level of male–male aggression, may be more important than simply the level of polygyny in explaining sexual differences in survival. Our results underline the advantages of long-term monitoring of marked individuals for the study of evolutionary ecology.

Key words: bighorn sheep; body mass; Capreolus capreolus; *capture–mark–recapture; isard;* Ovis canadensis; *roe deer;* Rupicapra pyrenaica; *senescence; sexual selection; survival; ungulate.*

INTRODUCTION

In humans, survival and reproductive capacity decrease with increasing age (Partridge 1993, Partridge and Barton 1993). Human senescence is characterized by specific diseases, a decrease of resistance to common diseases, poor ability to recover after perturbing events, and loss of sensorial faculties (Ricklefs and Finch 1995). Although senescence clearly occurs in humans, empirical evidence for senescence in wild mammals is equivocal (Promislow 1991, Wooler et al. 1992, Gaillard et al. 1994, Slade 1995) for two main reasons. First, because survival is <100% for all age classes, the probability of reaching a given age decreases as age increases, even in the absence of any senescence process (Sacher 1978). In natural populations, age-independent mortality is greater than in human populations, and it is possible that very few individuals reach the age at which their ability to survive would decrease because of senescence (Medawar 1952, Comfort 1979). Second, most studies cited in reviews claiming that senescence is commonly observed in mammals (Nesse 1988, Promislow 1991, Sibly et al. 1997) used questionable analytical methods. One of these methods, the maximum known longevity in captivity (Austad and Fischer 1991, 1992) is highly correlated with the number of individuals monitored and may bear little relationship to actual patterns of senescence (Comfort 1979, Krementz et al. 1989). Another, the life table technique (Miller 1988, Nesse 1988, Promislow 1991, Sibly et al. 1997) leads to errors in survival estimates unless several unrealistic assumptions are respected (including constancy of all vital rates over time or accurate assessment of age for recovered animals [Caughley 1977, McCullough 1979, Messier 1990]), especially for old age classes (Fryxell 1986). Although some recent studies based on capture–recapture methods have reported increases in mortality for older animals (Gaillard et al. 1993, McDonald et

Table 1. Body mass of males and females and sexual dimorphism in body mass (male mass divided by female mass) for three species of ungulates in five study areas. Data indicate the average mass of adults (4 yr of age and older) in late summer or early fall.

Species	Study area	Sex	Mass (kg)	Dimorphism
Isard	Orlu	male	26	1.08
		female	24	
Roe deer	Trois-Fontaines	male	26	1.08
		female	24	
	Chizé	male	24	1.09
		female	22	
Bighorn sheep	Ram Mountain	male	100	1.41
		female	71	
	Sheep River	male	105	1.40
		female	75	

al. 1996, Jorgenson et al. 1997), others have failed to reveal a senescent stage (Wooler et al. 1992, Loison et al. 1994, Slade 1995, Cransac et al. 1997, Nichols et al. 1997, Toïgo et al. 1997). As noted by most authors, this failure could result from either an insufficient number of years of monitoring or a senescent stage that begins later than expected. Evidence of senescence in wild populations thus must be reevaluated with long-term longitudinal monitoring of marked individuals (Gaillard et al. 1994, Nichols et al. 1997).

The methodological problem of describing patterns of senescence has impeded progress on the evolutionary problem of explaining a process that seems to decrease individual fitness (Bell 1984, Rose 1985). Senescence may be explained in an evolutionary context by the antagonistic pleiotropy hypothesis (Medawar 1946, Williams 1957, Hamilton 1966, Rose 1991) and the mutation-accumulation hypothesis (Edney and Gill 1968). Alternatively, senescence can be accounted for in a nonevolutionary context as an unavoidable by-product of metabolism (Sacher 1978). Recent long-term studies that have monitored the survival of marked individuals in large mammals provide a unique opportunity to describe senescence in wild populations, and to test hypotheses about its evolution.

Ungulates are particularly suitable for the study of senescence because different species vary considerably in mating system (Jarman 1983), fecundity (Bunnell 1987), and body mass (Peters 1983), all factors that may affect senescence (Stearns 1992). We investigated age-specific survival in Pyrenean chamois or isard (*Rupicapra pyrenaica*), roe deer (*Capreolus capreolus*), and bighorn sheep (*Ovis canadensis*), using recently developed statistical techniques to analyze capture–mark–recapture models (Lebreton et al. 1992) and long-term (12–22 yr) data for five populations. We first determined whether survival changed with age and analyzed the form of the relationship between age and survival, particularly for older age classes. Then, we considered three hypotheses related to age- and sex-specific survival probabilities in evolutionary ecology.

First, we tested whether senescence began with first reproduction, as predicted by the antagonistic-pleiotropy hypothesis (Medawar 1946, Williams 1957, Hamilton 1966). Second, we tested the hypothesis that male-biased mortality and the rate of decline in survival probabilities with age among males increased with the level of polygyny and of sexual size dimorphism. Most studies of ungulates report lower survival for males than for females (Clutton-Brock et al. 1982, 1985a, Gaillard et al. 1993, Owen-Smith 1993b, Jorgenson et al. 1997), but several exceptions exist (Berteaux 1993, Fancy et al. 1994, Cransac et al. 1997, Réale et al. 1997, Toïgo et al. 1997). A link between polygyny and male-biased mortality has been proposed (Ralls et al. 1980, Promislow 1992), but the supporting evidence is equivocal and often based on sex-ratio data that are not very reliable (Owen-Smith 1993b, but see Promislow 1992). We tested the prediction that sexual dimorphism in survival should be greatest for bighorn, which are polygynous and highly sexually dimorphic (Hogg 1984, Festa-Bianchet et al. 1996), and least for roe deer, which have very limited polygyny and sexual dimorphism (Danilkin 1996). Third, we tested the hypothesis that the rate of senescence (i.e., the rate of decline in survival probabilities with age) was related to metabolic rate and therefore decreased with increasing body size (Sacher 1978). Bighorn sheep are more than three times as heavy as roe deer or isard; therefore we expected greater longevity for bighorn sheep than for the other two species.

Study Species

The isard is a polygynous mountain-dwelling rupicaprin with a flexible mating system that can include harem defense (Lovari 1985). Males are ~10% heavier than females (Table 1). Both sexes complete mass accumulation by age three (Pépin et al. 1996). Litter size in our study area was always one. Roe deer are small cervids with sexual dimorphism similar to that of isard (Table 1). We studied roe deer in forested habitats, where their mating system involves male territoriality

TABLE 2. Characteristics of the five study populations of ungulates.

