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Authors: Sæther, Bernt-Erik, Solberg, Erling J., Heim, Morten, Stacy, John E., Jakobsen, Kjetill S., et al.

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Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment

Bernt-Erik Sæther, Erling J. Solberg, Morten Heim, John E. Stacy, Kjetill S. Jakobsen & Randi Olstad

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In most of Fennoscandia, moose *Alces alces* is intensively managed by the use of age and sex specific harvesting. This includes strong male biased harvesting, which over the last decade has resulted in a change in the sex and age composition of the populations. During the same period of time, a reduction in the proportion of male calves in the harvest has occurred all over Norway, probably reflecting a change in the secondary sex ratio. In order to examine for any causal link between these two patterns, we manipulated the structural composition of an isolated island population of moose in northern Norway and at the same time closely monitored the variation in the secondary sex ratio. In the first stage of the project, which was assumed to represent the conditions in a natural, unhunted moose population, the proportion of male calves increased significantly with the age of their fathers. Potentially, as a consequence of the high mean adult male age in the population, the secondary sex ratio was highly male biased. When we altered the male segment of the population, leaving only young (≤ 2½ years old) males as potential mates for the females, a significant increase in the proportion of female calves occurred in the population. Finally, in the last 3-years stage of the project, we reduced the adult sex ratio in the population to about 23% males and kept the adult male age relatively high. This again led to an increasing secondary sex ratio. These results suggest that the age composition of males in the population may affect the secondary sex ratio. The general significance of these results was supported by a larger temporal decrease in the proportion of males that were shot in the areas of Norway with larger changes in the sex composition of the hunting quotas than in the regions in which a less extreme harvest strategy were practised.

Key words: age-specific demography, Alces alces, harvest strategy, moose, secondary sex ratio

Bernt-Erik Sæther, Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway, and Norwegian Institute of Nature Research, Tungasletta 2, N-7485 Trondheim, Norway - e-mail: Bernt-Erik.Sather@bio.ntnu.no
Erling J. Solberg & Morten Heim, Norwegian Institute of Nature Research, Tungasletta 2, N-7485 Trondheim, Norway - e-mail addresses: erling.solberg@nina.no (Erling J. Solberg); morten.heim@nina.no (Morten Heim)
John E. Stacy, Affitech AS, Gaustadalleen 21, N-0349, Oslo, and Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N- 0316 Oslo, Norway
Kjetill S. Jakobsen, Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N- 0316 Oslo, Norway - e-mail: kjetill.jakobsen@bio.uio.no
Randi Olstad, Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

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Corresponding author: Bernt-Erik Sæther

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In ungulate populations, deviations of the secondary sex ratio from 50:50 are often explained as the result of individual variation among females in their ability to allocate resources to the sex with the greatest fitness returns (Trivers & Willard 1973, Frank 1990). Such variation may for instance arise due to individual variation in body condition among females (Hamilton 1967, Trivers & Willard 1973, Frank 1990, Clutton-Brock, Albon & Guinness 1984, Clutton-Brock, Guinness & Albon 1986, Hewison & Gaillard 1999 and references therein). More female offspring are predicted to be born by females in poor condition, and more male calves by females in good condition as it is assumed that there is a greater chance in polygynous species of achieving a higher reproductive success in males than in females. Accordingly, ungulate sex ratios may also respond rapidly to extrinsic changes that influence their living conditions of the polygynous species. In red deer *Cervus elaphus* on Rum, Scotland (Kruuk, Clutton-Brock, Albon, Pemberton & Guinness 1999), and at the west coast of Norway (Mysterud, Yoccoz, Stenseth & Langvatn 2000) the proportion of male calves decreased with population density, and similarly, an effect of climate on sex ratio was found in both studies. However, despite several results reported in support of the above predictions, it has been difficult to find a consistent pattern in mammals and to identify common individual characteristics (e.g. body condition) among females that can explain the deviations in the secondary sex ratio (e.g. Clutton-Brock & Iason 1986, Frank 1990, Hewison & Gaillard 1999). In addition, there may be significant underreporting of results due to lack of statistical significance or because results are not consistent with theory or expectations (Festa-Bianchet 1996, Palmer 2000).

