

REDUCED COST OF REPRODUCTION IN MOOSE *ALCES ALCES* THROUGH HUMAN HARVEST

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ABSTRACT: In life history theory there is a cost related with all resource allocation. For female moose (*Alces alces*), the cost of reproduction in terms of survival may be reduced for females if calves, or cows without calves, are selectively hunted during the fall. Cows with calves might experience higher hunting survival and therefore face a reduced trade-off between survival and reproduction. This hypothesis was tested during a 7-year study in northern Sweden. Female age and whether she had given birth or not best explained female moose survival during the hunting period, not the number of calves born or alive at the hunt. Still, the analysis suggests that the cost of reproduction was reduced for middle-aged females. Females not giving birth experienced a 3.2-fold greater risk of being harvested compared to those giving birth. This suggests that the application of life-history theory is crucial to fully understand the evolutionary consequences of management decisions on heavily harvested populations of ungulates.

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Classic life history theory rests on a central assumption of trade-offs among life history characters such as survival, reproduction, growth, body condition, number of offspring, and offspring size (Roff 1992, Stearns 1992). A trade-off occurs whenever an individual must allocate a fixed amount of resources in different ways. An individual that increases resource allocation to reproduction will have fewer resources to allocate to another character. The generally recognised trade offs with current reproduction are future reproduction, growth, condition, size, and survival (Williams 1966, Roff 1992, Stearns 1992). Several experimental manipulations have identified the existence of trade-offs between reproduction and other life history traits (e.g., Bell and Koufopanou 1986, Lindén and Møller 1989, but see Reznick 1992 for an opposing view). Well-known examples among vertebrate species are

Lack's bird studies in the 1960s (Lack 1968), and Clutton-Brock and co-workers' studies on red deer (*Cervus elaphus*; Clutton-Brock et al. 1982, 1983). In the latter study, reproductive females incurred a cost of reduced survival compared to non-reproductive females.

Reproductive females are more susceptible to predators than non-reproductive females (Magnhagen 1991 and references therein, Lee et al. 1996, Schaffer and Formanowicz 1996). In contrast, harvest regulations may increase the mortality of females without calves during the hunting season in cervids (Cederlund and Sand 1991, Fryxell et al. 1991, Clutton-Brock and Loneragan 1994, Cederlund and Liberg 1995, Solberg 1998, Van Ballenberghe and Ballard 1998).

In Sweden, moose with apparently low reproductive value are preferentially harvested (Swedish Environmental Protection

Agency 1994, Ball et al. 1999, Ericsson et al. 2000). Juveniles (calves) and males show the lowest survival during the harvest period, whereas adult females show the highest survival (Cederlund and Sand 1991, Ericsson and Wallin 2001, Ericsson et al. 2001). Nevertheless, the national strategy allows a considerable harvest of adult females (Swedish Environmental Protection Agency 1994, 2000). Official policy instructs hunters to harvest calves before their mothers, strongly discouraging the killing of female moose before their calves, and allowing many females to escape harvest (Thelander 1992, Swedish Environmental Protection Agency 1994). Females not accompanied by calves may be harvested as the hunters use the presence of calves as a pragmatic decision rule.

Therefore, where a female that invests heavily in reproduction may suffer increased mortality if predators are present, a female moose in Sweden that invests in reproduction might actually increase her survival. Here, I test the hypothesis that an investment in reproduction might allow female moose to escape human predation in Sweden. Do harvest regulations increase the survival of female moose if they invest in reproduction?

STUDY AREA

Data were collected in 1991-1997 in an area north of Umeå (64°12' N, 20°45' E) in the county of Västerbotten, northern Sweden. The area is located in the boreal zone close to the Bothnian Bay coast. Norwegian spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birches (*Betula pendula*, *B. pubescens*) are the dominant tree species in the area. The understorey consists mainly of blueberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idea*), and heather (*Calluna vulgaris*).

The winter moose population density in the area was estimated by aerial census at

0.7-0.9 per km² (K. Wallin, unpublished data). The density of roe deer is low and is concentrated mainly along the farmed areas near the coast (Cederlund and Liberg 1995). During November to April, semi-domestic reindeer herds occasionally use parts of the study area.

METHODS

Adult female moose were immobilised with etorphine and xylazine (Sandegren et al. 1987) between January and March from a helicopter with a dart gun. Each female was marked with a radio collar and uniquely numbered ear-tags.