	Study area				
Characteristic	Orlu	Trois-Fontaines	Chizé	Ram Mountain	Sheep River
Species	isard	roe deer	roe deer	bighorn	bighorn
Years of data	12	21	19	22	16
Years of monitoring	85–97	76–97	78–97	75–97	81–97
Marked males	70	202	173	265	139
Marked females	169	207	172	266	136
Predators on adults	none	none	none	wolf, cougar	wolf, cougar
Number of culled males	3	0	0	30	30
Number of culled females	3	0	0	0	2
Number of males known to have survived *at least* 8 yr of age	22	20	29	21	11
Number of females known to have survived *at least* 8 yr of age	107	56	63	71	40

and either monogamy or a very low level of polygyny (Danilkin 1996). Both sexes complete mass accumulation by age three (Hewison et al. 1996). Litter size varied from one to three, averaging 1.7 in both populations. Bighorn sheep are mountain-dwelling caprins, highly polygynous with a mating system based on male dominance (Hogg and Forbes 1997). Sexual dimorphism is pronounced (Table 1). Both sexes accumulate body mass until at least 7 yr of age (Festa-Bianchet et al. 1996). As in isard, litter size was always one. For all species, the earliest age of primiparity was 2 yr and the proportion of females aged 4 yr and older giving birth was usually >90% (Festa-Bianchet 1988*a*, Gaillard et al. 1992, Jorgenson et al. 1993*a*, Loison 1995).

STUDY AREAS AND POPULATIONS

We summarize the main characteristics of our study populations in Table 2. Here we provide brief descriptions and details of capture and marking methods for each study area. More information on our study areas and monitoring programs has already been published (Gaillard et al. 1993, Loison and Gaillard 1994, Jorgenson et al. 1997).

Isard

Isard were monitored in a protected area managed by the French Office National de la Chasse. Individuals were captured in traps and marked with colored collars. The National Game Reserve of Orlu in the Eastern French Pyrénées (42° N, 1° E) covers 42 km² at 900–2800 m elevation. The study population included about 1500 isards (Loison 1995). Marked individuals were monitored by resightings from May to October. Most deaths in mountain ungulates occur during winter and early spring, when food is limited and climate is harsh. In Orlu, no deaths have been reported for the May–October period (Loison 1995). Age at first capture was estimated by counting horn annuli (Schröder and Elsner-Schack 1985) and ranged from 1 to 14 yr for fe-

males and from 1 to 11 yr for males. Isard were not hunted in the game reserve but could be shot outside the reserve during the fall hunting season.

Roe deer

Two roe deer populations were monitored in fenced oak–beech forests managed by the Office National de la Chasse. Both populations were enclosed. About 20–35% of the deer were removed each year as part of ongoing management programs, but all marked individuals were released within the study area. About half of the roe deer were captured each January–February using drive nets (Gaillard et al. 1993). Animals caught were either removed and released elsewhere or individually marked with ear tags and numbered collars, then released in the study site. Recaptures of marked deer were used to monitor individual survival. Roe deer included in this analysis were of known age because they had been marked as fawns in their first winter. Trois-Fontaines (48° N, 3° E) covers 14 km². The roe deer population was estimated at about 250 individuals older than one year in March and throughout the study period (Gaillard et al. 1993). The National Game Reserve of Chizé (46° N, 0° E) covers 26 km². The population size estimated in March varied between 250 and 550 deer older than one year during the study period (Gaillard et al. 1993).

Bighorn sheep

The two bighorn sheep study areas were on public land in Alberta, Canada. Ram Mountain (52° N, 115° W, elevation 1082–2173 m) included ~38 km² of sheep habitat. Sheep were captured in a corral trap and monitoring of survival involved both recaptures and resightings from June to September, when mortality is negligible. Females were marked with collars, males with ear tags. Rams with horns describing at least four-fifths of a curl (''legal'' males) were hunted from late August through October. In 1972–1981, removals of

adult females kept the June population at 95–110 sheep (Jorgenson et al. 1993*b*). There was an average of 175 sheep in 1982–1997. Sheep River (50° N, 114° W, elevation 1420 to 2550 m) included the seasonal ranges of a migratory bighorn population. Sheep were captured by darting (Jorgenson et al. 1990) and marked with ear tags. Similar to Ram Mountain, the main resighting period occured from May to September. There were 93–153 sheep in March during our study, with changes in numbers caused partly by pneumonia in 1986 (Festa-Bianchet 1988*b*) and cougar (*Puma concolor*) predation in 1992–1995 (Ross et al. 1997). The winter range at Sheep River was a wildlife sanctuary where no hunting was allowed. Outside the sanctuary, males with horns of at least four-fifths of a curl were hunted in autumn (Festa-Bianchet 1989). A limited number of female permits resulted in six marked females being shot during our study. Of these only two were part of the sample analyzed here. Survival of marked sheep was monitored by resightings (Festa-Bianchet 1986*a*, *b*). Sheep were aged at first capture by counting the horn annuli (Geist 1966). Age at first capture for individuals included in this paper ranged from 1 to 4 yr for females, 1 to 8 yr for males. Bighorn males of legal horn size suffered ~35% annual hunting mortality (Festa-Bianchet 1989, Jorgenson et al. 1993*b*). Most males reached legal horn size at 4–5 yr at Sheep River and 5–6 yr at Ram Mountain, and few survived beyond 8–9 yr of age.

Methods

Survival estimation and model selection

We estimated the natural survival rates of marked individuals with capture–mark–recapture (roe deer) or capture–mark–resighting (isard and bighorn) models (Lebreton et al. 1992). For simplicity, we used the common term of ''recapture'' to designate both true recaptures and resightings. Marked individuals that died during capture (18 roe deer males and 24 roe deer females in Trois-Fontaines, 6 roe deer males and 6 roe deer females in Chizé, 1 bighorn male at Sheep River and 1 bighorn female at Ram Mountain), were shot by hunters (Table 2), removed (11 roe deer males and 16 roe deer females in Trois-Fontaines, 20 roe deer males and 23 roe deer females in Chizé, 11 bighorn females at Ram Mountain), or hit by vehicles (1 bighorn female at Sheep River) were all treated as losses during capture and withdrawn from the sample either in the year of death if they had been recaptured during that year, or in the last year of capture. The only species for which hunting was an important cause of death was bighorn. Because hunting is strictly regulated and registration of shot rams is compulsory, the probability that a hunter reported that he shot a marked individual can be assumed to be one. In both bighorn study sites, recapture

probabilities were also close to one (Jorgenson et al. 1997), and therefore it was not necessary to distinguish the probability of recapture from the probability of being hunted and reported.

