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Harvesting of males delays female breeding in a socially monogamous mammal; the beaver

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Human exploitation may skew adult sex ratios in vertebrate populations to the extent that males become limiting for normal reproduction. In polygynous ungulates, females delay breeding in heavily harvested populations, but effects are often fairly small. We would expect a stronger effect of male harvesting in species with a monogamous mating system, but no such study has been performed. We analysed the effect of harvesting males on the timing of reproduction in the obligate monogamous beaver (*Castor fiber*). We found a negative impact of harvesting of adult males on the timing of parturition in female beavers. The proportion of normal breeders sank from over 80%, when no males had been shot in the territories of pregnant females, to under 20%, when three males had been shot. Harvesting of males in monogamous mammals can apparently affect their normal reproductive cycle.

Keywords: *Castor fiber*; life history; management; phenology; seasonality

1. INTRODUCTION

The role of males as a factor in the life history and population dynamics of vertebrates has recently become more apparent (Mysterud *et al.* 2002; Le Galliard *et al.* 2005; Rankin & Kokko 2006). This is in part a result of recent findings showing that intensified harvesting often skews adult sex ratios to the extent that males become limiting for normal reproduction (Milner-Gulland *et al.* 2003). Among brown bears (*Ursus arctos*), harvesting of adult territorial males led to increased infanticide by immigrant males and reduced population growth (Swenson *et al.* 1997; Wielgus *et al.* 2001, see also Andreassen & Gundersen 2006 for voles). Most mammalian big game species are polygynous ungulates, in which the management paradigm is that the number of males is unimportant for population growth. Indeed, a reduced proportion of breeding female ungulates has only been seen in extreme cases of only 2% adult males in the population (Milner-Gulland *et al.* 2003). However, at less extreme sex ratios, females may delay breeding partly due to a reluctance to mate with younger males. This occurs typically in heavily harvested populations (Mysterud *et al.* 2002), though the delay is often just a few days (Noyes *et al.* 1996; Holand *et al.* 2003). In strongly seasonal environments, the timing of reproduction is considered crucial for fitness (Langvatn *et al.* 2004).

We would expect a stronger effect of male harvesting in socially monogamous species, since each male would not be expected to inseminate many females, but no such study has yet been done. The beaver (*Castor fiber*) is both territorial and obligately monogamous (Campbell *et al.* 2005), and an important game species (Novak 1987). We analysed the timing of female reproduction as a function of how many males had been shot in their respective territories prior to breeding.

2. MATERIAL AND METHODS

(a) Study area and beaver data

The study was conducted in Bø Township (59°25′ N, 09°03′ E; 266 km²), Telemark County, southeast Norway. The beaver colony density was typical for boreal forest habitats in southern Scandinavia and hunting pressure prior to the study had been light (Parker *et al.* 2002).

Beavers were shot between 13 March and 15 May 1997–1999 (Parker & Rosell 2001). Sexually mature individuals (adults) of both sexes were those aged 2 years or older (Wilsson 1971). The analysis included 37 pregnant females, 18 adult females, 21 adult males and 18 juveniles.

Animals were weighed to the nearest 0.1 kg, sexed by internal inspection of sex organs and aged after the methods in van Nostrand & Stephenson (1964). Female ovaries were examined for *corpora lutea* (Provost 1962) and uteruses were inspected for foetuses. Counts of corpora lutea of pregnancy provided estimates of litter size. Pregnant females were defined as those with one or more living foetuses, or with one or more corpora lutea for those females shot early in pregnancy before foetuses were visible (Provost 1962). Foetuses were removed and weighed individually to the nearest gram. Using a regression model for growth rate of beaver foetuses and a mean weight for foetuses at birth of 525 g (Parker & Rosell 2001), we predicted the parturition date for unborn litters of pregnant females shot. As five females were pregnant, but without foetuses, we know that offspring would have been born late, but not exactly how late. In the modelling (see below), we classified individual females into 'normal' (predicted parturition date 1–25 May, $n=28$) and 'late' breeders (four individuals with predicted parturition dates between 4 and 17 June, plus the five pregnant females without visible foetuses and thus even a later expected parturition, $n=9$).

The beaver tail functions as a fat storage organ (Aleksiuk 1970). As a measure of body condition, we used the ratio of tail size (seasonally variable) to body length (seasonally stable). Tail size was measured as tail length (from the tail tip forward to the start of hair line) times tail width measured at midpoint. Body length was measured as total length (from nose tip to tail tip) minus tail length. The tail fat index (I) was therefore expressed as

$$I = \frac{(A \times B)}{C},$$

where A is the tail length; B is the tail width; and C is the body length, i.e. larger values indicate a higher fat content and a better condition.

For each territory, we recorded the sequence of beaver shot. We calculated the number of juveniles, adult females and adult males shot from each pregnant female's territory prior to her own death during the 3 years of the study. The harvest of beaver during the study was considered high as the density of occupied territories during the 3 years on the study area declined by 46%, in part due to overharvesting of adults (Parker *et al.* 2002).