During the calving season (May-July) each female was located from the ground and approached every third day to determine the number of calves born. The marked cow was approached on foot using a hand-held radio receiver until a calf was found or until the end of July. Two to seven days before the onset of the harvest period in early September, the number of calves with each female was determined. If a female had given birth, but was found alone before the harvest period, she was always rechecked to confirm the absence of calves. An evaluation and a thorough description of the method used can be found in Swenson et al. (1999).

The harvest period is open from the first Monday in September to the last of December with a temporary closure during the rut (September 25 - October 10). For further descriptions of hunting practices, Swedish hunting regulations, and management see Bergström et al. (1992) and Ball et al. (1999). Hunters had to register calves that they harvested. All radio-marked females were checked immediately after the end of the harvest period to verify reported calves harvested. Occasionally a female lost a radio-collar or the radio ceased to transmit, so these are excluded in the analyses from the date of last signal.

In the present study, 129 different females were followed over several years with a sample size of 388 observations from the start of the harvest period. Only females aged 2 years and older were included in the analysis as yearlings do not give birth in the area (Ericsson et al. 2001).

Age of females was first determined by tooth wear and eruption during marking (Skuncke 1949). If females were later killed, the lower part of the jaw was retrieved and age determined by tooth cementum analysis (Fancy 1980). Age determination by tooth wear in this study population is an accurate method up to an age of 5 years (K. Wallin, G. Ericsson, and J. P. Ball, unpublished data). In the analysis with age as an independent variable, I use those that died and those estimated to be less than 6 years old at the first marking event. This reduced the sample size to 118 females and 363 observations from the harvest period for analysis, with age as an independent variable.

I performed all statistical analyses with SAS (SAS Institute 1989). The analyses were weighted by sample size. I applied logistic regression to model the survival probabilities during the harvest period as survival is a binary response variable (Collet 1994, Sokal and Rohlf 1995). I entered all variables manually, tested them according to the procedure outlined by Collet (1994), and used Aikike's information criterion (AIC) for the final model selection. For analytical purposes, females over 16 years ($n = 5$) were pooled in the 15-year-old group.

RESULTS

During the hunting periods in 1991-1997, 53 females died. Fifty-one were reported killed by hunters, and jaws were immediately retrieved by us. Two females were found dead (one with 2 calves, one barren) during the hunt, but not reported by

hunters. Post-mortem analysis could not eliminate crippling as a cause of death. Thus, it is likely that all mortality was from hunting.

For females entering the hunt without calves, survival was 0.834 ($n = 145$, SE = 0.0310), for females entering with 1 calf it was 0.895 ($n = 171$, SE = 0.0235). For females entering with 2 calves the survival was 0.847 ($n = 72$, SE = 0.0427). The survival during the hunting period did not differ among the 3 groups (logistic regression, $P = 0.546$)

Survival, Age, and Reproduction

Survival during the hunt was negatively related to female age ($P = 0.0046$, [$P(\text{survival}) = e^{(2.567 - 0.106 \cdot \text{AGE})} / (1 + e^{(2.567 - 0.106 \cdot \text{AGE})})$]). The highest survival among all groups of females was for cows entering with 1 calf that was harvested by the hunters ($s_x = 0.959$). Females entering the hunt with 2 calves that were both harvested had the lowest survival ($s_x = 0.800$). The difference between females entering the hunt without calves and those losing their only calf during the hunt was highly significant (Fisher Exact, $P = 0.001$). No other significant differences existed among groups ($P > 0.29$, Table 1). Females without calves thus appeared to pay a survival cost of not being accompanied by a calf.

Contrary to expectation arising from the applied harvest strategy, litter size at the onset of the hunt (0, 1, or 2 calves) was not related to female survival (Table 2, $P = 0.546$). The strongest relationship (other than age) was whether a female had given birth, but this was not significant (Table 2). Female age, together with whether a female had given birth, was the model that best explained female moose survival during the hunt (Table 2). The fit of this model was better according to the AIC-value than the model with age and number of calves born. Inspection of Fig. 1 further suggests

Table 1. Survival for female moose that entered the hunt with 2, 1, or no calves. Females that entered the hunt with 1 calf which was shot had a higher survival rate than females entering without a calf ($P = 0.001$). No other significant differences existed among groups ($P > 0.29$).