In this paper we only considered the survival of marked individuals from 1 yr of age, and focused on age-dependent patterns. The effects of year, cohort, density, or epizootics on capture probabilities and survival have been studied previously for each population (Gaillard et al. 1993, Loison 1995, Jorgenson et al. 1997). Other parameters that we had previously found to have important and significant effects on survival were included in the models presented here if their effect remained significant in the new analysis. This was, for example, the case for bighorn at Sheep River, which experienced a pneumonia epizootic in 1985. As a result, the number of parameters incorporated in the models considered in this paper was different among sex and species. The data sets used in this paper differed from those in our earlier publications in two ways. For all study areas, we added at least 2 yr of data (5 yr for roe deer). For bighorn sheep, our earlier analyses only included females first caught when aged 1 yr or less, and males aged 2 yr or less at first capture. Here we included males up to 8 yr old and females up to 4 yr old at first capture (see Loison et al. [1994] for technical details of including different ages at capture in the estimation procedure). These changes in the data sets increased the sample of individuals in older age classes and therefore allowed a more powerful test of senescence. Similarly to our previous work, we performed separate analyses for each sex in each population.

Goodness-of-fit (GOF) tests of the Cormack-Jolly-Seber (CJS) model are normally used as a starting point for fitting other models (Lebreton et al. 1992) and performed with the software RELEASE (Burnham et al. 1987). However, the CJS model only accounts for time variability in both survival and recapture rates, and neglects possible age effect. We therefore used modifications of the GOF test in order to test the GOF of models allowing for both age and time dependence. For roe deer and bighorn, we tested the GOF of a model with time dependence in recapture rates and two age classes (yearling vs. older) and time dependence in survival rates (see Gaillard et al. 1993, Jorgenson et al. 1997 for details). For bighorn, we performed this test by only including individuals first captured as yearlings, i.e., 91% of females and 84% of males at Ram Mountain, and 76% of females and 67% of males at Sheep River. The GOF tests of this model were not significant for roe deer (Trois-Fontaines males, $\chi^2 = 40.830$, df $= 72$, $P = 0.998$; Trois-Fontaines females, $\chi^2 = 69.064$, df $= 74$, $P = 0.645$; Chizé males, $\chi^2 = 50.908$, df $= 68$, $P = 0.937$; Chizé females, $\chi^2 =$

TABLE 3. Models fitted to investigate age-specific survival patterns in the five ungulate populations. Φ designates survival rates.

Model	Biological meaning	Notation
1	No age effect, no year effect	Φ
2	Complete age dependence + year effect + interaction	$\Phi_{a \times t}$
3	Complete age dependence + year effect	Φ_{a+t}
4	Complete age dependence	Φ_a
5	Caughley-like model (three age classes which differ in survival)	$\Phi_1\Phi_{2-7}\Phi_{\geq 8}$
6	Linear relationship between age and survival, yearlings excluded	$\Phi_1\Phi_{a1}$
7	Quadratic relationship between age and survival, yearlings excluded	$\Phi_1\Phi_{a1+a2}$
8	Linear relationship between age and survival between 2 and 7 yr of age, complete age dependency for old adults	$\Phi_1\Phi_{a1(2-7)}\Phi_{a(\geq 8)}$
9	Constant survival between 2 and 7 yr of age, complete age dependency for old adults	$\Phi_1\Phi_{2-7}\Phi_{a(\geq 8)}$
10	Constant survival between 2 and 7 yr of age, linear relationship between age and survival for old adults	$\Phi_1\Phi_{2-7}\Phi_{a1(\geq 8)}$

68.562, df = 66, P = 0.396), nor for bighorn sheep at Sheep River (males, χ^2 = 1.666, df = 4, P = 0.797; females, χ^2 = 12.289, df = 13, P = 0.504). At Ram Mountain, the GOF test was not significant for females (χ^2 = 2.988, df = 4, P = 0.560) but was significant for males (χ^2 = 55.668, df = 38, P = 0.032). However, this was due to only one cohort of males, and the test was not significant when this cohort was removed (χ^2 = 37.248, df = 36, P = 0.441). Because no effect appeared for females of the same cohort, we neglected this effect. For isard, the situation was more complex because age at capture ranged between 1 and 14 yr of age for females and 1 and 11 yr of age for males, with no age at capture predominating. We could not test models with both age and time because partitioning the data set by age at capture or by year of birth led to low sample sizes within each category. For females, we could partition the data according to year of birth. We therefore performed the GOF test for each cohort. By adding the GOF tests of all cohorts, we tested the fit of the model with interaction between age and time in both survival and recapture probabilities. Because of low sample size for some cohorts, we performed this analysis for females born from 1979 to 1989 (75% of the total number of marked females). The GOF test was not significant (χ^2 = 43.829, df = 73, P = 0.996). We could not perform a similar test for isard males because of low sample sizes within each cohort. We performed one GOF test of the model described for roe deer and bighorn with individuals captured as yearlings and one GOF test of the CJS model with individuals captured when older. Neither test was significant (yearlings, χ^2 = 6.598, df = 14, P = 0.949; older males, χ^2 = 34.582, df = 54, P = 0.982).

Model notation and biological meanings are summarized in Table 3. We first investigated age dependence by fitting a model including one survival estimate for each age and then a three-age-class model proposed as typical for ungulates by Caughley (1966) (the ''Caughley-like'' model, Gaillard et al. 1993). We considered the following age classes: yearlings, prime-age adults from 2 to 7 yr of age (see Gaillard et al. 1993 and Jorgenson et al. 1997 for justification of this cut-off age) and old adults from 8 yr of age onward. We then tested whether a continuous function could provide a good description of the relationship between survival and age and we examined at which age survival began to decrease. We modeled survival rate as polynomial functions (first and second order) of age on the logistic scale (see Newton and Rothery 1997, Nichols et al. 1997 for similar approaches). We considered these relationships excluding yearlings, which often have survival rates that are lower than those of older individuals for reasons other than senescence (Gaillard et al. 1993, Loison et al. 1994, Jorgenson et al. 1997). The minimum number of individuals known to have survived until at least 8 yr of age is reported in Table 2.

Mortality rates are usually thought to increase exponentially with age (the ''Gompertz mortality law,'' Gompertz 1825), although the generality of this empirical law has been questioned (Abrams 1991, 1993, Abrams and Ludwig 1995). The Gompertz model corresponds to a linear function between survival rates and age, on a log–log scale (log(–log(survival rate))). However, the deviance of models with the complementary log–log and logistic links never differed by more than one unit. Hence, we considered the linear function with a logistic link as an approximation of the Gompertz model because this procedure allowed us to compare the Gompertz with other models fitted with the same link.

We investigated three possible relationships between survival and age: (1) whether the rate of decline in survival probability with age (hereafter called ''senescence rate'') increased with age, by comparing the model with a linear-logistic function of survival with age (that assumed no increase of senescence rate with age) and the model with a quadratic-logistic function

TABLE 4. Deviance, number of free parameters (in parentheses), and Akaike Information Criterion (in italics) of models fitted for bighorn, isard, and roe deer populations. Bold lettering indicates the selected model.

