

Early onset of reproductive senescence in domestic sheep, *Ovis aries*

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A central theme in life history theory is to determine how reproduction varies with age in iteroparous organisms. Evidence of ageing and senescence, defined as the progressive loss of function accompanied by decreased performance with age, remains poorly documented for large herbivores, in particular as it relates to reproduction. Analyses of body weight of 87 532 domestic sheep lambs demonstrates that onset of reproductive senescence in ewes occurs already at 5 and 6 years of age when measured, respectively, as lamb weight and litter size produced. This provides convincing evidence of early onset of reproductive senescence in this highly domesticated sheep breed. As this is earlier than indicated for other *Ovis* species as well as for the Soay sheep, an ancient and lightly domesticated sheep, we hypothesize that there may be a cost of selection for large litter size in mammalian herbivores.

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A central theme in life history theory is to explain how reproduction varies with age in iteroparous organisms (Stearns 1992). The theory of terminal investment predicts that parents should invest more in their offspring as their own potential for future reproduction fails (Gadgil and Bossert 1970, Trivers 1972, Pianka and Parker 1975, Clutton-Brock 1984). The proportion of resources a mother invests is therefore expected to increase toward the end of her life span, when the number of offspring she can expect to rear in the future is low (Clutton-Brock et al. 1982, Green 1990). However, ageing and senescence, defined as the progressive loss of function accompanied by decreased performance with age (Kirkwood and Austad 2000), may act as a constraint to increased investment with age. There has been some controversy regarding senescence in survival in mammalian populations (Promislow 1991, Gaillard et al. 1994, Sibly et al. 1997), which in part is a result of

the scarcity of observed individuals living to the onset of senescence in natural populations (Loison et al. 1999).

Ungulates are highly suited for studies of senescence, as they are long-lived and reproduce at the same time each year, in contrast to rodents where senescence may be confounded with seasonality (Slade 1995). Recently, decreased survival with increasing age was reported in isard *Rupicapra rupicapra*, roe deer *Capreolus capreolus*, bighorn sheep *Ovis canadensis* (Loison et al. 1999) and Soay sheep (*Ovis aries*) (Catchpole et al. 2000), while data on reproductive senescence are scarce. To test the hypotheses of possible reproductive senescence, we extracted data on litter size and body weight of 87 532 lambs from ewes of known age and from the heavily domesticated Dala breed (Drabløs 1997), which had been free-ranging at pastures in Norway during the summer.

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Material and methods

Study area and husbandry practice

The study area is the western part of southern Norway. Data come from 19 municipalities in the counties Rogaland (3), Hordaland (3), Sogn and Fjordane (4), Møre and Romsdal (3), and Sør-Trøndelag (6). In general, temperature and precipitation decline from south to north and from coast to inland, while snow depth increases (Langvatn et al. 1996, Mysterud et al. 2000). In summer both the length of the growing season and total degree-days decline from south-west to north-east (Langvatn and Albon 1986). Topography is generally steeper in the inland (Mysterud et al. 2001a).

During winter, sheep are fed both grain feeds/concentrates and hay/ensilage, and this practice has been stable during the study period and between regions. During summer, the sheep are free-ranging from June/July through September/October (Mysterud et al. 2001b). Stocking densities of sheep on pastures are generally low, compared e.g. to Scotland (Simpson et al. 1998), ranging from 5 to somewhat above 50 sheep per km² (Mysterud 2000). Sheep are mostly grazing in the alpine and subalpine zone (Abrahamsen et al. 1977).

Sheep data and statistical analyses

Data on body weight, sex, breed, age of ewe (years), age of lamb (days), litter size, location (municipality) and year (1989–98) of 87 532 lambs of the Dala breed were retrieved from the Sheep control database (“Sauekontrollen”) in Norway (Table 1). These are lambs that have been free-ranging all summer, and that are weighed shortly after they are gathered from the pastures. Age of ewes and lambs were known precisely since year and date of birth was recorded. To account for possible confounding effects of location (municipality) and year (e.g. climate and density), these were entered as covariates in all models.