(b) Statistical analysis

We used logistic regression to determine the relationship between the timing of breeding (normal versus late) and the candidate explanatory variables. Female age and condition may also affect the timing of reproduction in mammals (Langvatn *et al.* 2004). The candidate terms were female condition (tail fat index), age, litter size, year (categorical) plus adult male, adult female and juvenile harvest in each pregnant female's colony prior to her own death.

Table 1. Predictive logistic regression models of expected parturition time (normal versus late) with a variable number of males in the population harvested in Norway. (d.f., degrees of freedom; G, a test statistics for model fit that is $-\chi^2$ distributed; P model, test for overdispersion in the model; AICc, Akaike information criterion corrected for sample size; ΔAICc, difference in AICc value relative to the best model (boldfaced); AICc-w, AICc weights.)

parameter	residual deviance	d.f.	G	P (model)	AICc	ΔAICc	AICc-w
age of female	41.024	35	1.172	1.000	45.388	8.792	0.011
condition of female	40.356	34	1.187	1.000	*	8.135	0.015
number of corpora lutea	38.452	35	1.099	1.000	42.816	6.220	0.039
year (categorical)	37.455	34	1.102	1.000	43.819	7.223	0.024
no. of harvested juveniles	40.973	35	1.171	1.000	45.337	8.741	0.011
no. of harvested adult males	**32.232**	**35**	**0.921**	**1.000**	**36.596**	**0.000**	**0.879**
no. of harvested adult females	39.707	35	1.134	1.000	44.071	7.475	0.021

* AICc not given due to one missing value; ΔAICc is given relative to the best model with the same sample size.

We used the Akaike information criterion (AICc) corrected for sample size to compare models (Burnham & Anderson 2002) and goodness-of-fit to assess model fit to avoid overdispersion (table 1).

3. RESULTS

Harvesting adult males in colonies markedly delayed parturition in females (figure 1; the proportion of normal breeders $= 2.128$ (s.e. $= 0.613$) $- 1.365$ (s.e. $= 0.534$) $\times$ male harvest; $Z = -2.556$, $p = 0.011$). Adult males were shot either in the same year as pregnant females (but before them; y_0, $n = 12$), 1 year before (y_{-1}, $n = 7$) or 2 years before (y_{-2}, $n = 2$), but estimates were little affected by time since harvest (estimates: $y_{0,-1} = -1.177$; $y_0 = -1.084$; $y_{-1} = -1.099$). Harvesting adult females or juveniles had no effect on the timing of parturition (table 1). Likewise, female age, body condition, litter size and year of harvest were not related to the proportion of normal breeders (table 1).

4. DISCUSSION

The timing of reproduction is considered crucial for fitness in iteroparous animals breeding annually in strongly seasonal environments (Gosling *et al.* 1988; Langvatn *et al.* 2004). Late-born young are at a disadvantage as they are smaller in autumn and more likely to die during their first winter (Hogg *et al.* 1992; Langvatn *et al.* 2004). Prolonging offspring investment into the autumn may benefit them, but at the expense of the mother's own condition and the next breeding cycle (Hogg *et al.* 1992). When forced to breed late, females avoided depriving their own condition in autumn at the expense of offspring size (Holand *et al.* 2006). Since the heavy harvesting of adult males apparently delayed breeding, it may also have led to reduced offspring survival. Indeed, Parker *et al.* (2002) recorded a decline in the proportion of juveniles in the harvest from 26 to 3% during the 3 years of the study. They attributed this primarily to a heavy harvesting of adult females, though reduced survival of late-born young might also have contributed. The high population harvest rate (25%) observed in this study, particularly of adults (Parker *et al.* 2002), appears to have hindered sufficient adult male recruitment and dispersal. This may have led to repeated ovulations and the late breeding in females. Little information is currently available regarding how long it takes to
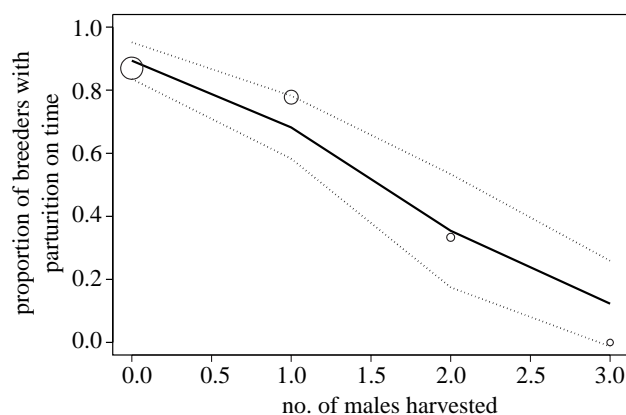

Figure 1. The relationship between the predicted parturition time ('normal' or 'late') in spring-shot Eurasian beaver ($n = 37$) and the number of adult males harvested from each female's territory during the study (1997–1999) prior to her own death, southeast Norway. Dotted lines are 95% confidence intervals and circle size is directly proportional to the sample size (i.e. the number of pregnant females).

replace a territory holder that has been harvested, and how this may vary depending on the saturation of beaver in nearby areas. Our own anecdotal observations from areas with a saturated population suggest that they are quickly replaced by young males, and if so, female reluctance to mate with them may explain the delay in breeding, but more solid studies are needed to confirm such a suggestion. Our study thus provides an example that harvesting may affect populations beyond the actual removal of individuals.

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