

# Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality

H. Sand, C. Wikenros, P. Ahlqvist, T.H. Strømseth, and P. Wabakken

**Abstract:** Predators commonly select prey of inferior quality compared with the average animals found in the population. Consequently, predation may often be compensatory to other sources of mortality. We tested whether wolves (*Canis lupus* L., 1758) in Scandinavia selected moose in poor body condition by comparing mandibular marrow fat (MMF) of wolf-killed moose (*Alces alces* (L., 1758)) with harvested moose. Model selection analyses indicated that MMF levels were lower for wolf-killed moose compared with harvested moose, but an unbalanced sample design between years for the two causes of death (wolves and harvest) may have confounded a clear interpretation of the results. Nevertheless, corrected MMF levels (to 1 April) showed that a significantly ( $p = 0.006$ ) higher proportion of the wolf-killed calves (18.5%) were below the level often assumed to reflect acute malnutrition (<20% MMF) compared with harvested moose calves (3.3%). For wolf-killed yearlings and adult females, 5.6% and 8.3%, respectively, had MMF below this level compared with 0% for harvested individuals. As a result, 15.1% of the total number of wolf-killed moose and 1.6% of the harvested moose during winter appear to be compensatory to mortality from starvation. Differences in body condition, and thus levels of compensatory mortality, found between wolf-killed and harvested moose in this study may reflect a stronger selection for individuals in poor body condition by wolves.

**Key words:** compensatory predation, marrow fat, moose (*Alces alces*), prey selection, wolves (*Canis lupus*).

**Résumé :** Les prédateurs sélectionnent souvent des proies de qualité inférieure à celle des animaux moyens retrouvés dans la population. En conséquence, la prédation peut s'avérer être compensatoire par rapport aux autres sources de mortalité. Nous vérifions si les loups (*Canis lupus* L., 1758) en Scandinavie choisissent les élan en mauvaise condition corporelle en comparant la graisse de la moelle de la mandibule (MMF) chez des élan (*Alces alces* (L., 1758)) tués par les loups et d'autres élan récoltés. Des analyses de sélection de modèles indiquent que les concentrations de MMF sont plus basses chez les élan tués par les loups que chez les autres élan récoltés, mais un plan d'échantillonnage non équilibré entre les années pour les deux causes de mortalité (loups et récolte) peut avoir causé de la confusion dans l'interprétation des résultats. Néanmoins, les concentrations corrigées de MMF (jusqu'au 1 avril) montrent qu'une proportion significativement plus élevée ( $p = 0,006$ ) de jeunes tués par les loups (18,5 %) se situent sous le niveau généralement présumé refléter une malnutrition aiguë (<20 % MMF) par comparaison avec les jeunes élan récoltés (3,3 %). Chez 5,6 % des jeunes de l'année et 8,3 % des femelles adultes tués par les loups, les concentrations sont sous ce seuil, par comparaison à 0 % des individus récoltés. En fin de compte, 15,1 % du nombre total des élan tués par les loups et 1,6 % des élan récoltés durant l'hiver semblent représenter de la mortalité compensatoire à la mortalité par inanition. Les différences de condition corporelle, et ainsi les niveaux de mortalité compensatoire, trouvés entre les élan tués par les loups et les élan récoltés dans notre étude peuvent refléter une plus forte sélection par les loups des individus en mauvaise condition physique.

**Mots-clés :** prédation compensatoire, graisse de moelle, élan (*Alces alces*), sélection des proies, loup (*Canis lupus*).

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## Introduction

The type of selection pattern by predators may be important for the dynamics of predator-prey populations for at least two reasons. First, selected prey individuals may con-

tribute differently compared with an average individual to the annual growth of the prey population because their reproductive value is dependent on age and sex (Gaillard et al. 2000). Second, predation impact on prey populations is dependent on the compensatory nature of predation mortality

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(Caughley 1977). For large ungulate populations limited by high harvest rates, most predation mortality is assumed to be additive to other sources of mortality (McCullough 1979; Bartmann et al. 1992). This is because high harvest rates may regulate populations at levels below where density-dependent resource limitation may occur and thus restrict the potential for compensation through increased reproduction or survival.