We used mainly general additive models (GAM; Hastie and Tibshirani 1990) with smoothing splines to analyse variation in weight of lamb and litter size, as these relationships were expected to be nonlinear with

regard to age of ewe. Splines are piecewise polynomials that are smooth (twice differentiable) in the spline knots (the control points of the splines) (Bjørnstad et al. 1999). The complexity of the curve (i.e. the number of degrees of freedom; df_{spline}) associated with the smoothing spline was selected by repeated fitting of the GAM with varying df_{spline} for one variable (1–12), while holding df_{spline} of the other variables constant. The fit of the different models was then tested in an ANOVA setting (see Venables and Ripley 1994: 251–252), and the selected df_{spline} was then used in the graphical presentation. Weight of lamb was ln-transformed to stabilize the variance.

To accurately determine at what age onset of reproductive senescence in domestic sheep started, we entered age of ewe as a factor and used the “treatment” contrast within a linear modelling setting that adjusted for multiple comparisons (i.e. a family wise comparison with the Tukey method in S-Plus; Venables and Ripley 1994). Based on results from the GAM (see below), we restricted this analysis to ewes between 3 and 7 years of age.

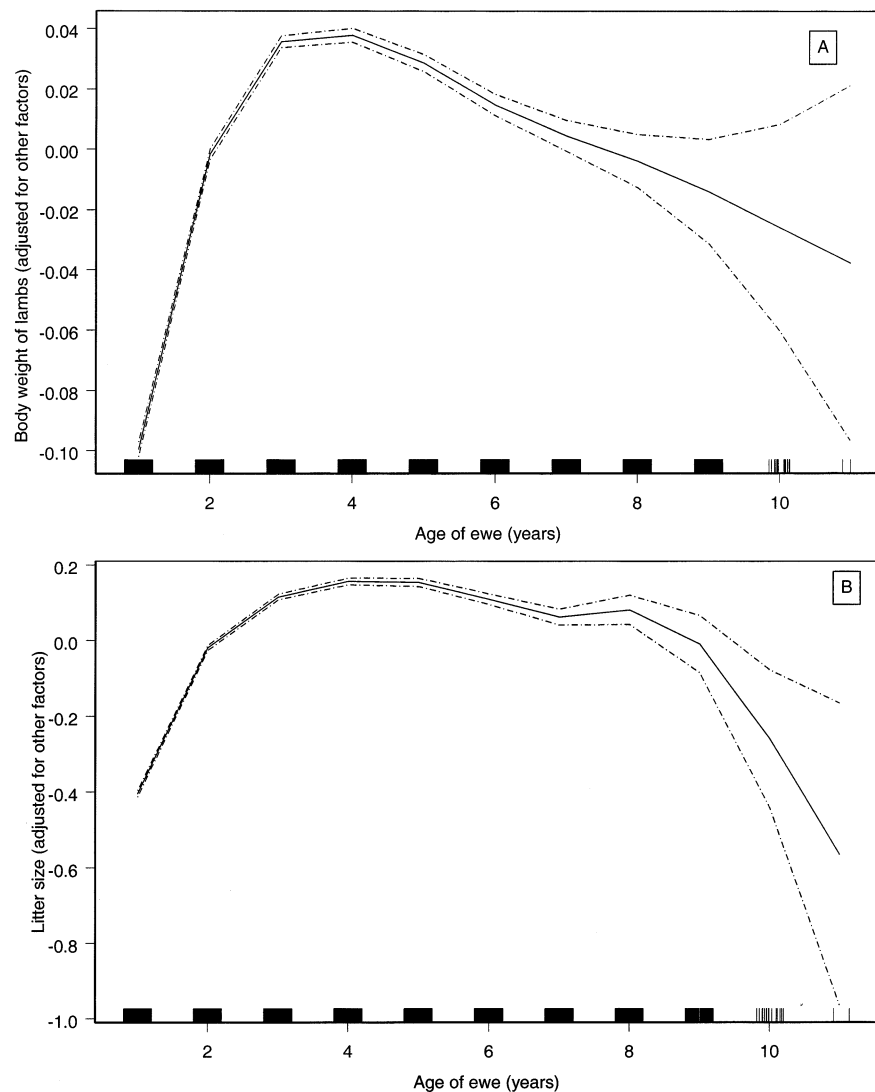
Results

There was a clear peak in production of lambs at 4 and 5 years of age when measured, respectively, by body weight of lambs (Table 1, Fig. 1A, $df_{\text{spline}} = 5$ vs. 6, $df = 1,86478$ $F = 13.333$, $p < 0.001$) and litter size (Fig. 1B, $df_{\text{spline}} = 7$ vs. 8, $df = 1,87056$ $F = 5.490$, $p = 0.019$). We controlled for that body weight of lambs increased with age of lamb ($df_{\text{spline}} = 10$ vs. 11, $df = 1,86478$, $F = 4.515$, $p = 0.034$), was higher in males than in females ($df = 1,86479$, $F = 5827.404$, $p < 0.001$), was negatively related to litter size ($df = 1,86487$, $df_{\text{spline}} = 2$ vs. 3, $df = 1,86479$, $F = 35.282$, $p < 0.001$), and showed significant variation also due to location ($df = 1,86928$, $F = 126.528$, $p < 0.001$) and year ($df = 1,86487$, $F = 157.908$, $p < 0.001$). We also controlled for the significant variation in location ($df = 1,87063$, $F = 216.030$, $p < 0.001$) and year ($df = 1,87080$, $F = 30.157$, $p < 0.001$) when analysing litter size. The contrast analysis supported that onset of reproductive senescence in domestic sheep was 5 and 6 years when measured, respec-

Table 1. Sample sizes of lambs, average litter size and average mean body weight of 87 532 lambs from ewes of different ages.

Age of ewe (years)	1	2	3	4	5	6	7	8	9	10	11
