

Patterns of reproductive effort in male ungulates

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Abstract

In ungulates, males and females have contrasting life histories, as usually only the females raise the young. How reproductive effort in males varies with individual level and population level characteristics has received little attention in the literature. Using published information on direct (weight loss during the rut) and indirect (rut-related changes in activity budgets, fighting frequency, etc.) measures of reproductive effort, we tested whether effort in males increased with (H₁) increasing age, (H₂) increasing body size, (H₃) decreasing population density, (H₄) increasingly female-biased sex ratio and with a younger male age structure. Consistent with H₁, reproductive effort was consistently higher in prime-aged than in younger males in a large number of studies. Among younger males, sub-adult males had an equal or higher effort than yearling males. Prime-aged males had more typical rutting behaviour (e.g. roaring, tending, fighting and chasing frequencies) and they often lowered their intake of forage during the rut. However, reproductive effort usually declined for very old age classes. Reproductive effort increased with size (H₂) also after accounting for age. Data on effort vs (H₃) density and (H₄) sex ratio/male age structure were inconclusive. Clearly, far more studies relating effort to population characteristics are needed before the rutting ecology of male ungulates can be understood.

Key words: ungulates, reproductive effort, males

INTRODUCTION

In ungulates, males and females have contrasting life histories. Usually only the females take care of the young (Clutton-Brock, 1989; Davies, 1991). Thus, while female reproductive success depends on raising young successfully, male reproductive success depends on fighting for access to females during a short rutting season (Clutton-Brock, Guinness & Albon, 1982; Clutton-Brock, Albon & Guinness, 1988). Reproductive effort in males therefore originates from fighting with other males for access to females, patrolling territories, roaring (McComb, 1987) and tending females (general reviews: De Vos, Brokx & Geist, 1967; red deer *Cervus elaphus*: Lincoln, Youngson & Short, 1970; reindeer *Rangifer tarandus*: Espmark, 1964; Lent, 1965; Henshaw, 1970; Skogland, 1989; fallow deer *Dama dama*: Braza, Garcia & Alvarez, 1986; mouflons *Ovis orientalis*: Cavallini, 1987; moose *Alces alces*: Lent, 1974; elk *Cervus elaphus*:

Struhsaker, 1967; mountain goat *Oreamnos americanus*: Geist, 1964; Soay sheep *Ovis aries*: Grubb & Jewell, 1973; Grubb, 1974). Female ungulates are the more important component for the dynamics of populations as they produce and raise the young. Recent reviews of life history of ungulates therefore concentrate entirely on females (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al.*, 2000). Some models of optimal male mating strategies have been reported (Hogg, 1984; Gosling, 1986; Dunbar, Buckland & Miller, 1990; Sandell & Liberg, 1992; Forchhammer & Boomsma, 1998), but generally the life history of males has received much less attention. The somatic weight loss during an annual cycle in males is equal to (Bobek, Perzanowski & Weiner, 1990) or greater than it is in females (Leader-Williams & Ricketts, 1981; Pérez-Barbería, Mutuberria & Nores, 1998), and there is often a high frequency of antler wounding (Kitchen, 1974; Geist, 1986).

In polygynous ungulates, reproductive success is much higher among prime-aged males (Squibb, 1985; Pemberton *et al.*, 1992; Asa, 1999), and they are usually the harem holders (Clutton-Brock *et al.*, 1982). However,

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Table 1. Patterns of reproductive effort measured with indirect measures (such as rut-related changes in activity budgets) and direct measures (such as weight loss during rut) and how this relates to (H₁) male age (Y, yearling; SA, sub-adult; PA, prime-aged; O, old, senescent individuals), (H₂) body size (S, small; M, medium sized; La, Large), (H₃) population density (L, low density; H, high density), and combined for (H₄) sex ratio and male age structure (F, female biased, young male age structure; E, more even sex ratio, male age structure)