Among mammals, predators commonly prey selectively on the most vulnerable individuals in a population (Errington 1946; Mech 1970; Curio 1976; Pole et al. 2003), but see Andersen et al. (2007) for an alternative result. The pattern of prey selection by predators have generally been investigated by using different proxies of prey vulnerability including individual characters such as age, sex, disease, debilitation, abnormalities, and different measurement of body condition. Selection of inferior individuals of a particular prey species is sometimes related to the difficulty for the predator to capture individuals of that species with a stronger selection for inferior prey with increased difficulty to capture and kill individuals (Temple 1987). In particular, predators that live on prey species with a body size much larger than themselves may be expected to show such a pattern. In temperate and boreal regions, winter conditions usually constrain ungulates so that body condition deteriorates with time during winter (Caughley and Sinclair 1994; Franzmann and Schwartz 1998), making them more vulnerable to predation (Mech et al. 2001). One commonly used measure of body condition for ungulates is marrow fat content in various skeletal bones (Cheatum 1949; Neiland 1970; Franzmann and Arneson 1976), which is among the last body resources to be metabolized during times of food shortage (Dauphine 1971; Mech and DelGiudice 1985). Low marrow fat levels (<10%–30%) indicate individuals in very poor condition that have an elevated risk of dying from starvation in late winter (Franzmann and Arneson 1976; Ballard et al. 1987). Evidence for selection of prey with low marrow fat levels will therefore have important implications for the extent of additive versus compensatory mortality and thereby on the magnitude of predator limitation on prey population growth and abundance (Gasaway et al. 1992).

In Scandinavia, wolves (*Canis lupus* L., 1758) prey mainly on moose (*Alces alces* (L., 1758)), a formidable prey species being three to nine times larger (depending on age) than wolves in winter (Sand et al. 2005, 2006a). Wolves select moose on individual characters such as age and sex with a strong preference for calves and old females (Sand et al. 2005, 2008). In this paper, we test the hypothesis that wolves actively select prey in poor body condition by comparing mandibular marrow fat content (MMF) of wolf-killed and harvested moose, assuming that harvested individuals represent what is available in the moose population. We also quantify the extent to which wolf predation may be compensatory to other mortality by assuming that predation on moose that show acute malnutrition (using variable levels of MMF: 10%–30%) represent compensatory predation (Gasaway et al. 1992). Our analyses are restricted to the time of year (winter) when body condition should be lowest (Huggard 1993; Mech et al. 1995) and therefore the potential for selection should be highest.

## Materials and methods

### Study area

Moose currently inhabit all parts of the Scandinavian peninsula (Sweden and Norway) with populations showing high annual growth rates with annual harvest quotas commonly being 25%–30% of the total preharvest population size in areas without large predators (Lavsund et al. 2003). Winter population densities (postharvest) normally range between 5 and 15 moose per 10 km<sup>2</sup>. The proportion of calves in the harvest commonly constitutes 40%–50% (Lavsund et al. 2003; Rönnegård et al. 2008), whereas their proportion in the winter population after harvest normally ranges between 25% and 35% (H. Sand and C. Wikenros, unpublished data). The distribution of wolves in Scandinavia is largely limited to southern Norway and south-central Sweden, which was recolonized in the early 1980s (Wabakken et al. 2001). During the 1990s, the wolf population increased in numbers and range with a total population size of 252–291 wolves in the winter of 2009–2010, including a total of 49–52 (resident) pair and pack territories (Wabakken et al. 2010). Moose are by far the most important prey for wolves in Scandinavia, generally constituting more than 95% of the biomass ingested in winter (Olsson et al. 1997; Sand et al. 2005). Predation on moose is strongly directed towards a high proportion of calves in both winter (~70%; Sand et al. 2005) and summer (~90%; Sand et al. 2008). Other prey species include roe deer (*Capreolus capreolus* (L., 1758)), beaver (*Castor fiber* L., 1758), and in Norway, red deer (*Cervus elaphus* L., 1758) and wild reindeer (*Rangifer tarandus* (L., 1758)).