		Bighorn†				Isard§	
		Ram Mountain		Sheep River‡		Orlu	
Model no.	Model	Male	Female	Male	Female	Male‖	Female
1	Φ	1189.93 (2) *1193.93*	1052.89 (2) *1056.89*	433.01 (3) *439.01*	551.20 (3) *555.20*	418.63 (13) *444.63*	1133.62 (12) *1157.62*
2	$\Phi_{a \times t}$	976.98 (199) *1374.98*	711.58 (241) *1193.58*	237.16 (134) *505.16*	340.87 (161) *662.87*	309.82 (131) *571.82*	1031.03 (220) *1471.03*
3	Φ_{a+t}	1142.12 (36) *1214.12*	949.07 (42) *1033.07*	391.11 (30) *451.11*	490.61 (33) *556.61*	374.39 (39) *452.39*	1162.19 (45) *1252.19*
4	Φ_a	1171.02 (14) *1199.02*	984.99 (20) *1024.99*	416.83 (16) *448.83*	516.28 (19) *554.28*	402.95 (28) *458.95*	1194.16 (33) *1260.16*
5	$\Phi_1 \Phi_{2-7} \Phi_{\geq 8}$	1182.90 (4) *1190.90*	1003.47 (4) *1011.47*	424.80 (6) *436.80*	531.55 (6) *543.55*	417.60 (15) *447.60*	1230.55 (15) *1260.55*
6	$\Phi_1 \Phi_{a1}$	**1176.43 (4)** ***1184.43***	**996.77 (4)** ***1004.77***	**423.13 (6)** ***435.135***	526.59 (6) *538.59*	417.26 (15) *447.26*	**1214.66 (15)** ***1244.66***
7	$\Phi_1 \Phi_{a1+a2}$	1176.43 (5) *1186.43*	996.73 (5) *1005.73*	422.89 (7) *436.89*	**520.40 (8)** ***534.40***	410.11 (16) *442.11*	1214.42 (16) *1246.42*
8	$\Phi_1 \Phi_{a1(2-7)} \Phi_{a(\geq 8)}$	1173.00 (10) *1193.00*	986.57 (16) *1018.57*	419.52 (12) *443.52*	519.09 (15) *549.09*	404.55 (24) *452.55*	1197.84 (28) *1253.84*
9	$\Phi_1 \Phi_{2-7} \Phi_{a(\geq 8)}$	1179.57 (9) *1197.57*	989.47 (15) *1019.47*	422.47 (11) *444.47*	517.63 (14) *545.63*	407.07 (23) *453.07*	1198.42 (27) *1252.42*
10	$\Phi_1 \Phi_{2-7} \Phi_{a1(\geq 8)}$	1182.81 (5) *1192.81*	998.84 (5) *1008.84*	424.80 (7) *438.80*	521.37 (7) *535.37*	413.58 (16) *445.58*	1214.83 (16) *1246.83*
6′	$\Phi_{a(1-3)} \Phi_{a1}$	... ...	... ...	... ...	... ...	**411.51 (17)** ***445.51***	... ...
7′	$\Phi_{a(1-3)} \Phi_{a1+a2}$	... ...	... ...	... ...	... ...	409.90 (18) *445.90*	... ...
8′	$\Phi_{a(1-3)} \Phi_{a1(4-7)} \Phi_{a(\geq 8)}$	... ...	... ...	... ...	... ...	404.31 (26) *456.31*	... ...
9′	$\Phi_{a(1-3)} \Phi_{4-7} \Phi_{a(\geq 8)}$	... ...	... ...	... ...	... ...	404.44 (25) *454.44*	... ...
10′	$\Phi_{a(1-3)} \Phi_{4-7} \Phi_{a1(\geq 8)}$	... ...	... ...	... ...	... ...	410.80 (18) *446.80*	... ...

† Resighting probabilities were constant over years at both Ram Mountain and Sheep River. Hence, only one parameter was needed to model recapture probabilities.

‡ All models took into account that survival was lower during 1985 because of a pneumonia epizootic. One value of yearly survival was therefore estimated for 1985/1986 and a second value for all other years. Similarly, the intercept of the logistic regression relating survival to age was estimated separately for 1985/1986 and for other years. Thereby, two additional parameters were estimated for models 4–10 compared to models that would have ignored the epizootic.

§ Resighting probabilities were time-dependent both for males and for females. Hence, 12 parameters were needed to model resighting probabilities.

‖ The survival of young males (1–3 years of age) can be confounded with dispersal (see *Discussion*). Therefore, we fitted models 6–10 estimating survival for these three age groups independently (noted $\Phi_{a(1-3)}$). Models were denoted 6′, 7′, 8′, 9′, and 10′.

¶ In Chizé, recapture probabilities depended on three periods. Hence, three parameters were needed to model the recapture probabilities.

In Trois-Fontaines, the recapture probability was constant over years. Therefore, only one parameter was needed to model the recapture probabilities.

of survival with age (that assumed an increase of senescence rate with age); (2) whether a decrease in survival with increasing age could be detected within prime-age adults (2 to 7 yr of age) by comparing the model with a constant survival for prime-age adult and the model in which survival rates from 2 to 7 yr of age were a linear-logistic function of age; and (3) whether the age-related decrease in survival was discontinuous so that it could not be described by a single function; we therefore compared the model with either a linear or quadratic function of survival with age to a model with constant survival between 2 and 7 yr followed by a linear-logistic decrease in survival with age beginning at 8 yr.

We used the Akaike Information Criterion (AIC) to select the most parsimonious model (see Burnham and

TABLE 4. Extended.