#calves pre-hunt	#calves killed	Hunting survival	SE	<i>n</i>
2	2	0.800	0.126	10
2	1	0.905	0.064	21
2	0	0.829	0.059	41
1	1	0.959	0.028	49
1	0	0.889	0.031	122
0	-	0.834	0.029	145

that this was most pronounced for females in the age interval of 5-10 years that gave birth. I further tested this by using the 3 age classes emerging from Fig. 1 (2-4, 5-10, 11, and older). This revealed that females aged

5-10 that had not given birth had a significantly lower survival rate than females that gave birth (Fig. 2, logistic regression, $P = 0.018$). This was not significant for the other 2 age classes ($P > 0.65$). Middle-aged females (5-10 yr) not giving birth experienced a 3.2 times higher mortality risk during the hunting period.

Restricting the analysis to middle-aged females without calves in August (pre-hunt), there was a tendency towards higher survival for cows that gave birth but lost their calves before the onset of the hunt versus those that did not give birth (Fisher Exact, $P = 0.08$). None of the 15 middle-aged females that gave birth and lost their calves before the hunt was killed during the hunt ($s_x = 1.0$), but 8 of the 34 that did not give birth were killed by hunters ($s_x = 0.765$).

DISCUSSION

The general idea that calves may shield a moose female from human predation was not supported by the analysis; more calves per se were not better with respect to survival during the hunting period. However, the management emphasis on survival of reproductive cows and heavy harvest may apparently reduce part of the cost of

Table 2. Analyses of the contribution of age and reproduction on survival during the hunting period ($n = 363$). The best fit was for the logistic model that took both female age, and if she had given birth or not, into account. R is a binary variable with a value 1 if the female had given birth, 0 if she did not give birth. For R Aug the value is 1 if a female entered the hunt with calves, 0 if she entered without calves.

Variable	-2logL	Δ -2logL	df	<i>P</i>	AIC
Null model	301.811				304.440
Age(0-15)	294.036	7.775	1	0.005	298.036
Age, Born litter (0,1,2)	291.038	10.773	2	0.005	297.038
¹ Age, R	291.006	10.805	2	0.004	297.006
Age, Litter Aug	293.129	8.682	2	0.013	299.129
Age, R Aug	291.707	10.104	2	0.006	297.707

¹ Best model.

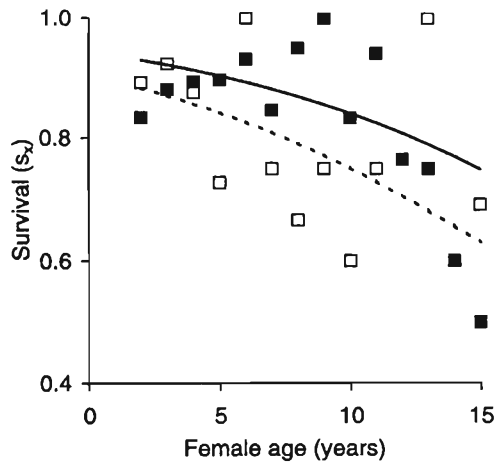


Fig. 1. Female moose survival during the hunt in relation to age and whether she had given birth (filled squares) or not (open squares). Broken line indicates age-related survival of barren females; solid line aggregated survival of females with at least 1 calf. Female age, together with whether a female had given birth, best explained female moose survival during the hunt. This was pronounced for females in the age interval of 5-10 years that gave birth.

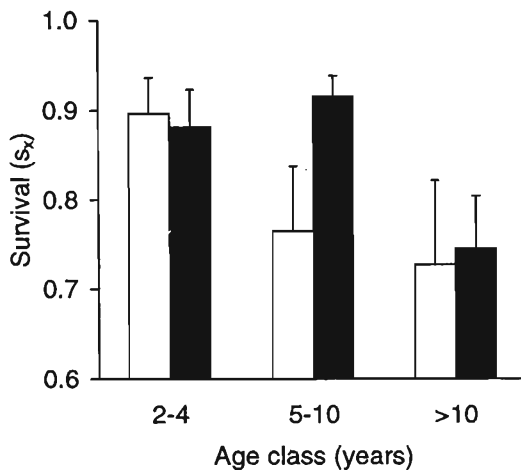


Fig. 2. Survival of moose females in different age classes (2-4, 5-10, and >10 years old) in relation to whether they did not give birth (open bars) or gave birth to at least 1 calf (solid bars). Middle-aged females without calves had a 3.2 times greater risk of being shot than those still with calves during the hunt. In young and old age classes this was highly non-significant.

reproduction (in terms of survival) for the middle-aged segment in the moose population.

