

# The role of males in the dynamics of ungulate populations

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## Summary

1. In this review, we focus on how males can affect the population dynamics of ungulates (i) by being a component of population density (and thereby affecting interpretation of log-linear models), and (ii) by considering the mechanisms by which males can actively affect the demographic rates of females.

2. We argue that the choice of measure of density is important, and that the inclusion or exclusion of males into models can influence results. For example, we demonstrate that if the dynamics of a population can be described with a first-order auto-regressive process in a log-linear framework, the asymmetry between the effects of females on the male dynamics and vice versa can introduce a second order process, much in the same way that the interaction between disease and host or predator and prey can. It would be useful for researchers with sufficient data to explore the affects of using different density measures.

3. In general, even in harvested populations with highly skewed sex ratios, males are usually able to fertilize all females, though detailed studies document a lower proportion of younger females breeding when sex ratios are heavily female biased. It is well documented that the presence of males can induce oestrus in females, and that male age may also be a factor. In populations with both a skewed sex ratio and a young male age structure, calving is delayed and less synchronous. We identify several mechanisms that may be responsible for this.

4. Delayed calving may lower summer survival and autumn masses, which may lead to higher winter mortality. If females are born light, they may require another year of growth before they start reproducing. Delayed calving can reduce future fertility of the mother. As the proportion of calves predated during the first few weeks of life is often very high, calving synchrony may also be an important strategy to lower predation rates.

5. We argue that the effects of males on population dynamics of ungulates are likely to be non-trivial, and that their potential effects should not be ignored. The mechanisms we discuss may be important – though much more research is required before we can demonstrate they are.

*Key-words:* calving dates, calving synchrony, demography, log-linear models, second-order processes, sexual body-size dimorphism.

*Journal of Animal Ecology* (2002) **71**, 907–915

## Introduction

The aim of population ecology is to understand why populations of animals fluctuate in size over time. This is important for a plethora of disciplines ranging from conservation to evolutionary biology (Gaillard, Festa-

Bianchet & Yoccoz 1998). For example, we are more likely to successfully manage a species if we understand why and how populations fluctuate. In evolutionary biology, we can only really start to understand selection if we know how and why ecological processes determine the frequency distribution of the fundamental biological processes of birth and death. To do this requires an understanding of how and why individuals vary (phenotypically, morphologically, behaviourally and genetically) and the consequences such variation has for the dynamics of populations.

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Two approaches to understanding the dynamics of populations are currently popular in ecology. First, to use log-linear models and describe dynamics by simple autoregressive processes (e.g. Bjørnstad, Falck & Stenseth 1995), making the assumption that the population is homogenous. The second approach is to focus explicitly on population heterogeneity and to propose a link between a certain ecological process and population dynamics (e.g. Sutherland 1996). In this essay, we are guilty of using both approaches: we focus on how males may affect population dynamics of ungulates (1) by being a component of population density (and thereby affecting the interpretation of log-linear models), and (2) by considering the mechanism by which males actively affect demographic rates of females.

### Males as a part of population density

The density or size of a population is associated with variation in age- and sex-specific vital rates and population dynamics (e.g. Nicholson 1933; ungulates: Sæther 1997; Gaillard *et al.* 1998; Gaillard *et al.* 2000). Although density-dependence is an important biological process both in demographic and population dynamic studies, it is commonly measured in different ways (Table 1). Because the choice of density measure could affect interpretation of results, it is important to consider what is likely to be the most biologically sensible estimate of density.

The total number of individuals within a population is the measure most commonly chosen, but many studies concentrate on the total number of males or females, the number of adult males or females, or estimates of biomass (Table 1). In those few cases when a choice of density measure is discussed, the justification for the choice is typically based on the degree of habitat or diet overlap between the sexes. For example, studies of survival, fecundity and dispersal rates of red deer (*Cervus elaphus* L.) on the Isle of Rum, Scotland have used the total number of adult females as a measure of density (Clutton-Brock, Guinness & Albon 1982; Coulson *et al.* 1997). The justification for this is that there is little overlap in habitat use between the sexes (Conradt, Clutton-Brock & Thomson 1999). Indeed, in several species of polygynous ungulates, adult males only visit female ranges during the rut (Dubois *et al.* 1996).