Roe deer			
Chizé¶		Trois-Fontaines#	
Male	Female	Male	Female
1284.06 (4)	1752.74 (4)	1302.57 (2)	1938.96 (2)
1292.06	*1760.74*	*1306.57*	*1942.96*
1155.77 (148)	1593.84 (188)	1151.77 (149)	1779.07 (192)
1451.77	*1969.84*	*1449.77*	*2163.07*
1240.78 (35)	1684.58 (39)	1239.55 (32)	1875.16 (39)
1310.78	*1762.58*	*1303.55*	*1953.07*
1264.18 (17)	1714.83 (20)	1289.57 (14)	1895.10 (18)
1295.18	*1754.83*	*1317.57*	*1931.10*
1278.18 (6)	1732.41 (6)	**1294.28 (4)**	1914.03 (4)
1290.18	*1744.41*	***1302.28***	*1922.03*
1273.56 (6)	**1730.03 (6)**	1297.02 (4)	**1905.2 (4)**
1285.56	***1742.03***	*1305.02*	***1913.27***
1272.39 (7)	1729.92 (7)	1295.59 (5)	1905.02 (5)
1286.39	*1743.92*	*1305.59*	*1915.02*
1270.44 (13)	1716.93 (16)	1295.60 (10)	1899.40 (14)
1294.44	*1748.93*	*1315.60*	*1927.40*
1270.44 (12)	1717.21 (15)	1288.22 (9)	1900.80 (13)
1294.44	*1747.21*	*1306.22*	*1926.80*
1272.58 (7)	1729.99 (7)	1294.08 (5)	1907.53 (5)
1286.58	*1743.99*	*1304.08*	*1917.53*
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Anderson 1992, Lebreton et al. 1992, Burnham et al. 1995 for justification of this criterion in the CMR context). The AIC is calculated as the deviance. The deviance equals $-2 \text{Ln}(L)$ plus twice the number of free parameters of the model, where L is the likelihood, $L = \Pi \, p_i \exp(x_i)$, x_i is a capture–recapture history, and p_i is the probability of occurrence of the capture–recapture history with i varying between 1 and 2 $\exp(n - 1)$ for n years of recaptures. The selected models are those with the lowest AIC. To test specific hypotheses among nested models, we also used classical likelihood-ratio-tests.

Comparison of survival and senescence patterns among sexes and species

To compare senescence patterns between sexes and species, we compared the parameters of the quadratic-logistic function of survival (Φ) with age [logit(Φ) = $\alpha + \beta x + \gamma x^2$], where x is age. This function has three parameters, the intercept (α), the coefficient of the lin-

ear term (β), and the coefficient of the quadratic term (γ). We chose to standardize this relationship so that survival from 8 to 9 yr of age (start of the old-adult age class) corresponded to the logit of the intercept (logit $\Phi_8 = \alpha$). In other words, we rescaled the age variable so that $x = \text{age} - 8$, in order to interpret the intercept as the survival rate at the beginning of the old-adult age class, the coefficient of the linear term as the slope of the decrease of survival at 8 yr of age, and the coefficient of the quadratic term as the acceleration of the senescence rate. Moreover, rescaling the explanatory variable (age in our case) around its mean value reduces the correlation among the coefficients of a quadratic regression (Hocking 1996). Eight yr of age is a good compromise given the longevity of each sex–species group (Table 7) and given that we had to choose a common age for all groups. Therefore, we used quantitative measures (the coefficients of the quadratic-logistic function) with which we could test statistical hypotheses about differences in senescence among sex–species groups.

We performed an ANOVA to investigate effects of species and sex on the three coefficients of the quadratic-logistic function. Because these coefficients were estimated with varying levels of precision, we weighted each of the estimates by the inverse of the variance of the estimate. We also performed an ANCOVA for each coefficient according to average body mass of the species and sex to test whether survival at 8 yr of age (α), the slope of the decrease of survival at 8 yr of age (β), or the acceleration of senescence (γ) were related to differences in mass when the effect of sex was controlled.

RESULTS

Model selection and decrease in survival with age

Survival changed with age in both sexes of all five populations (Table 4) because the complete age-dependent model or the Caughley-like model had lower AICs than the model without any age effects, except for male isard in Orlu. In every case except males in Orlu, the Caughley-like model (model 3) was a more parsimonious descriptor of survival than the complete age model (model 2), and survival was lower for old individuals than for prime-aged ones. In all populations, senescence occurred for both sexes. Emigration from the study area likely explained the low apparent survival for 2- and 3-yr-old male isards in Orlu (Loison 1995). Therefore, for male isards, we fitted models 3 to 8 again excluding survival from 2 to 4 yr (Table 4). The best model for describing the survival data differed among populations. Nevertheless, the Gompertz model (linear-logistic, model 4) was the best (with respect to AIC values) in 8 of 10 cases (Table 5). For female bighorn in the Sheep River population, however, the

TABLE 5. Model selected, mean annual survival from 2 to 7 years of age from the Caughley-like model, and test of the difference between male and female prime-age survival rate (Wald test) in five ungulate populations.

Species	Population	Sex	Model selected	Prime-age survival	Male vs. female
Bighorn	Rain Mountain	M	$\Phi_1\Phi_{a1}$	0.85 ± 0.01	$W = 5.70$
		F	$\Phi_1\Phi_{a1}$	0.94 ± 0.01	$P < 10^{-4}$
	Sheep River	M	$\Phi_1\Phi_{a1}$	0.88 ± 0.02	$W = 1.71$
		F	$\Phi_1\Phi_{a1+a2}$	0.92 ± 0.01	$P = 0.044$
Isard	Orlu	M	$\Phi_{a(1-3)}\Phi_{a1}$	0.93 ± 0.03	$W = 0.54$
		F	$\Phi_1\Phi_{a1}$	0.94 ± 0.02	$P = 0.295$†
Roe deer	Chizé	M	$\Phi_1\Phi_{a1}$	0.86 ± 0.02	$W = 4.03$
		F	$\Phi_1\Phi_{a1}$	0.95 ± 0.01	$P < 10^{-4}$
	Trois-Fontaines	M	$\Phi_1\Phi_{2-7}\Phi_{\geq 8}$	0.83 ± 0.02	$W = 4.03$
		F	$\Phi_1\Phi_{a1}$	0.92 ± 0.01	$P < 10^{-4}$

Note: Wald tests are one-tailed because we expected lower survival for males than for females.

† Prime-age survival for isard is estimated excluding the survival rates from 2 to 4 years of age because of the possible dispersal of young males. Including young males suggests a mean survival between 2 and 7 years of age of 0.87 ± 0.03 and a significant sex difference ($W = 2.28$, $P = 0.021$).

Gompertz model was significantly different from the one selected (quadratic-logistic model vs. linear-logistic model: $\chi^2 = 6.19$, df = 1, $P = 0.013$). Similarly, the AIC of the Gompertz model had three units more than the AIC of the Caughley model for male roe deer in Trois-Fontaines. Therefore, for male roe deer in Trois-Fontaines, the Gompertz model did not provide a good description of the age-related decrease in survival, which occurred in a step-like fashion. Male roe deer at Trois-Fontaines were the only sex–species group for which survival did not decrease continuously with age.

To compare sex–population groups, we required one common model that could reasonably be accepted in all cases. Such a common model should not differ significantly from the selected model in each instance in order to provide an accurate description of senescence patterns. The quadratic-logistic model fulfilled this criterion and was used as a common model because it satisfactorily described the survival data in all sex–population groups (Table 4), although it was not the most parsimonious model when the linear-logistic one had a lower AIC. For female bighorn sheep, the quadratic-logistic model differed significantly from the linear-logistic model. Therefore, the quadratic-logistic model was used to compare species and sexes in the following analysis (see Table 6 for the coefficients of the quadratic-logistic relationship).