Species	Parameter	<i>n</i>	H ₁ age	H ₂ size	H ₃ density (index used)	H ₄ sex ratio/ male age structure	Reference
Indirect measures							
<i>Alces alces</i>	Foraging time		PA only				Schwartz <i>et al.</i> , 1987
<i>Alces alces</i>	Fighting intensity		Y/SA < PA/O	S < La			Peek, Van Ballenberghe & Miquelle, 1986
<i>Alces alces</i>	Foraging time	45		S < La			Miquelle, 1990
<i>Antilocapra americana</i>	Interaction frequency		Y/SA < PA/O				Kitchen, 1974
<i>Bison bison</i>	Activity pattern	105	Y < SA < PA > O				Maher & Byers, 1987
<i>Bison bison</i>	Tending frequency		Y/SA < PA/O				Berger, 1989
<i>Bison bison</i>	Aggressive interactions/ tending frequency		Y < SA < PA < O				Komers, Meisser & Gates, 1992
<i>Bison bison</i>	Tending time		SA < PA				Komers, Messier, Flood <i>et al.</i> , 1994
<i>Bison bison</i>	Feeding time/aggressive interactions		SA < PA			Y: F > E	Komers, Messier & Gates, 1994a,b
<i>Bison bonasus</i>	Tending frequency		Y/SA < PA/O				Cabon-Raczynska <i>et al.</i> , 1987
<i>Capra pyrenaica</i>	Activity pattern		Y < SA < PA < O				Alados, 1986a, Lincoln, 1971
<i>Cervus elaphus</i>	Rutting activity		Y/SA < PA				Clutton-Brock <i>et al.</i> , 1982
<i>Cervus elaphus</i>	Fighting frequency		Y < SA < PA/O		L > H (female density)		Clutton-Brock <i>et al.</i> , 1982
<i>Cervus elaphus</i>	Length of rutting season		Y < SA < PA/O				Pépin <i>et al.</i> , 2001
<i>Cervus elaphus</i>	Roaring frequency	3	SA < PA				Bobek <i>et al.</i> , 1990
<i>Cervus elaphus</i>	Rumen fill	115					R. Langvatn, pers. comm.
<i>Cervus elaphus</i>	Rumen fill	81	Y < SA < PA		L = H (total harvest)		Struhsaker, 1967
<i>Cervus elaphus</i>	Feeding time		Y < SA < PA				Bowyer, 1981
<i>Cervus elaphus</i>	Interaction rate		Y < PA				Harper <i>et al.</i> , 1967
<i>Cervus elaphus</i>	Roaring rate		Y/SA < PA/O				Miura, 1984
<i>Cervus nippon</i>	Chasing frequency		Y < SA < PA/O				Alvarez, 1993
<i>Dama dama</i>	Fighting frequency				L < H		Komers, Pélabon & Stenström, 1997
<i>Dama dama</i>	Activity pattern		Y/SA < PA/O				Pélabon & Komers, 1997; Pélabon <i>et al.</i> , 1999b
<i>Dama dama</i>	Fighting frequency				L < H (population/ male density)		Pélabon <i>et al.</i> , 1999a
<i>Dama dama</i>	Interaction frequency			Y: S < La			McElligott, O'Neill & Hayden, 1999
<i>Dama dama</i>	Roaring rate		Y/SA < PA/O				Braza <i>et al.</i> , 1986
<i>Dama dama</i>	Activity pattern		SA < PA/O				Ozoga & Verme, 1985
<i>Odocoileus virginianus</i>	Courtship behaviour		Y < PA				Forchhammer, 1995
<i>Ovibos moschatus</i>	Foraging time		Y = SA < PA				
<i>Ovis canadensis</i>	Male interaction frequency			S < M < L		F < E (SA: F > E)	Singer & Zeigenfuss, 2002
<i>Ovis dalli</i>	Male interaction frequency			S < M < L		F < E (SA: F > E)	Singer & Zeigenfuss, 2002
<i>Ovis dalli</i>	Foraging rates		Y/SA < PA/O	S < M > La			Singer <i>et al.</i> , 1991
<i>Ovis gmelini</i>	Activity pattern		Y/SA < PA/O				Bon <i>et al.</i> , 1995
<i>Rangifer tarandus</i>	Rutting activity		Y/SA < PA/O				Espmark, 1964
<i>Rangifer tarandus</i>	Foraging time	7	Y < SA < PA				Kojola, 1991
<i>Rangifer tarandus</i>	Foraging time		Y/SA < PA				Kojola, 1986