So what measure of density is most appropriate? The answer is likely to vary between study systems, and will be related to the mechanism(s) generating the density-dependent response. If density dependence is regulating population growth through resource availability by elevating mortality rates or depressing fecundity rates, then the choice of density measure should be a function of the degree of resource overlap. If resource overlap is small, then male vital rates or population dynamics are presumably a function of the number of males in the population, and female dynamics a function of the

**Table 1.** Studies providing examples of density dependence in vital rates or abundance of ungulate populations with a focus of what density estimate that has been used. Data on sexual body size dimorphism is from Mysterud (2000)

| Species  | Sexual body size dimorphism (m/f) | Vital rates/abundance                     | Density estimate                          | Reference                          |
|--|-----------------------------------|---|---|------------------------------------|
| Roe deer   | 1.04                              | Winter mortality                          | Total abundance                           | Gaillard <i>et al.</i> (1993)      |
| Red deer   | 1.48                              | Harvest number (total, male and female)   | Harvest number (total, male and female)   | Forchhammer <i>et al.</i> (1998)   |
| Red deer   | 1.48                              | Body mass (male and female)               | Total harvest                             | Mysterud <i>et al.</i> (2001)      |
| Red deer   | 1.48                              | Harvest sex ratio (calves)                | Female harvest                            | Post <i>et al.</i> (1999)          |
| Red deer   | 1.48                              | Proportion of females breeding            | Female abundance                          | Clutton-Brock <i>et al.</i> (1982) |
| Bighorn sheep  | 1.61                              | Neonatal survival                         | Female abundance                          | Portier <i>et al.</i> (1998)       |
| Moose  | 1.33                              | Total density                             | Total density                             | Messier (1991)                     |
| Soay sheep   | 1.40                              | Total abundance                           | Total abundance                           | Grenfell <i>et al.</i> (1992)      |
| Red deer, roe deer, moose, European bison, wild boar | 1.49, 1.04, 1.33, 1.70, 1.74      | Total biomass (combined for all species)  | Total biomass                             | Jedrzejska <i>et al.</i> (1994)    |
| Red deer, roe deer, moose, European bison, wild boar | 1.49, 1.04, 1.33, 1.70, 1.74      | Total density (separate for each species) | Total density (separate for each species) | Jedrzejska <i>et al.</i> (1997)    |

number of females. Should the number of female adults or the number of female adults plus the number of associated young be used in analyses of female dynamics? This will depend on the number of mouths consuming food at the time of year that food availability is limiting. The next obvious question is whether small and large mouths (juveniles and adults) should be given equal weight? The answers to these questions, and the consequent most sensible measure of density will be system-specific. We would welcome more frequent biological justification of the choice of density.

### Density in the log-linear world

Perhaps the choice of density measure does not really matter. Maybe all indices of density are correlated and the form of the statistical relationship between density and the response variable is identified accurately regardless of the measure. For some systems this is probably true, but for many it is not. In sexually dimorphic ungulate species, male and female densities are not necessarily highly correlated even if diet overlap between the sexes is high. This is because male mortality rates are typically higher than those of females (Owen-Smith 1993), even when males and females have similar body size (Gaillard *et al.* 1993), and the interaction between density and environmental stochasticity is more pronounced in males (Coulson *et al.* 2001; Gaillard, Festa-Bianchet & Yoccoz 2001). Furthermore, differences in life history between males and females can generate different density-independent associations with vital rates between the sexes (Coulson *et al.* 2001).

Most studies do not have the level of detail to consider such subtle heterogeneities. The most common form of ungulate population data is of annual counts of population sizes (Post & Stenseth 1999) – possibly split into the number of males and females – data that frequently are analysed using log-linear autoregressive (AR) methods. Theoretically the choice of density measure should matter within this framework. In a resource-limited population the analysis of only male (or female) numbers in relation to the population density of only males (or females) should generate only a first order (AR(1)) estimate. However, if feedback between the male and female components exists (i.e. there is resource overlap), analyses incorporating population density of males and females is predicted to also generate a second order (AR(2)) estimate in the same way that feedback between predators and prey or host and parasite or disease does. Let us illustrate this by considering the following population model:

$$\begin{aligned} N_t^{(x)} &= N_{t-1}^{(x)} \exp(f(N_t^{(x)}, N_{t-1}^{(y)}), \epsilon_t) \\ N_t^{(y)} &= N_{t-1}^{(y)} \exp(g(N_t^{(x)}, N_{t-1}^{(y)}), \epsilon_t) \end{aligned} \quad \text{eqn 1}$$