Number of lambs	14 844	22 792	18 031	13 560	9113	5754	2563	689	159	21	2
Adjusted mean litter size	1.53	1.95	2.04	2.08	2.08	2.03	1.97	2.00	1.92	1.76	1.00
Adjusted mean weight (kg) of singleton lamb	42.9	47.1	48.2	48.6	48.2	47.7	47.3	46.4	46.2	43.1	45.0
Adjusted mean weight (kg) of twin lamb	38.2	43.3	44.9	45.0	44.7	43.9	43.3	43.6	42.4	40.1	
Adjusted mean weight (kg) of triplet lamb	39.1	41.0	42.2	41.8	41.4	41.3	40.2	39.5	41.3	44.8	

Fig. 1. The relationship between (A) body weight of lamb and age of ewe and (B) litter size and age of ewe in domestic sheep, based on data from 87 532 lambs. Results are presented as a result of fitting an additive model to the data on body weights with smooth functions on continuous predictor. The dashed lines are 95% pointwise confidence intervals (Venables and Ripley 1994).



tively, as weight of lambs (Fig. 2A) and litter size (Fig. 2B).

Discussion

There was compelling evidence of reproductive senescence in domestic sheep, as both litter size and body weight of lambs during autumn clearly decreased after ewes reached, respectively, 5 and 6 years of age (Fig. 1; Table 1). Some earlier studies of wild ungulates indicate reproductive senescence measured as proportion of females breeding (Festa-Bianchet 1988, Garrott et al. 1991, Langvatn et al. 1996, Green 1990, Bérubé et al. 1999). Also, senescence in domestic sheep has earlier been reported (in the agricultural literature) for litter size (Turner 1969, Dickerson and Glimp 1975, Gates 1993), but with no formal (i.e. tabular data, Gates

1993) or inadequate statistical testing (i.e. forcing a symmetrical quadratic curve with age on an asymmetrical relationship, Dickerson and Glimp 1975) for onset of senescence. Our study is the first reporting reproductive senescence both in litter size and weight of offspring. A possible confounding factor is that sheep farmers usually remove less productive ewes from the herd. This was clearly evident also in our material as number of sheep ewes decreased sharply after 7 years of age, and sheep 8 years or older was rare in our data files (Table 1). However, this increased heterogeneity would lower the slope estimates between litter size/body weight of lamb and ewe age after onset of senescence and make our test more conservative (Vaupel and Yashin 1985). Restricting the analysis to ewes between 3 and 7 years of age clearly showed that ewes aged 3 and 4 years produced the heaviest lambs (Fig. 2A) and ewes aged 4 and 5 produced the largest litters (Fig. 2B).

As onset of senescence in domestic sheep was earlier than previously reported for wild ungulates (Table 2), there is time to look for possible explanations for the comparative pattern of senescence in large herbivores.