One set of alternative explanations involves mechanisms where male quality or time of insemination influences the sex ratio (e.g. James 1983, Clutton-Brock & Iason 1986). Because males in most mammals are the heterogametic sex, differences in the male production of X and Y-spermatozoa or differential probability of conception by X and Y-spermatozoa may affect the sex ratio. For instance in humans, some evidence indicate that timing of insemination in relation to time of ovulation influences the probability of an ovum being fertilised by X or Y-spermatozoa (James 1983, 1996, Martin 1997 and references therein). More precisely, male conceptions are most likely when insemination occurs some time before or some time after ovulation, whereas no differences should be expected close to ovulation, possibly due to higher penetration rates of Y-spermatozoa than X-spermatozoa through the cervical mucus when the gonadotrophin levels are lower prior to or after ovulation (e.g. Roberts 1978, James 1996, Martin 1997 and references therein). Similar arguments have also been used to explain deviations in secondary sex ratios in other mammalian species (James 1996), although these mechanisms to date have mainly been examined in humans. However, to the extent that such mechanisms are important for determining the offspring sex, we may also expect a relationship between the variation in male qualities within a population and/or the structural composition of the population and the secondary sex ratio (e.g. Verme & Ozoga 1981, Richter & Labisky 1985). Here, we report on results indicating such a relationship in moose *Alces alces* and argue that this may occur following behavioural changes that influence the timing of insemination relative to the time of ovulation.

Selective harvesting of adult males is one of the most powerful tools to increase the annual yield from natural populations (Caughley 1977, Sæther, Engen & Solberg 2001). During the last decades, this strategy has been employed in the management of most Fennoscandian moose populations (Haagenrud, Morow, Nygren & Stålfelt 1987, Solberg, Loison, Sæther & Strand 2000), with the consequence that a large fraction of the males are now shot even before they reach the age of 3½ years. This has resulted in a substantial decrease in the proportion of adult males (Fig. 1A) and probably also of the mean age of males in many populations. Thus, such a management scheme provides a unique opportunity to examine how a large-scale perturbation of an intrinsic variable, i.e. the structural composition of the population, may affect the secondary sex ratio.

A decrease in the proportion of male calves shot during the hunting season has occurred in Norway (Fig. 1B) and Sweden (Reuterwall 1981) during the last 30 years. From being strongly male biased, often with more than 60% male calves of a harvest in the early 1970s (see Fig. 1B, and see also Reuterwall 1981), the sex ratio is currently close to even. Because summer mortality of moose calves in many populations is relatively small (Stubsjøen, Sæther, Solberg, Heim & Rolandsen

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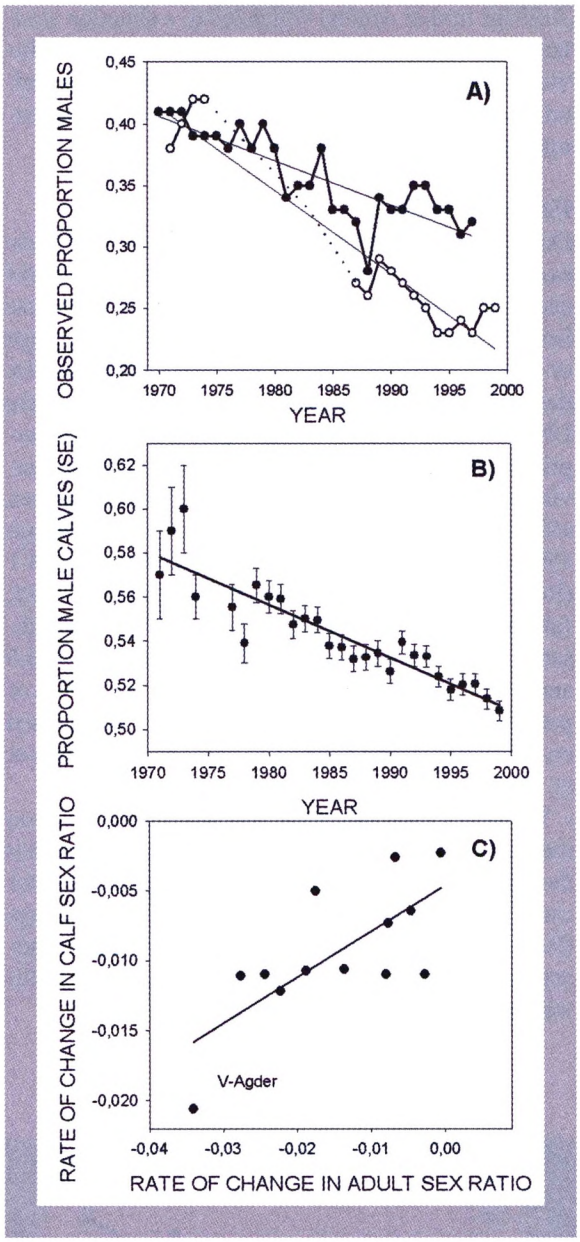