where  $N_t^{(x)}$  and  $N_t^{(y)}$  are the abundances of females and males in year  $t$ , the coefficients are the within sex and between sex density dependencies, and the  $\epsilon_t$  is a

random noise element (independent and identically distributed). Note we are assuming that the error term is identical for both sexes, but it would be easy to relax this assumption. This model may be further specified as

$$\begin{aligned} N_t^{(x)} &= N_{t-1}^{(x)} \exp(a_{11}x_{t-1} + a_{12}y_{t-1} + \epsilon_t) \\ N_t^{(y)} &= N_{t-1}^{(y)} \exp(a_{21}x_{t-1} + a_{22}y_{t-1} + \epsilon_t) \end{aligned} \quad \text{eqn 2}$$

( $x_{t-1}$  and  $y_{t-1}$  are the corresponding log-transformed abundances). If  $a_{11} = a_{22} = a_{12} = a_{21}$ , the model given by equation 2 will, for the total population, correspond to an order one process.

The model given by equation 2 may be written as

$$\begin{aligned} x_t &= (1 + a_{11})x_{t-1} + a_{12}y_{t-1} + \epsilon_t, \\ y_t &= a_{21}x_{t-1} + (1 + a_{22})y_{t-1} + \epsilon_t. \end{aligned} \quad \text{eqn 3}$$

Combining and rearranging equation 3 gives:

$$\begin{aligned} x_t &= (2 + a_{11} + a_{22})x_{t-1} + (a_{12}a_{21} - a_{11} - a_{22} - a_{11}a_{22} - 1)x_{t-2} \\ &\quad + \epsilon_t + (a_{12} - a_{22} - 1)\epsilon_{t-1}, \\ y_t &= (2 + a_{11} + a_{22})y_{t-1} + (a_{12}a_{21} - a_{11} - a_{22} - a_{11}a_{22} - 1)y_{t-2} \\ &\quad + \epsilon_t + (a_{21} - a_{11} - 1)\epsilon_{t-1}. \end{aligned} \quad \text{eqn 4}$$

Examination of this equation demonstrates that if the two sexes have symmetrical effects on one another, there should be a significant first order effect. If the two sexes have asymmetrical effects on one another there should be a significant second order effect. Interestingly, as long as  $(a_{12} - a_{22} - 1)\epsilon_{t-1} \neq 0$  (or  $(a_{21} - a_{11} - 1)\epsilon_{t-1} \neq 0$ ) there will also be a moving average term.

The consequence of choosing a biologically inappropriate measure of density (for example, ignoring males in a system with some diet overlap) will result in an overestimate of the order of the autoregressive processes.

If the male and female components of the population have asymmetrical effects on each other, we would expect  $b_1$  to be significant and  $b_2$  to be non-significant in analyses of male and female dynamics that consider only the population density of their own sex. However, we would expect both  $b_1$  and  $b_2$  to be significant in analyses of male and females dynamics that consider the population density of males and females combined.

### Demography of ungulates

Female ungulates usually produce and raise offspring alone, and they are therefore obviously the most important component with regard to population dynamics. For this reason, some recent reviews of demography of ungulates and how it relates to population dynamics have focused entirely on females (Gaillard *et al.* 1998, 2000). Although males are often neglected, we have a good understanding of the patterns and processes affecting both female and male demography and how it is dependent on age. In general, males have lower survival than females (Gaillard *et al.*

**Table 2.** Evidence for how sex ratio and male age structure affect demographic rates of polygynous ungulates. '+' indicates a positive relationship, while '0' indicates no relationship. Note that a young male age structure are often correlated with a female-biased sex ratio (Ginsberg & Milner-Gulland 1994), and only a few studies have controlled for this (Sæther *et al.* 2001; Holand *et al.* 2003)