(1) *Body size.* Due to allometric effects, we may expect that larger animals have a later onset of senescence than smaller ones (Peters 1983). Indeed, onset of reproductive senescence was at 9 years of age in the small roe deer (27 kg; Gaillard et al. 1998b), while it is at age 13 in bighorn sheep (72 kg; Bérubé et al. 1999), and somewhere between 13 and 17 in red deer (108 kg; Langvatn et al. 1996). However, ewes from the Dala sheep breed used in this study weigh about 80–100 kg (Drabløs 1997), and there is thus no simple relationship between reproductive senescence and body size in large herbivores. Similarly, it was no simple relationship between body size and senescence in survival (Loison et al. 1999).

(2) *Costs of reproduction.* The evolutionary based hypotheses of senescence, the mutation-accumulation hypothesis (Medawar 1946, Edney and Gill 1968) and the antagonistic pleiotropy hypothesis (Medawar 1946, Williams 1957, Hamilton 1966, Rose 1991), are both based on the diminishing strength of selection against deleterious mutations after first reproduction (Hamilton 1966).

A cost of reproduction, where an increase in reproductive effort reduces future survival or fecundity, might be the kind of pleiotropic gene action that generates senescence (Gustafsson and Pärt 1990, Stearns 1992, Bérubé et al. 1999). The disposable soma theory (Kirkwood 1981, 1990, Abrams and Ludwig 1995, Kirkwood and Austad 2000), a physiological variant of the antagonistic pleiotropy hypothesis, also suggests that there is a trade-off between today's reproduction and soma repair (and hence between reproductive effort and longevity; Cichon 1997). In female ungulates, longevity is considered a major determinant of lifetime reproductive success (Clutton-Brock et al. 1988, Gaillard et al. 2000). We expect strong selection to avoid mortality, and prime-aged females have indeed generally a high survival rate (Caughley 1966, Gaillard et al. 1998a). This may be a result of reduced reproductive effort to avoid mortality (Eberhardt 1985). Litter size is an important factor for cost of reproduction (Robbins and Robbins 1979, Stearns 1992). Both bighorn sheep and red deer are generally monotoxic species, while roe deer, with an earlier onset of senescence (Gaillard et al. 1998b), is polytocous (Sæther and Gordon 1994). The comparative pattern therefore does not suggest a simple relationship between reproductive senescence and reproductive effort.

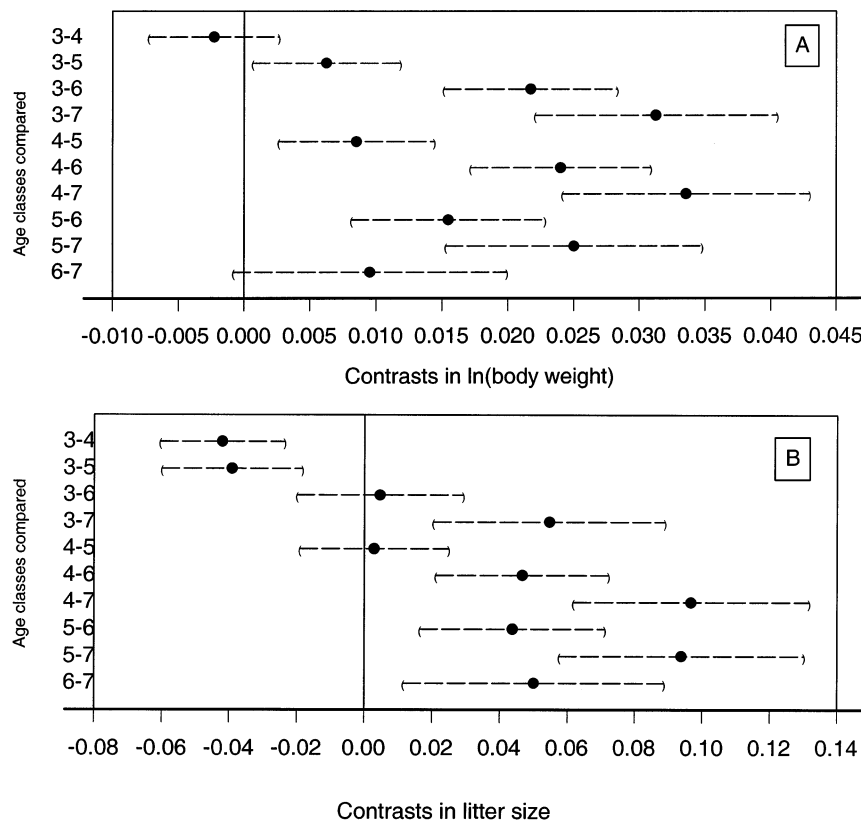


Fig. 2. Results from contrast-analyses comparing differences between ewes of different ages to determine onset of reproductive senescence as measured by (A) body weight of their lambs and (B) litter size. If error-bars do not include zero, then age-classes compared are significantly different from each other.