Figure 1. Annual variation in the proportion of observed males of all adult (≥ 1 year old) moose during the hunting season (A) within the areas Vefsn (○) and Trøndelag (●). For the period 1971-1974, data are from Haagenrud & Lørdahl (1979). Slopes are estimated by least squares regression. B) shows the decline in the proportion (± 1 SE) of male calves among moose calves harvested in the 13 counties that were most important for moose hunting in Norway during 1971-1999 (N = 188, 107). C) shows the relationship during 1977-1999 between the rate of decline in the male bias of the calf sex ratio and the rate of change in the proportion of males in the adult harvest within the 13 counties that were most important for moose hunting in Norway. The rate of change in the proportion of males among calves and in the adult harvest, respectively, was estimated as the slope of the logistic regression of the ratio on time. The Spearman rank correlation between the regression coefficient was r = 0.72, df = 13, P = 0.006. When omitting the outlier (the county of Vest-Agder), the relationship was still significant (r = 0.64, P = 0.025).

2000), this pattern is likely to reflect a change in the secondary sex ratio of the population. However, these large-scale changes in the secondary sex ratio may not necessarily be related to structural changes of the population (e.g. age composition of males or adult sex ratio), but could also be the result of confounding correlation with other variables. For instance, a decrease in the proportion of adult males is often closely associated with an increase in density (Solberg & Sæther 1994), which in turn may affect the secondary sex ratio (Kruuk et al. 1999, Mysterud et al. 2000).

To examine for the presence of a relationship between the structural population composition and the secondary sex ratio, we first examined the effect of male age on the sex of the calves in an isolated island moose population in northern Norway by means of DNA fingerprinting. We then manipulated the age and sex structure of the moose population while simultaneously monitoring the change in the secondary sex ratio. During the whole study, we kept the winter population size relatively constant. By this set-up we wanted to examine if male age may be an important component in determining the sex of the calf.

Study area

The study was conducted on the island of Vega (65°40'N, 11°55'E) off the coast of Helgeland in northern Norway, about 30 km from the mainland. Most parts of the main island are relatively flat, except for one mountain (800 m a.s.l) in the southwestern part. The total area of the main island is 119 km^2. A mixture of grazing fields, small forests, marshes and heather *Calluna vulgaris* areas chacterise the landscape. The climate is oceanic with only shorter periods of snow cover during most winters.

The moose population on Vega was founded in 1985, when three animals arrived after swimming from the mainland to the island. In the winter of 1992, at the start of the study, the population size was 25 animals.

Methods

Collection of population data

During 1992, 21 animals (five males, eight females and eight calves) were captured from helicopter or by foot using a remote drug-delivery system (Dan-Inject, Børkop, Denmark) and were equipped with 142 mHz radio collars. The remaining four (one male and three females) animals were captured throughout the following year either from helicopter or by foot. Thus, from

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the winter of 1993 and onwards, all individuals on the island were radio collared. Each winter throughout the study period all calves and immigrants were radio collared, and animals with malfunctioning transmitters or lost radio collars were recaptured.