A most striking pattern was that females not giving birth in the most reproductive segment (5-10 yr) displayed a significantly higher hunting mortality than those that give birth. I see two potential explanations for this. First, females with calves may use different habitats than females not giving birth, and may more actively select habitat to avoid predators. The latter has been documented for moose when wolves were present (e.g., Edwards 1983, Stephens and Peterson 1984). Second, females not giving birth may rut earlier and therefore be more vulnerable to hunting early in the season (Ericsson and Wallin 1996). This clearly deserves further attention but the selective harvest may potentially alter the trade-off between reproduction and survival in middle-aged females. Further investigation would require that one compared survival of reproductive females versus non-reproductive females in the complete absence of predation (including hunting) to fully reveal the underlying trade-off between their survival and reproduction. In the absence of predation, females that just give birth to 1 calf, or those that do not give birth every year, may actually have a higher evolutionary fitness as reproduction is prolonged over a longer period. However, as argued here, this may at least partly be the opposite under a human selection regime that favours female moose that raise a calf in consecutive years.

At first, the long (~ 4 months) hunting season may contradict the applied strategy as cows may lose their calves and then may get killed by hunters who perceived her as a cow without calves. We do not believe this happens for many females. The majority (75%) of the total female harvest in the area was taken before September, and there is also a temporal division between females

in the most reproductive segment (3-10 yr) and in females in low-reproductive ages (1-2 yr, > 10 yr, Fig. 1; Ball et al. 1999, Ericsson et al. 2001). The normal strategy for hunting groups is to try to cull bulls, single females, and calves (in that order) before the temporary closure for the rut September 25. When the season reopens, if their quota is not filled, the hunters tend to focus on calves and single individuals of both sexes.

Will the hunters selective strategy have an evolutionary impact? A rule of thumb in quantitative genetics is that in an outbred population like moose there will be genetic variation for almost every character (Hartl and Clark 1989). Thus, one may expect a genetic basis for selection concerning litter size to exist. However, temporary differences in the environment may have stronger impact on litter size than permanent genetic differences between female moose (sensu Hartl and Clark 1989). Hence, most of the observed variation in litter size may be of non-genetic origin, but the elevated survival for middle-aged reproductive females may still result in increased reproduction in the population given that the selection regime persists. But how soon would such an increase be possible to observe in the moose population? Commercial harvest of fish by humans acts as a selective force on demographic parameters (e.g., Murphy 1967, Garrod 1988, Hutchings and Myers 1994). Furthermore, those changes may occur relatively quickly in an evolutionary sense (i.e., 30-60 generations; Crowl and Covitch 1990, Reznick et al. 1990). For a moose population it means that it may take 200-500 years before we can detect a change given that the same selection regime persists. Alternatively, the change can be rather fast and observable due to phenotypic plasticity (Ridley 1993). This has implications for the study of moose with their relatively long generation time. First, it is hard to observe changes induced by harvest regimes for life

history traits. That life-history traits in general show low heritability reinforce this (e.g., Falconer 1989). Second, despite this, it will still be possible for selection to act although it will proceed at a slower rate. Third, if we notice a rather fast change in a life history trait, the reason may well be phenotypic plasticity in the genome.

To conclude, no effective management of any harvested population can ignore the underlying principles of population biology (Landa 1997). I suggest that in heavily harvested populations, one must also consider life-history theory because harvest regimes may alter the trade-offs that have been important in the evolutionary history of the species in question. By focusing on populations that are selectively harvested, we may be able to take the study of life history trade-offs to another level: from controlled laboratory settings to full-scale "natural" settings. Thus, instead of regarding exploited ungulate populations as less suitable for such studies, they may in fact be better, because they can be used to study life-history trade-offs and the potential evolutionary consequences of harvest (Skogland 1989, Hartl et al. 1991, Ginsberg and Millner-Gulland 1994, Solberg 1998).

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