<i>Rangifer tarandus</i>	Chasing, grunting frequency	Y/SA < PA/O	Hirovani, 1994
<i>Rangifer tarandus</i>	Rubbing frequency	Y/SA = PA/O	Adams <i>et al.</i> , 2001
<i>Tragelaphus strepsiceros</i>	Tending frequency	SA < PA/O	Owen-Smith, 1993
Direct measures			
<i>Alces alces</i>	Weight loss	3 2–10% in PA	Franzmann <i>et al.</i> , 1978
<i>Alces alces</i>	Weight loss	9949 Y < SA < PA > O	Mysterud <i>et al.</i> , 2004
			Y: F = E PA: F < E
			L = H
<i>Bison bison</i>	Subcutaneous fat	37 SA < PA	Komers, Heisser & Gates 1994b
<i>Cervus elaphus</i>	Weight loss/ kidney fat loss	115 Pooled for > 5	Bobek <i>et al.</i> , 1990
<i>Cervus elaphus</i>	Weight loss	48 Y/SA < PA/O	Dzięciolowski <i>et al.</i> , 1996
<i>Cervus elaphus</i>	Weight loss/ kidney fat loss	? Pooled for 6–11	Milner, Alexander & Griffin, 2002
<i>Cervus elaphus</i>	Weight loss	13913 Y < SA < PA > O	Yoccoz <i>et al.</i> , 2002
			Y: L = H PA: L < H O: L < H (total harvest)
<i>Dama dama</i>	Weight loss	32 PA only	McElligott <i>et al.</i> , 2003
<i>Rangifer tarandus</i>	Weight loss	7 Y < SA < PA	Kojola, 1991
<i>Rangifer tarandus</i>	Weight loss	54 Y = SA < PA	Mysterud <i>et al.</i> , 2003
			Y: F > E
			Y: L = H (total density during rutting season)

young males also take an active part during rut, and sometimes a quite high reproductive success has been found among young males (Stevenson & Bancroft, 1995; Hogg & Forbes, 1997; Coltman *et al.*, 2002).

We here test the following hypotheses based on empirical evidence of reproductive effort in male ungulates reported in the literature, both related to individual level (H_{1-2}) and population level characteristics (H_{3-4}):

H_1 (age): reproductive effort is predicted to increase with age (e.g. Clutton-Brock *et al.*, 1982; Clutton-Brock, 1984).

H_2 (body size): reproductive effort is predicted to increase with size (Komers, Messier & Gates, 1994b).

H_3 (population density): reproductive effort is predicted to decrease with density (e.g. Clutton-Brock *et al.*, 1982; Clutton-Brock, Rose & Guinness, 1997).

H_4 (sex ratio and male age structure): a female-biased sex ratio is usually correlated with a young male age structure. Young males should increase effort with increasingly female-biased sex ratios (e.g. Solberg & Sæther, 1994), and young males should increase effort when adult prime-aged males are not present (e.g. Komers, Messier & Gates, 1994b).

We include both studies using direct (patterns of weight loss or condition during the rutting season) and indirect measures of effort such as rut-related changes in time-budgets, the last with a stricter focus on mechanisms.

RESULTS

Data directly on somatic weight loss of males during rutting were remarkably scarce; most reported evidence of reproductive effort was from indirect measures on time budget data, such as frequency of fighting, roaring, tending of females and foraging activity (Table 1).

H_1 (age): there was compelling evidence that reproductive effort increased from young to the prime-aged stage (Table 1). For young age classes, sub-adults had a higher or equal reproductive effort when compared to yearlings. Few studies provided explicit data on the transition from prime-age to the old, senescent stage, but effort decreased from prime-aged to the senescent stage, as shown for red deer (and partly for moose) (somatic weight loss) and bison (activity budget), which is inconsistent with H_1 .

H_2 (body size): in most studies, age and size are correlated, and the general pattern for age implies that effort increases with size, as younger males are smaller than prime-aged males. After controlling for age, one study reported increased effort with increasing body size among yearlings and one for prime-aged males (Table 1).