Comparison of sex and species survival patterns

A linear-logistic decrease of survival rates with age was observed for both males and females in all populations except for female bighorn sheep at Sheep River and male roe deer at Trois-Fontaines. Based on the Caughley-like model (model 3), the survival rate of prime-aged adults was higher for females than for males with the exception of isard (Table 5).

It appeared that the sex difference in survival increased for older ages (Fig. 1), except for bighorns at Sheep River, for which data on males older than 8 yr were available for only 11 individuals. We expected that survival differences between sexes should be more evident for the more polygynous species. Instead, sex differences in survival were not related to the level of polygyny, being high in both populations of roe deer, the least polygynous species, low in the highly polygynous isard, and variable in the two populations of bighorn, a species which is also highly polygynous (Table 5).

Species had no significant effect on the coefficients of the quadratic-logistic regression of survival with age (Table 7). The effect of sex was significant only for the intercept (Table 7). Males had a lower intercept than females (averaged over species: $\alpha_{female} = 2.098 \pm 0.114$, $\alpha_{male} = 1.314 \pm 0.226$) indicating that survival from 8 to 9 yr was consistently higher for females than for males (average of 0.89 for females and 0.79 for males). In contrast, the decrease in survival from 8 yr of age (β) and the increase of mortality rate with age (γ) were not significantly different between sexes (Table 7), despite an apparent pattern of increasing difference of survival with age. For isard and roe deer, the sex differences in the absolute values of the linear and quadratic coefficients were consistent with expectations: both terms were larger for males than for females (Table 6). Body mass had no significant effect on the three coefficients (Table 7), possibly because of the high variability of each of the coefficients among species (Table 7).

Onset of senescence, maximum known longevity and body mass

When we considered the entire data set for any sex–population group, the best model often implied a de-

TABLE 6. Intercept, coefficient of the linear term, and coefficient of the quadratic term of the quadratic-logistic model relating survival and age, according to species, population, and sex, for five populations of ungulates.

Species	Population	Sex	Intercept (α) [M < F]	Linear term (β) [M > F]	Quadratic term (γ) [M > F]
Bighorn sheep	Sheep River	M	1.719 ± 0.298	−0.032 ± 0.156	0.012 ± 0.026
		F	2.150 ± 0.198	−0.197 ± 0.038	−0.025 ± 0.010
			[yes]	[no]	[no]
	Ram Mountain	M	1.028 ± 0.183	−0.165 ± 0.096	0.0006 ± 0.017
		F	2.059 ± 0.143	−0.172 ± 0.028	−0.001 ± 0.006
			[yes]	[=]	[no]
Isard	Orlu	M	2.284 ± 0.372	−0.091 ± 0.084	−0.035 ± 0.022
		F	2.238 ± 0.160	−0.124 ± 0.044	−0.002 ± 0.005
			[=]	[no]	[yes]
Roe deer	Chizé	M	1.435 ± 0.217	−0.208 ± 0.064	−0.018 ± 0.017
		F	2.348 ± 0.167	−0.152 ± 0.047	−0.004 ± 0.007
			[yes]	[yes]	[yes]
	Trois-Fontaines	M	1.122 ± 0.233	−0.222 ± 0.108	−0.026 ± 0.023
		F	1.725 ± 0.178	−0.225 ± 0.040	−0.006 ± 0.011
			[yes]	[=]	[yes]

Notes: The headings in square brackets indicate whether we expected male coefficient values to be larger or smaller than female values (M > F or M < F, respectively). The table entries in square brackets indicate whether the difference between male and female values followed the expected pattern for a given population [yes], opposite to that expected [no], was not >5% of the lowest value [=].

crease in survival beginning at age two (Table 4). However, when testing for an effect of age on survival between 2 and 7 yr of age, we found that survival actually decreased over this age range only for male bighorn sheep at Ram Mountain. In the other nine cases the slopes of survival and age were not significantly different from zero and in three cases they were positive (Table 8). Therefore for most population–sex groups, we could identify a ''prime-age'' phase during which survival was relatively high and constant compared to other age classes (see also Fig. 1).
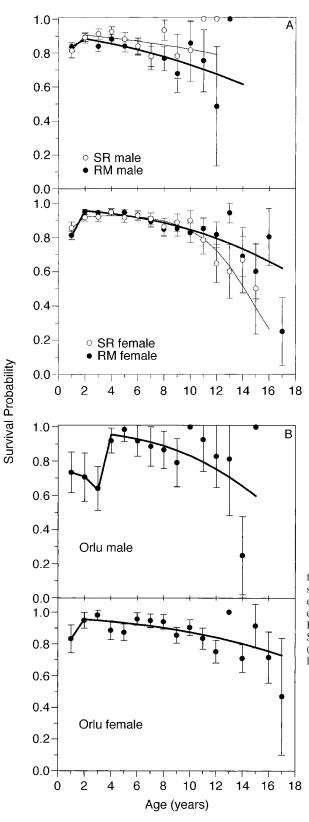
There was no evidence that the onset of senescence coincided with age of first reproduction in females. The yearly survival rate of females aged 2–7 yr estimated from the Caughley-like model was consistently high, between 0.92 and 0.95, whatever the species and the population. The survival rates for prime-aged females in all populations were remarkably similar (Table 5), despite a mass range from 22 kg in roe deer to 75 kg in bighorn sheep. Maximum recorded longevities were also similar across species: the oldest males died at 13 yr in bighorn, 14 yr in roe deer, and 16 yr in isard; while the oldest females reached 18 yr in roe deer, 19 yr in bighorn, and 21 yr in isard. In all populations, the oldest known female was 4–6 yr older than the oldest known male.

DISCUSSION

Our study is the first empirical comparison of interpopulation and interspecific variability in the shapes of mammalian survival curves based on estimates obtained from marked animals. Survival rates decreased with age for both sexes in five wild populations of three

ungulates, providing strong evidence for effects of senescence on survival. The pattern of senescence, however, differed among sexes, populations, and species. We will first consider some methodological problems that could affect survival estimates, then discuss sex differences in relation to sexual selection theory and finally examine the relevance of our results for evolutionary and nonevolutionary theories of senescence.