During the calving season (May-July) from 1992 to 2000, the females were approached on foot every 3-4 days until calves were present. We determined the age of the calves by their size, behaviour and the physical condition of their mothers. Thus, the calving date could usually be determined within a range of ± 1 day. This procedure, combined with behavioural observations of the mothers, makes it unlikely that calves were born and died without being detected. In late summer or early autumn, the calves were approached on foot and their sex determined by visual observation. Harvesting was done by local hunters during the hunting season (September-October).

Manipulation of the population structure

First, we studied variation in reproductive success of radio collared males and females from 1992 to 1994. Because only a very limited number of animals had been shot prior to the start of the study, we assume that this period represents the situation in an unmanaged moose population (with a mean adult sex ratio of 49% males). Then, after the rutting season of 1994, we shot all adult (≥ 1 year old) males, leaving only very young males as potential mates for the females during the rutting seasons of 1995 (only yearlings) and 1996 (five yearlings and eight 2½ years old; Table 1). This stage of the project represents a situation with low male age, but a relatively balanced adult sex ratio (with a mean adult sex ratio of 41%; see Table1). Finally, in the last period of the project (rutting seasons of 1997-1999), we removed males to obtain a skewed adult sex ratio (with a mean adult sex ratio of 23%), but leaving some old males in the population (see Sæther, Solberg & Heim 2003 for further details) which led to a situation similar to the current adult sex ratio found in many Norwegian populations (see Fig. 1A). During the whole period, we maintained a winter population of approximately 30 animals (Sæther et al. 2003).

Table 1. Annual variation in the age and sex composition of the moose population at Vega at the onset of the rutting season during the three experimental periods.

		Male age				Female age			
Period	Year	Calves	1½	2½	≥ 3½	Calves	1½	2½	≥ 3½
1	1992	12	6	2	3	8	2	5	7
	1993	12	6	6	5	5	8	1	10
	1994	9	9	5	8	6	5	4	9
2	1995	8	9	0	0	4	6	3	10
	1996	8	5	8	0	10	2	1	10
3	1997	6	4	1	2	12	6	2	11
	1998	9	3	1	2	11	5	5	12
	1999	11	3	1	2	12	4	4	13
	2000	17				10			

Paternity analysis

During the first unmanipulated part of the study, we examined the parental relationship between the calves and their fathers using DNA-fingerprinting. DNA was isolated by the CTAB method from tissue ear cartilage or muscle of animals captured for radio collaring or shot during the hunting season. Approximately 5 μg were DNA digested with Dde I over night. The DNA-fingerprinting protocol and probe labelling was done as previously described (Refseth, Mjølnerød & Jakobsen 1994, Refseth, Nesbø, Stacy, Vøllestad, Field & Jakobsen 1998). The probes used were M13, 33.6 and MOMS 1 (Refseth et al. 1994, Jeffreys, Wilson & Thein 1985, Jakobsen, Stacy, Refseth & Thoresen 1996) at hybridisation temperatures of 55°C (MOMS 1) and 60°C (33.6 and M13). Paternity was determined by exclusion of potential fathers through sharing of exclusive bands based on DNA-fingerprint scoring as outlined by Refseth et al. (1994).

The age of each individual was determined based on them either having been radio-collared as a calf or that their jaws were collected after harvesting. In the latter case, tooth replacement patterns in calves and yearlings (Peterson 1955) and the number of layers in the secondary dentine of the incisors in adults (Haagenrud 1978) were used as age estimation methods.

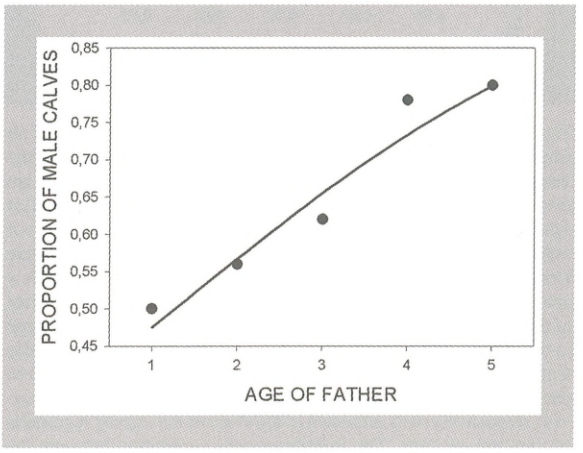


Figure 2. Proportion of male calves (N = 57 calves of 14 mothers) in relation to the age of their fathers on the island of Vega during the pre-manipulation period of 1992-1994.