| Variable             | Female fecundity   | Ovulation date   | Calving date  | Birth synchrony  |
|----------------------|--|--|---|--|
| Male presence        |  | Red deer <sup>1</sup> : +<br>Moose <sup>2</sup> : +<br>White-tailed deer <sup>3</sup> : +<br>Dom. sheep <sup>4-8</sup> : +<br>Dom. goats <sup>9-15</sup> : + |   |  |
| Male age (old/young) | Bighorn sheep <sup>16</sup> : 0<br>Black-tailed deer <sup>17,18</sup> : +<br>Elk <sup>19,20</sup> : 0<br>Fallow deer <sup>21</sup> : +<br>Mouflon <sup>23</sup> : 0<br>Reindeer <sup>23</sup> : 0<br>White-tailed deer <sup>24</sup> : 0 | Elk <sup>19</sup> : +<br>Fallow deer <sup>21</sup> : 0   | Black-tailed deer <sup>17</sup> : +<br>Reindeer <sup>23</sup> : 0 | Bighorn sheep <sup>16</sup> : 0<br>Elk <sup>19</sup> : +<br>Reindeer <sup>23</sup> : 0 |
| Sex ratio (m/f)      | Caribou <sup>25</sup> : +<br>Elk: 0 <sup>26</sup> /+ <sup>27</sup><br>Moose: 0 <sup>28-30</sup> /+ <sup>29,31,32</sup><br>Mule deer <sup>27</sup> : +<br>Reindeer <sup>23</sup> : 0  |  | Reindeer <sup>23</sup> : +<br>Moose <sup>28,32</sup> : +          | Reindeer <sup>23</sup> : 0   |

<sup>1</sup>McComb (1987); <sup>2</sup>Miquelle (1991); <sup>3</sup>Verme *et al.* (1987); <sup>4</sup>Watson & Radford (1960); <sup>5</sup>Schinckel (1954a); <sup>6</sup>Schinckel (1954b); <sup>7</sup>Pearce & Oldham (1988); <sup>8</sup>Knight & Lynch (1980); <sup>9</sup>Shelton (1960); <sup>10</sup>Ott *et al.* (1980); <sup>11</sup>Chemineau (1983); <sup>12</sup>Chemineau (1987); <sup>13</sup>Walkden-Brown *et al.* (1993a); <sup>14</sup>Walkden-Brown *et al.* (1993b); <sup>15</sup>Walkden-Brown *et al.* (1993c); <sup>16</sup>Shackleton (1991); <sup>17</sup>Hines & Lemos (1979); <sup>18</sup>Hines, Lemos & Hartmann (1985); <sup>19</sup>Noyes *et al.* (1996); <sup>20</sup>Larkin *et al.* (2002); <sup>21</sup>Komers *et al.* (1999); <sup>22</sup>Bon *et al.* (1992); <sup>23</sup>Holand *et al.* (2003); <sup>24</sup>Ozoga & Verme (1985); <sup>25</sup>Bergerud (1974); <sup>26</sup>Bender & Miller (1999); <sup>27</sup>White *et al.* (2001); <sup>28</sup>Taquet *et al.* (1999); <sup>29</sup>Markgren (1974); <sup>30</sup>Laurian *et al.* (2000); <sup>31</sup>Solberg *et al.* (2002); <sup>32</sup>Sæther *et al.* (2001).

1993; Owen-Smith 1993), and prime-aged females have a higher survival and reproductive rate than younger and older age classes of females (Caughley 1966; Gaillard *et al.* 1998, 2000). Because of more intensive rutting of prime-aged males (Yoccoz *et al.* 2002), they may sometimes have a higher winter mortality than young individuals (Festa-Bianchet 1989; Ditchkoff *et al.* 2001). What we know much less about is how the proportion of males and their age structure can affect demographic rates of females, apart from the fact that they are a part of population density as reviewed above.

### The role of male ungulates

Most large herbivores have a polygynous mating system, and males typically do not help females raise young (Davies 1991). Only a few males are required to ensure fertilization in production systems (Haigh & Hudson 1993). A single male is capable of inseminating a large number of females within a short period of time; 10 female fallow deer (*Dama dama* L.) (Jabbour *et al.* 1991) and 50 female reindeer (*Rangifer tarandus* L.) (Skjenneberg & Slagsvold 1968) were successfully served in one rut. From single sire farmed deer production systems in small enclosures, it is evident that male : female ratios must be very skewed in order to get reduced productivity (caribou 1 : 12 (Bergerud 1974); red deer 1 : 10 if young males vs. 1 : 50 if prime-aged males (Haigh & Hudson 1993); elk 1 : 5 if young

males vs. 1 : 25 if prime-aged males (Haigh & Hudson 1993)).