Methodological questions and evidence of senescence

Before attributing age-specific survival patterns to senescence (defined as an intrinsic decrease of survival capacity: Williams 1957, Abrams 1991), we must examine other factors that may affect the estimation of age-specific survival rates obtained with capture–recapture methods, including selective hunting or removals and age-specific dispersal. As explained in the *Methods* section, we did not include in our analysis deaths caused by hunting or removals. Nevertheless, if hunting or removals were not random (with respect to age, sex, body size, or trophy size), they could bias the results and possibly act as a selective force modifying demographic characteristics of populations (Heimer et al. 1984, Skogland 1989, Jorgenson et al. 1997). If hunters shot the largest individuals, then we would estimate ''natural'' survival rate on the remaining set of smaller and possibly weaker individuals, and hence may underestimate actual survival rates. Hunting is unlikely to affect our results for roe deer and isard, given the low number of culled individuals (Table 2). In the roe deer populations, unmarked yearlings to be removed were randomly chosen among those captured; therefore the marked sample was representative of the
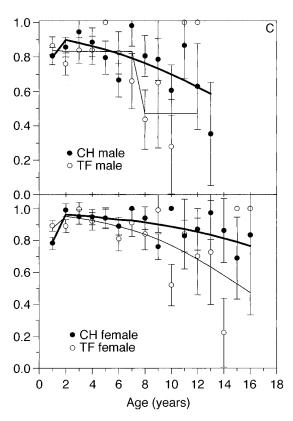
FIG. 1. Annual survival rate as a function of age (in years) for three species of ungulates. Solid and open circles are survival rates estimated from the age-dependent model (model 2) and are shown with standard errors. Lines link age estimates obtained from the selected model in each case. Bolded lines correspond to black circles. (A) Bighorn sheep, SR, Sheep River population; RM, Ram Mountain population. (B) Isard, Orlu population. (C) Roe deer, CH, Chizé population; TF, Trois-Fontaines population.

TABLE 7. Tests for the effects of sex, species, and body mass on the three coefficients of the quadratic-logistic regression between age and survival (see Table 6 for values).

Tests (and models)	Intercept (α)			Linear term (β)			Quadratic term (γ)		
	df	F	P	df	F	P	df	F	P
Two-way ANOVA									
Interaction sex and species	2, 4	0.603	0.590	1, 4	0.437	0.673	2, 4	1.290	0.370
Species	2, 6	0.677	0.543 (18.4)	2, 6	2.623	0.152 (46.6)	2, 6	0.173	0.882 (4.1)
Sex	1, 8	15.661	0.004	1, 8	0.011	0.920	1, 8	0.516	0.493
ANCOVA									
Body mass	1, 7	0.183	0.682	1, 7	<0.001	0.995	1, 7	<0.001	0.984
Sex	1, 7	12.423	0.010	1, 7	0.010	0.925	1, 7	0.434	0.531

Notes: Because none of the interactions between sex and species were significant, the test for species effect was performed using a two-way ANOVA without interaction. Similarly, because the species effect was not significant, the sex effect was tested using a one-way ANOVA. The effect of body mass was tested using an ANCOVA with sex as a categorical variable. The percentage of the variability in α, β, and γ explained by the interspecific differences are indicated in parentheses.

population. Ewe removals at Ram Mountain in 1972–1980 were not based on morphological criteria, and female hunting at Sheep River was irrelevant as only two females included in our analyses were shot. In both populations of bighorn sheep, however, males with fast-growing horns may become legal one or two years before slow-growing males (Jorgenson et al. 1998). Hunting had two possible effects on our analysis of senescence in bighorn males. First, because we could only monitor a few old males, senescence could not be described as confidently as for the other sex–population groups. Second, hunting modified the age structure of males compared to unhunted populations. The scarcity of males 8 years of age and older may allow males to breed at a younger age than in unhunted populations. Early participation in the rut may increase mortality of young adult males (Jorgenson et al. 1997). In unhunted populations of bighorn sheep senescence in males may occur later than in our study populations. Because hunting pressure was similar in our study sites, however, it is unlikely that hunting could explain the differences in survival seen among bighorn males at Sheep River and at Ram Mountain (Fig. 1).

Age-dependent dispersal could bias survival estimates because capture–mark–recapture methods only estimate local survival; mortality and dispersal cannot be distinguished. The roe deer populations were enclosed and therefore dispersal was impossible. For isard and bighorn, female dispersal is very uncommon (Festa-Bianchet 1986a, Loison 1995), especially among adults. Male dispersal in bighorn sheep is almost absent at Sheep River, and is uncommon at Ram Mountain, where we either saw most emigrant males in a neighboring population or obtained tag reports from hunters (Festa-Bianchet 1986b, Jorgenson et al. 1997). Therefore, dispersal was unlikely to affect our survival estimates for bighorn males. Dispersal probably had a strong effect on our analysis of survival for young male isard: the apparently high ''mortality'' of males aged 2–3 yr (Fig. 1) was mostly due to emigration. Because five of eight male isard that were known to emigrate were aged 1–3 yr (Loison 1995), however, dispersal was unlikely to affect our analysis of survival of males 4 yr of age and older.

Age-specific reproductive features and age-specific survival patterns

Relationships between age-specific reproduction and age-specific survival are crucial to understanding life history strategies (Stearns 1992) and evaluating theo-

TABLE 8. Slopes and 95% confidence intervals of the relationship between age and survival from 2 to 7 years of age in five ungulate populations.

Species	Population	Sex	Slope	Confidence interval
Bighorn sheep	Sheep River	male	−0.172	−0.350, +0.006
		female	0.056	−0.088, +0.201
	Ram Mountain	male	−0.170	−0.305, +0.036
		female	−0.139	−0.302, +0.023
Isard	Orlu	male	0.193	−0.738, +1.123
		female	−0.132	−0.444, +0.180
Roe deer	Chizé	male	−0.166	−0.399, +0.066
		female	−0.093	−0.431, +0.246
	Trois-Fontaines	male	0.123	−0.197, +0.443
		female	−0.254	−0.517, +0.010

ries on the evolution of senescence. Within this context, we compared (1) males and females, which have different reproductive features, (2) gender differences in species that have different mating systems, and (3) different populations of the same species for roe deer and bighorn.

Three general patterns were evident in our results: survival of males was lower than survival of females, the gender differences in survival tended to increase among old individuals, and sex-biased survival appeared unrelated to the level of polygyny. Because of the predominantly polygynous mating system, in most mammal species males are expected to have lower survival than females (Ralls et al. 1980, Promislow 1992). Evidence of higher survival rates for females than for males has been found in several mammals (Clutton-Brock et al. 1982, Owen-Smith 1993*b*), but many studies have found no sex differences or even a male bias in survival in dimorphic polygynous species (Van Vuren and Bray 1986, Berteaux 1993, Fancy et al. 1994, Compton et al. 1995, Toïgo et al. 1997 Cransac et al. 1997). Some studies may have failed to find sex differences in survival despite polygynous mating systems because they monitored expanding populations for which food resources were not limited. Males appear to be more sensitive than females to starvation (Clutton-Brock et al. 1985*a*), and sex differences in survival may not occur when resources are abundant. Among our study populations, we found a significant sex difference in survival, except for isard at Orlu, which nevertheless exhibited a trend for greater female survival.