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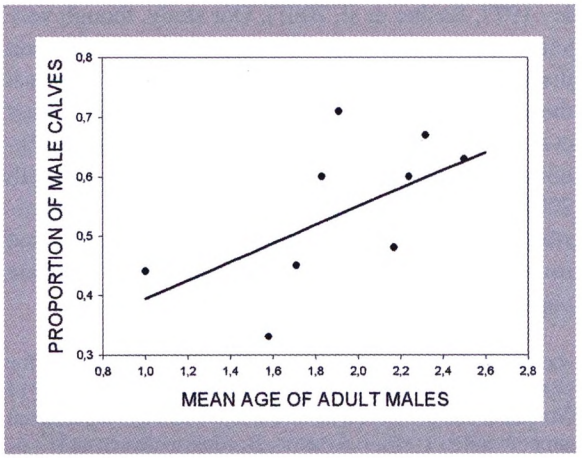


Figure 3. Annual variation during 1992-2000 in the sex ratio of moose calves on Vega in relation to the mean age of adult males (≥ 1 year old) prior to the rutting season the previous year. The trend line was fitted to the logistic equation; $y = e^{(-1.06 + 0.63x)} / (1 + e^{(-1.06 + 0.63x)})$, where y is calf sex (male or female) and x is mean adult male age. See text for further information on statistics and Table 1 for sample sizes.

Results

During the first period of the project, the probability of giving birth to a male calf increased with the age of the father (PROC GENMOD; SAS Inc. 1996: $\chi^2 = 34.63$, df = 3, $P < 0.001$ after correcting for underdispersion in the data; Fig. 2), whereas no significant effects ($P > 0.1$) of maternal age or body mass, litter size or calving date were found on the sex ratio. Accordingly, the secondary sex ratio also changed after manipulation of the age and sex composition of the population (PROC GENMOD: $\chi^2 = 3.85$, df = 7, $P = 0.0497$; Fig. 3). In the first unmanipulated stage of the project, an average of 64% of the calves were males. This proportion decreased to a female-biased sex ratio among calves born after the rutting seasons with only young males present in the population (see Table 1). Then it increased again in the final period of the project when the adult sex ratio was biased, but with a higher mean age of the adult males (see Table 1 and Fig. 3). Thus, there was an association between the variation in secondary sex ratio and the fluctuations in the mean age of the male segment during the previous rutting season (see Fig. 3).

Discussion

The manipulation of the structural composition of the moose population at Vega demonstrates the potential of a large and rapid change in the secondary sex ratio of an ungulate population (see Fig. 3). It is, however, often difficult to interpret the generality of the results from such small-scale population perturbations because unknown ecological variables, or the particular sample of individuals, may influence the results. Two lines of evidence suggest that the results reflect some general processes in moose populations. First, as expected from the results on the island of Vega, the proportion of male calves shot during the hunting season in the Vefsn valley in northern Norway (65°20'-66°00'N, 12°30'-14°30'E) decreased significantly with the mean age of adult males in the harvest (logistic regression: $\chi^2 = 4.28$, df = 1, $P = 0.038$). The fluctuations in the size and composition of this population have been studied for more than 30 years by means of moose observations by hunters, virtual population analysis based on the age composition of shot animals (Quinn & Deriso 1999) and annual variation in age specific body masses (Solberg & Sæther 1994, Solberg & Sæther 1999, Solberg, Sæther, Strand & Loison 1999, Solberg et al. 2000). Neither annual variation in mean body mass of yearling females nor fluctuations in population size could explain a significant ($P > 0.1$) proportion of the variance in the calf sex ratio. Second, the decrease over time in the proportion of male calves shot was higher in the areas of Norway where the larger changes in the sex composition of the hunting quotas occurred than in regions where a less extreme harvest strategy was practised (Fig. 1C). This suggests that changes in the adult sex ratio may affect the rates at which male and female calves are born into a moose population, and these changes in the secondary sex ratio may operate through an effect of changes in the mean age of the adult males.