Table 2. A review of studies showing senescence in life history traits related to reproductive effort of female ungulates.

Species	Body weight (kg)	Life history trait	Onset of senescence (yr)	Reference
Moose (<i>Alces alces</i>)	331	Litter size	13	Ericsson et al. 2001
Roe deer (<i>Capreolus capreolus</i>)	27	Productivity	9	Gaillard et al. 1998b
		Implantation failure	>8	Hewison and Gaillard 2001
Bison (<i>Bison bison</i>)	450	Proportion breeding	12	Green 1990
Red deer (<i>Cervus elaphus</i>)	108	Ovulation rate	13–17	Langvatn et al. 1996
Feral horses (<i>Equus caballus</i>)	358	Proportion breeding	>15	Garrott et al. 1991
Domestic sheep (<i>Ovis aries</i>)	80–100	Offspring body weight	5	This study
		Litter size	6	This study
Soay sheep (<i>Ovis aries</i>)	24	Offspring mortality	7	Catchpole et al. 2000
		Fecundity	Not found	Doney et al. 1974, T. Coulson pers. comm. (updated unpubl. results)
Bighorn sheep (<i>Ovis canadensis</i>)	72	Proportion breeding	>9	Festa-Bianchet 1988
Reindeer (<i>Rangifer tarandus</i>)	69	Proportion breeding	13	Bérubé et al. 1999
		Offspring body weight	9	Weladji et al. 2001

However, we argue that the pattern may be depending also on phylogeny. In contrast to wild *Ovis* species that have small litter sizes (up to about 1.2), which is the common pattern for wild grazing ungulates (Couturier 1962, Sæther and Gordon 1994), domestic sheep have been artificially bred for large litter sizes (Clutton-Brock 1981, Clutton-Brock et al. 1997). Early onset of senescence will therefore be expected in domestic herbivores such as sheep if there is a trade-off between early and late reproductive effort. Interestingly, our analyses found an earlier onset of senescence than in the similar sized bighorn sheep (Bérubé et al. 1999). Further, the well studied population of primitive domestic sheep from the islands of St. Kilda in the Outer Hebrides of Scotland, known as the Soay sheep (Jewell et al. 1974, Clutton-Brock et al. 1991, Grenfell et al. 1998), has undergone little artificial selection since it was first taken to St. Kilda during the neolithic period, i.e. 6000–3800 B.P (Clutton-Brock 1981). Soay sheep produces one or two lambs (average 1.15 for adults producing young; yearlings never produce twins; 20% do not reproduce; Coulson et al. 2000), while the sheep in our population produced between one and five offspring (average 1.9, Table 1). Data for onset of reproductive senescence for Soay sheep using body weight of lambs (though for a low sample of ewes) found no decrease within 10 years of age (Doney et al. 1974). Recent analysis on a much larger sample confirms that there is no evidence of senescence in fecundity in Soay ewes (T. Coulson, unpubl. results), despite the smaller body size of Soay sheep compared to the Dala breed (Table 2). However, yearling mortality (12–24 months) varied as a function of age of ewe (Clutton-Brock et al. 1992), and increased mortality of yearlings started when mothers reached 7–8 years of age. In sum, reproductive senescence seems to occur much later in the lightly domesticated Soay sheep with low litter size compared with the heavily domesticated Dala breed from Norway with larger litter sizes.

Studies on more species and breeds are needed before we can say that we understand why some ungulate species have an earlier onset of reproductive senescence than other species. It may also be variation within species related to density (Mysterud et al. 2001c). Our analysis at least indicates that it may be worthwhile to relate onset and rate of senescence to reproductive effort. If this is the case, there may be a cost of selection for large litter size in large mammalian herbivores, and demonstrates the usefulness of using domesticated animals to advance the understanding of the possible life-history trade-off between senescence and selection for increased reproductive effort in large herbivores in general.

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