H_3 (population density): there was evidence from two studies of red deer and one for moose that effort decreased with increasing density. In one study on red deer, the decreased effort with increasing density was more marked for older individuals. In contrast to predictions, two studies on fallow deer found increased effort with increasing density, and studies on reindeer found no effect of density on effort of young males.

H₄ (sex ratio and male age structure): four studies reported variation in reproductive effort relative to population sex ratio and/or male age structure. Two studies reported that yearlings, as predicted, had a higher reproductive effort as population sex ratio becomes more female-biased and with a younger male age structure. However, a study including prime-aged individuals, showed that in dall sheep and bighorn sheep, effort decreased with increasingly female-biased sex ratios, but this result seemed somewhat variable depending on male age. In moose, there was no relationship between effort and population sex ratio.

DISCUSSION

Individual level characteristics: age and size

Most observations of reproductive effort in male ungulates fit the well-known pattern that younger males (yearlings and subadults) spend less time in rutting activity (i.e. a lower effort) than the prime-aged males (Table 1). This was evidenced from time budget data during rut such as frequency of fighting, roaring, tending of females and foraging activity, and from a few studies using data directly on somatic weight loss of males during rutting (Table 1). Some more variation was evident when comparing effort of yearling vs sub-adult males. Sub-adult males had either similar or a higher level of reproductive effort. While the pattern for young and prime-aged males is therefore well documented, data from very old, senescent individuals are limited to only four studies. Data from red deer (somatic weight loss; Yoccoz *et al.*, 2002), moose (Mysterud, Solberg & Yoccoz, 2004) and bison (activity budget; Maher & Byers, 1987) show that reproductive effort declines for very old age classes, while one study shows increased effort (aggressive interactions/tending frequency) also for the oldest males (Komers, Messier & Gates, 1992).

Male age and size are often closely correlated (Mysterud *et al.*, 2001), and their effects are often difficult to separate. The general pattern for age implies that effort increases with size, as younger males are smaller than prime-aged males. Since size is a better predictor for dominance than age in males (Clutton-Brock *et al.*, 1982), body size may be a better predictor than age for the level of reproductive effort. After controlling for age, one study reported increased effort (interaction frequency) with increasing body size among yearling fallow deer (Pélabon *et al.*, 1999a). Body condition at the start of the breeding season was the most important determinant of reproductive effort also in prime-aged fallow deer (McElligott *et al.*, 2003). Large-sized yearling males are more frequently harassed by adult, territorial roe deer *Capreolus capreolus* (Wahlström, 1994). Other reports seem less reliable. In *Ovis dalli*, the general pattern was that effort increased with age, but it was suggested that effort may be largest for the next to largest rams (Singer *et al.*, 1991).

The principal mechanisms behind the age-dependent pattern of reproductive effort appear to be: (1) prime-aged males eat less or stop eating completely; (2) 'rutting behaviour' (fighting with other males, roaring, wallowing, urinating, tending females) is more pronounced in prime-aged males; (3) prime-aged males seem to be rutting for a longer period of time. It is likely that each of these mechanisms contribute to the reported age-specific pattern, though little is at present known regarding the relative role of the specific mechanisms. Part of the reduction in body condition in ungulates is due to lower voluntary feed intake (Kay, 1979; Schwartz *et al.*, 1987; Miquelle, 1990). Feed intake is partly controlled by sexual hormones. Castrated males have a lower reduction in voluntary feed intake and may gain weight during the rutting period (Kay, 1979; Ryg, 1982).

Population level characteristics: density, sex ratio and male age structure

Data on density dependence in reproductive effort are limited, and reported patterns are not consistent. Reproductive effort in male red deer decreased with increasing density, as demonstrated both from reduced somatic weight loss (Yoccoz *et al.*, 2002) and from reduction in frequency of fights with increasing density (Clutton-Brock *et al.*, 1982). In Norwegian red deer, the effect of density on weight loss during the rut was found to be weak in young males, but increased considerably with advancing age, also after prime age was reached. In moose, effort also decreased with increasing density, but in yearlings only (Mysterud *et al.*, 2004). There was no effect of density on effort of yearling reindeer (Mysterud *et al.*, 2003), but in this case, only rutting densities differed giving males a similar condition at high and low density.