Many, if not most, large herbivore populations are heavily harvested. Harvesting may have a considerable impact on population dynamics by removing individuals (Solberg *et al.* 1999), and whenever the harvesting is sex- and/or age-biased it may largely affect the remaining age and sex structure of the population (Beddington 1974; Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999). Even in many harvested populations, there are no effects of a skewed sex ratio or male age structure on the proportion of females breeding (Table 2). However, detailed studies document a lower proportion of younger females breeding when sex ratios are heavily skewed (Ginsberg & Milner-Gulland 1994; Solberg *et al.* 2002). Preliminary simulations suggest that male capacity to inseminate females can be limiting when the adult sex ratio is severely skewed (Gruver, Guynn & Jacobsen 1984; Ginsberg & Milner-Gulland 1994). A female-biased sex ratio is often correlated with a young male age structure in harvested populations (Ginsberg & Milner-Gulland 1994). Young males are known to inseminate successfully (Coltman *et al.* 2002), but younger males may not have the same capacity to inseminate a large number of females as prime-aged males. At present, there are only a few manipulations that have attempted to differentiate the two or take into account other possible confounding factors such as density or the age structure of the female populations (Sæther *et al.* 2001; Holand *et al.* 2003).

Recently, studies of demographic rates in harvested populations with a skewed sex and age structure suggest that males also may affect population dynamics by quite subtle mechanisms (Table 2).

#### BIRTH DATE AND SYNCHRONY

A skew in sex ratio and/or in the male age structure may result in delayed calving and lead to a less synchronous calving season (Table 2). The adaptive value of timing of birth in ungulates has been related to plant phenology and peak protein levels (e.g. Bunnell 1982; Côté & Festa-Bianchet 2001). For example, late-born bighorn sheep (*Ovis canadensis* Shaw) lambs have a lower probability of survival, probably because of inadequate nutritional status of their mothers (Festa-Bianchet 1988). Earlier born bison (*Bison bison* L.) were socially dominant to late-born peers (Green & Rothstein 1993). Delayed calving may therefore lower summer survival (Festa-Bianchet 1988), and lower autumn masses (Holand *et al.* 2003) which may lead to a higher winter mortality (Loison, Langvatn & Solberg 1999). Light born females may also need an extra year of growth to reach the body mass necessary to reproduce (Langvatn *et al.* 1996). This is hence a possible mechanism to explain why the proportion of young females breeding declines with a skew in sex ratio (see above). If females are born light, it may require another year of growth before they start reproducing (Langvatn *et al.* 1996). Also, delayed calving may reduce future fertility of the mother (red deer: Clutton-Brock, Iason & Guinness 1987; caribou: Cameron *et al.* 1993). Red deer females on Rum, Scotland, suffered a 1% reduction in fertility for every day past the date of median conception in the previous year (Clutton-Brock *et al.* 1987). As the proportion of calves predated during the first few week of life is often very high (Linnell, Aanes & Andersen 1995), calving synchrony may also be an important strategy to lower predation rates (Rutberg 1984; Ims 1990; Bowyer 1991; Sinclair, Mduma & Arcese 2000; Gregg *et al.* 2001), through a swamping effect (Estes 1976; Leuthold 1977).

#### CONCEPTION DATE AS A MECHANISM FOR DELAYED CALVING

How the proportion of males in a population and male age structure may affect birth dates can be explained by understanding the behavioural ecology of rutting; more specifically an understanding of how conception is affected by the interaction between male presence, female choice and female distributions when certain high-quality males are present (Table 2).

The presence of males may induce oestrus in both wild and domestic ungulates (Table 2) as well as in several other species (McClintock 1983). The proximate mechanisms are related to both sound and smell. In red deer, experimental playback of roaring by male stags induced oestrus in females (McComb 1987). Female

red deer also selected males with a high roaring frequency (McComb 1991), which are the (prime-aged) males that most often won fights and had the highest reproductive success. However, the presence of males had an additional effect to roaring, indicating that smell and/or vision may also play a role (McComb 1987). Male urine contains odiferous compounds (Whittle *et al.* 2000), and concentration of some of these are related to male age (Miller *et al.* 1998). Cow moose (*Alces alces*) aggressively compete for access to bull urine (Miquelle 1991), and male urine may play an important role in synchronizing reproduction. That females not only respond with oestrus to male presence, but also to age of available males was demonstrated in fallow deer (Komers, Birgersson & Ekvall 1999).