Contrary to our expectations, female-biased adult survival was not related to either sexual size dimorphism or to level of polygyny. The strongest female bias was for roe deer, the least dimorphic and the least polygynous of the species we studied. In the highly polygynous and sexually dimorphic bighorn and in the polygynous isard, sex differences were smaller than in roe deer. Population-specific features and changes in resource availability cannot explain our results: the roe deer populations consistently showed strong sex differences in survival despite differences in population dynamics, density, and food availability (Gaillard et al. 1993, 1996). We therefore question the assumption that sexual dimorphism in adult survival is related to the costs for males of polygyny and of sexual size dimorphism. Lower survival is expected for males in polygynous species because of intrasexual competition and the costs of large body size (Clutton-Brock et al. 1982, 1985*b*, Clutton-Brock and Albon 1985, Promislow 1992). However, polygyny in itself may be a poor measure of the level of competition and of the energetic expenditures devoted to reproduction by males. Owen-Smith (1993*b*) suggested that in several small, weakly

dimorphic and weakly polygynous antelopes, the female bias in sex ratio among adults was as high as in more dimorphic and more polygynous species. Different mating systems could involve important differences in risk of injury from male–male combat and in the energetic expenditure required for access to females. Reproductive costs in males could be higher for a weakly polygynous but territorial species such as roe deer than for promiscuous but nonterritorial species such as isard (Lovari and Locati 1991) and bighorn sheep (Hogg 1984). The major costs of reproduction for ungulate males originate from fighting with other males, not from copulations (Geist 1986, Gosling et al. 1987, Festa-Bianchet et al. 1990, Alvarez 1993, Komers et al. 1994). A highly polygynous mating system with low frequency of male–male combats (Owen-Smith 1984, 1993*a*) may not lead to greater male mortality than a less polygynous system.

Our earlier examinations of survival patterns in roe deer and bighorn sheep suggested low variability of adult survival rates among populations (Gaillard et al. 1993, Jorgenson et al. 1997). In this paper, by adding several years of data, we confirmed that prime-age survival of females is similar in different populations of the same species (Tables 3 and 6). In addition, we found that prime-age female ungulates of different species also have very similar survival rates. All survival estimates for prime-age females were within 3% of each other, despite substantial differences in body mass, in reproduction (isard and bighorn always produce singletons, while roe deer regularly produce twins and sometimes triplets), and in predation pressure (bighorn coexisted with wolves and cougars, the other species had no large predators). When we considered patterns of senescence, however, we found marked differences among populations of the same species. A relatively small proportion of the variability in the coefficients describing the shape of the senescence curve (from the quadratic-logistic function) was explained by the species effect (Table 7). If species-specific life history patterns have been shaped by natural selection, then we would expect greater variability in survival for older than for prime-aged individuals among populations of the same species, as selective pressures acting upon older animals would be weaker than those acting upon younger animals (Hamilton 1966, Caswell 1989).

Evaluation of senescence hypotheses

We found that senescence did not occur earlier and did not increase faster for small species or for the smaller sex (females) than for large species or for the larger sex (males). Our results therefore concur with earlier empirical studies (Austad and Fisher 1991, 1992), showing no support for nonevolutionary hypotheses

relating senescence patterns to body mass and metabolic rate (Sacher 1978).

Our analysis confirmed that maximum known longevity is a misleading measure of senescence patterns (Comfort 1979). In our study populations, maximum known longevities were very similar: despite differing patterns of senescence, the oldest known female in four of five populations died at 18 or 19 yr of age. In bighorn sheep, maximum known male longevity was 13 yr in both populations, despite much lower survival and faster senescence at Ram Mountain than at Sheep River.

As shown empirically by our study and theoretically by Abrams and Ludwig (1995), many models can possibly describe age-specific survival rates. The Gompertz model, which describes senescence with a single parameter and is therefore widely used for interspecific comparisons (e.g., Promislow 1991), is only one of them. When other models provide a better fit to observed age-specific survival patterns, the decline of survival rate with age is not constant but varies with age. Senescence is therefore not easily defined and compared between species or populations (Abrams and Ludwig 1995). We chose here to base the sex–species group comparison on a general and flexible model (the quadratic-logistic model), which was not the most parsimonious in every sex–species group, but which could be accepted as a common description of senescence patterns.

Both the mutation-accumulation hypothesis (Medawar 1952) and the pleiotropy hypothesis (Williams 1957) are based on the diminishing strength of selection against deleterious mutations after first reproduction (Hamilton 1966). Our results do not support the prediction that the decrease of survival rates begins at the age of first reproduction. Age of primiparity was 2 yr in all of our study populations, yet female survival varied little between 2 and 7 yr of age. Other studies confirm that prime-age survival of female ungulates is usually high and constant (see Benton et al. 1995 for red deer, *Cervus elaphus,* Loison et al. 1994 for chamois, *Rupicapra rupicapra,* Gaillard et al. 1998 for a review). In female ungulates, longevity is a major determinant of lifetime reproductive success (Clutton-Brock et al. 1988), and high survival of prime-aged females could result from strong selection to avoid mortality, perhaps by reducing reproductive effort (Eberhardt 1985). Recent results based on long-term monitoring of long-lived birds suggest similar patterns in survival (Aebisher and Coulson 1990, Weimerskirsch 1992, Holmes and Austad 1995, McDonald et al. 1996). These studies found that although survival decreased with age, at least after an age threshold, adult survival was high over an extended range of ages (Ollason and Dunnett 1988). Until long-term data on the survival of old birds became available, it was believed that the survival rates of adult birds were not age dependent (Lack 1954). The short-term negative effects of reproductive effort on survival appear to be weak in species for which high survival over an extended prime-age stage has a strong effect on fitness. As pointed out by McDonald et al. (1996), there can be differences between the observed decrease of survival with age, or "actuarial senescence," and degenerative senescence, which implies irreversible physiological changes. Documenting actuarial senescence in wild populations and comparing different species is complementary to the genetic and experimental approaches (Gustafsson and Part 1990). Ungulates are iteroparous species, for which individual age has a strong effect on reproductive patterns and for which age distributions affect population dynamics (Gaillard et al. 1989). The study of evolutionary problems in ungulates requires long-term monitoring of marked individuals, which can be achieved in a limited number of populations in which experimental manipulations are difficult and usually compromise the long-term monitoring program. We submit that the comparative and descriptive approach, when based on reliable methodology as used in this paper, can provide valuable insights into trade-offs and environmental constraints, allowing an understanding of the evolution of life histories.

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