In contrast to predictions, two studies from populations of non-lekking fallow deer reported increased frequency of fighting with increasing density (Alvarez, 1993; Pélabon, Komers & Höglund, 1999b). Reproductive effort in males may possibly be related to the mating strategy (Yoccoz *et al.*, 2002), but at present, there are not sufficient data to test this interspecifically. Population density may affect effort either by reducing condition of males prior to rut (Yoccoz *et al.*, 2002), or indirectly as population density is often correlated with sex ratio (Clutton-Brock *et al.*, 1997). If so, the density measure used, and whether or not the sex ratio is controlled for, may strongly influence results and provide another possible solution to the different patterns reported.

A female-biased sex ratio is usually correlated with a young male age structure (e.g. Mysterud, Coulson & Stenseth, 2002). Variation in reproductive effort relative to population sex ratio/male age structure was available from four studies (Table 1). Consistent with the hypothesis, yearling bison bulls (Komers, Meisser & Gates, 1994b) and yearling male reindeer (Mysterud *et al.*, 2003) had a higher reproductive effort as population sex ratio becomes more female-biased and when prime-aged males were absent. In moose, there was no relationship between

effort and sex ratio for either prime-aged or yearling males (Mysterud *et al.*, 2004). Studies on dall sheep and bighorn sheep found that effort generally decreased with increasingly female-biased sex ratios (Singer & Zeigenfuss, 2002). However, sub-adult males seemed to increase their effort when adult males were scarce or absent (Singer & Zeigenfuss, 2002). Therefore, such changes in demographic structure may affect yearling, sub-adult and prime-aged males differently. Intra-sexual competition may be less intense for the prime-aged males, while opportunities for young males to start rutting early and hence increase their effort may increase when the demographic structure is more skewed towards females and younger males. Therefore, we propose that reproductive effort will increase for young males and decrease for prime-aged males with increasingly female biased sex ratios and a young male age structure. For yearling males, effort will likely only increase if there are also few subadult males to take over the role of prime-aged males (cf. Singer & Zeigenfuss, 2002).

Reproductive effort vs investment

Reproductive investment is, by definition, 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring' (Trivers, 1972; Evans, 1990). In the context of a male ungulate (which does not invest in the offspring, but only in the propagation of his own genes), this is the effort devoted in one rutting season relative to the chances of surviving and subsequently reproducing in another year. We have focused on reproductive effort, which is regarded irrespective of its cost (Evans, 1990). Surprisingly, in fallow deer, mass loss of prime-aged males was not related to either mating success or the behaviours associated with mating success (McElligott *et al.*, 2003). This indicates that males of higher quality were more efficient at converting energy into reproductive success, and that there maybe differences in costs for the same effort. Males have a more variable mortality rate than females (Toïgo & Gaillard, 2003). Intrasexually, yearling males are reported to have both a lower (Ballard, Whitman & Reed, 1991; Owen-Smith, 1993; Ditchkoff *et al.*, 2001) and a higher rate of natural mortality than prime-aged males (Clutton-Brock *et al.*, 1982; Catchpole *et al.*, 2000; Festa-Bianchet, Gaillard & Côte, 2003). In Soay sheep, precocial maturity in males did carry a survival cost, as was shown in comparing the survival of castrated and non-castrated males (Stevenson & Bancroft, 1995). Survival of young rams was also lower in populations with skewed sex ratio (Singer & Zeigenfuss, 2002). Patterns of survival of young compared to prime-aged males therefore follow a less consistent pattern than reproductive effort. Although present evidence is quite scarce, it also seems that costs of reproduction in terms of mortality follow a different pattern than reproductive effort for older males. While reproductive effort decreased for the oldest age-classes (Maher & Byers, 1987; Yoccoz *et al.*, 2002; Mysterud

et al., 2004); mortality of males increased more with density than female mortality (Clutton-Brock *et al.*, 1997). Although one study has reviewed male age-dependent mortality patterns for the genus *Ovis* (Festa-Bianchet, 1989), a more thorough look at male mortality patterns in ungulates related to age, population density and sex ratio is clearly needed before firm conclusions regarding investment patterns can be drawn. A better understanding of male rutting behaviour may also give a better insight into details of population dynamics (Mysterud *et al.*, 2002).

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