The female distribution patterns during the rut may also vary with sex ratio and male age structure and hence affect the likelihood of a synchronous calving season. Mating strategies in mammalian herbivores are mainly thought to be determined by female and not male distribution (Ims 1988; Davies 1991). However, recent studies document that variation in female spatial organization during peak rut can occur depending on the availability of males. In red deer, the number of females using rutting areas increased during the rut (Carranza & Valencia 1999). Females in larger harems were less frequently harassed. Similar results have been observed in lekking fallow deer, in which females join large herds to avoid harassment (Clutton-Brock, Price & MacColl 1992; McComb & Clutton-Brock 1994). Females may gain direct benefits of mating with older males. Some evidence suggest that young males have a less well-developed social behaviour and often harass females (Valdez, Cardenas & Sanchez 1991; Komers *et al.* 1999), but evidence is contradictory (Shackleton 1991; Valdez *et al.* 1991). In captivity, female fallow deer confined with young males lost more mass than when confined with older males during the rut (Komers *et al.* 1999). In a manipulated herd of reindeer with an even sex ratio and male age structure, the female distribution was best described as one large floating harem (M.E. Smith *et al.*, unpubl.). Most of the females were easily accessible for the males and vice versa during the main rut. With a skewed sex ratio, females gathered in several distinct harems throughout the main rut and quite a few females were always in transit between harems although the frequency decreased during peak rut (M.E. Smith *et al.*, unpubl.). Therefore, the presence of high-quality, prime-aged males may lead to females being less dispersed and hence increasing the probability of a more synchronous rut.

There is certainly a cost to being choosy, as delayed conception is expected to delay birth date (see above). In the more extreme scenario, a failure to conceive leads to reovulation 2–3 weeks later (see roe deer *Capreolus capreolus* L. for an exception; Sempere, Maugeat & Maugeat 1998) or, of course, failure to reproduce at all. Most researchers usually assume a constant

gestation length, although very few studies have documented this. In bison, gestation was reduced by 6 days for females in good condition when conception was delayed, possibly because of the benefits of giving birth at the optimal time (Berger 1992). More studies are clearly needed on gestation length in ungulates.

An alternative and less studied issue is that young males often start rutting later than prime-aged males (Espmark 1964; Hines & Lemos 1979; Clutton-Brock, Rose & Guinness 1997; Yoccoz *et al.* 2002). This may also provide a mechanism by which birth dates are delayed when there are only young males available to females, but no study have reported if young males also start rutting later when no prime-aged males are present.

#### OTHER EFFECTS OF MALES

At present, there are a few other potential mechanisms by which the males may affect population dynamics. It is well known that aggression by dominant males is sometimes the proximate cause of dispersal in ungulates (roe deer: Strandgaard 1972; Wahlström 1994). However, this is mainly related to the dispersal of male offspring, and it is therefore as yet speculation that a skewed sex ratio or male age structure may also lead to a different pattern of dispersal. In carnivores (Swenson *et al.* 1997; Wielgus & Bunnell 2000; Wielgus *et al.* 2001), primates (Robbins 1995) and rodents (Trulio 1996), male infanticide may be important for population dynamics. Although male infanticide has been observed in several captive species (e.g. captive horses *Equus caballus* L. Duncan 1982; plains zebra *Equus burchelli* Pluhacek & Bartos 2000), there is no evidence that this is frequent in wild ungulates, though the hippopotamus (*Hippopotamus amphibius* L.) may be an exception (Lewison 1998). Invading males were reported to induce abortion in wild horses (Berger 1983). Recently, male age structure was reported to affect the offspring sex ratio in moose (*Alces alces* L.; Sæther *et al.* 2001). The sex ratio was female-biased in a period with younger males, while the sex ratio was male-biased when older males performed most matings. The mechanism is unknown, but Sæther *et al.* 2001 speculated that sperm with a Y chromosome (necessary to produce a male) have higher mortality than sperm with an X chromosome. Since insemination may be delayed when only young males are around, this may explain why fewer males are born when only young males are present.

#### Conclusion

In this paper, we use two common but quite different approaches in population ecology (see Introduction) to make two points. First, that although log-linear approaches have greatly advanced our understanding of population ecology, great care is required in interpreting the causes of second order processes. Second,

the detail matters – we argue that the effects of males on population dynamics of ungulates are non-trivial, and the potential effect should not be ignored. The mechanisms we discuss may be important – though much more research is required before we can demonstrate they are.

#### Acknowledgements

We gratefully acknowledge the financial support of the Research Council of Norway to A.M. and NERC to T.C.

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Received 10 December 2001; revision received 14 May 2002