Variation in mammalian sex ratios are often considered to be adaptations to changes in the factors that influence the relative fitness gained by the females who produce offspring of either of the two sexes (Frank 1990, Hewison & Gaillard 1999). For instance, nutritional stress is assumed to favour production of females (Trivers & Willard 1973, Frank 1990, Hewison & Gaillard 1999). This may occur following differential pre- or neonatal mortality of males and females, which in most cases will be associated with a fall in the number of offspring (Clutton-Brock & Iason 1986, Hewison & Gaillard 1999). On Vega, however, the productivity of moose is among the highest recorded in Norway (e.g. pregnancy rate of 55% and 95% of yearlings and adults, respectively, and 55% of adults produce twins; B-E. Sæther, E.J. Solberg & M. Heim, unpubl. data), and no significant variation in fecundity was recorded among the three stages of the study despite large variation in the calf sex ratio (B-E. Sæther, E.J. Solberg & M. Heim, unpubl. data). Thus, the large variation in sex ratio was

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apparently not a result of a differential neonatal mortality. Similarly, the secondary sex ratio was not correlated with any maternal characteristics, but only with the age of the fathers (see Fig. 2). An adaptive alteration of the sex ratio as a response to changes in the structural composition therefore seems unlikely.

Instead, we suggest that variation in the sex ratio may have been induced by changes in the mating behaviour during the rutting season following the change of the population sex and age structure. If we assume that ovulation in moose occur one to two days after onset of estrous, as found in many ungulates (e.g. Asher, Fisher, Smith, Jabbour & Morrow 1990, Asher, Fisher, Jabbour, Smith, Mulley, Morrow, Veldbizen & Langridge 1992 and references therein), and that the probability of conceiving a male is higher some time prior to ovulation, as found in humans (Guerrero 1974, Martin 1997), insemination at the start of estrous is more likely to result in male offspring. In moose, the estrous period is short, normally less than two days (Lent 1974, Schwartz & Hundertmark 1993), indicating that even a short delay in insemination may affect the sex ratio. When only young or few males are present, we may expect that the period between mating and onset of estrous increases. This may occur through a mating preference by the female for older males, making her less ready to accept a young male as a mate, or through difficulties by the female to find an available mate. Older males may also have a more developed courtship behaviour, semen production and mating capacity (Bubenik 1998), and are found to mate more often than younger males (Van Ballenberghe & Miquelle 1993, 1996). They may therefore ensure that more females are mated earlier in their estrous period than younger males.

Such a mechanism, in which the structural composition of the population influences the secondary sex ratio, has been suggested also by others (Verme & Ozoga 1981, Richter & Labisky 1985 and references therein), but often in the opposite direction. For instance, Verme & Ozoga (1981) showed that increasing proportions of male offspring were born in white-tailed deer *Odocoileus virginianus* when the period between mating and onset of estrous increased. However, Verme & Ozoga (1981) assumed ovulation to occur 12-14 hours after termination of estrus, whereas studies of captive red deer and fallow deer *Dama dama* have shown that ovulation occur on average one day after the onset of estrus (Asher et al. 1990, 1992).

Demographic analyses of vertebrate populations often only consider the female part of the population, and generally assume that a sufficient number of males is present to secure fertilisation of all available females (Caughley 1977, Sæther et al. 2001). Our study, though very small-scale, provides the first experimental indication that the composition of the male segment may influence the demography of a moose population (see also Sæther et al. 2003). Because such effects may be a general phenomenon in ungulates (Mysterud, Coulson & Stenseth 2002), we encourage other studies to evaluate this possibility before recommending harvest strategies that involve manipulation of the male segment of ungulate populations.

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