### Wolves studied

Wolves were immobilized from the air following procedures presented in Arnemo and Fahlman (2007) and described in detail in Sand et al. (2006b). Wolves were equipped with GPS neck collars (GPS-Simplex (TVP International, Lindsberg, Sweden) or GPS-plus (Vectronic Aerospace, Berlin, Germany)). Winter (1 December – 30 April) predation was studied during 1999–2009 for 25 (18 based on GPS and 7 based on VHF) intensive study periods (mean = 70 days, range = 33–132 days) distributed on 17 different wolf territories for a total of 1747 days. In addition, search for wolf killed prey occurred during occasional snow tracking of VHF-collared wolves in one territory.

### Wolf-killed moose

We searched for wolf-killed prey by visiting locations where GPS- and VHF-collared wolves had stopped for extended periods following Sand et al. (2005). Information recorded at kill sites included body parts, tracks, blood, and wolf scats, and were used to determine the species, age, and sex of prey, time of death, proportion of the carcass consumed, and whether the carcass actually resulted from a wolf kill. Species of ungulate carcasses found were identified from hair and skeletal remains, whereas sex was determined by visual inspection of reproductive organs, or by presence of antler pedicles. Age of ungulates was classified into juvenile (<1 year old) or adult (≥1 year old) in the field and the mandibles were collected and later used for age determination by counting cementum annuli in the first molar (Markgren 1969) and estimation of body condition in terms of marrow fat

(MMF) content (Neiland 1970). Examination of wolf-killed carcasses and collection of the mandibular in the field occurred within 1–2 weeks after the assumed date of death (Sand et al. 2005), thus minimizing the risk of dehydration of marrow fat. For a more detailed description of methods used in studies of wolf predation see Sand et al. (2005, 2008).

### Harvested moose

In the Grimsö research area (130 km<sup>2</sup>), situated within the wolf range, moose were harvested throughout fall and winter thereby providing data on moose that could be used for comparison of marrow fat content with wolf-killed moose during winter. Harvested moose were aged and sexed and all samples and measurements taken were handled by research personnel. Harvest is strongly selective in terms of age and sex of moose (Rönnegård et al. 2008) and based on general harvest strategies to maximize yield. This harvest regime is not likely to result in a selection according to body condition of animals. A subsample of harvested moose during October through November included occasions where female moose were killed with one or both of her calves. These data were used to test for any relationships in body condition (carcass mass, MMF) of the calves and that of the mother including maternal age.

### Condition of wolf-killed and harvested moose

Estimation of MMF from wolf-killed and harvested moose was performed using the Neiland (1970) method with bone marrow weighed and dried at 70 °C for 14 days, then weighed again, and fat content calculated as the ratio of dry and wet mass. For comparison of differences between wolf-killed and harvested moose, we restricted our data to moose killed from 1 December to 30 April and using date of collection (the number of days from 1 July) as covariate in the analyses. For classifying individual moose as suffering from acute malnutrition that eventually will lead to starvation mortality, we used a 10%, 20%, and 30% threshold level of marrow fat (Franzmann and Arneson 1976; Ballard et al. 1987). The three variable levels of marrow fat were chosen because there is no known distinct threshold that will lead to the death of an animal and throughout the literature these levels have been commonly used to indicate severe starvation.

### Estimation of compensatory mortality

Assuming that the 20% threshold of MMF correctly reflects the level below which all moose starve to death in the moose population, we calculated the quantity of wolf predation and human harvest that should be compensatory to mortality from starvation. The proportion of moose below this threshold was calculated for calves and for the pooled sample of yearlings and adult females. To estimate the total proportion of wolf-caused mortality that should be compensatory to starvation in the moose population during winter, we also need to include the age distribution of moose in wolf kills. The proportion of moose calves in wolf kills during winter is approximately 70% (Sand et al. 2005), whereas the proportion of calves in the winter population is, on average, 30% (H. Sand and C. Wikenros, unpublished data). We estimated the proportion of harvested moose that would be compensatory in the same way but with the difference that calves con-

stituted 50% among killed moose as usually applied to human harvest in this area (Rönnegård et al. 2008). We calculated the proportion of compensatory mortality  $c$  for the different cause of death (wolf-killed or harvested) using

$$[1] \quad c = \sum_{m=1}^m s_m p_m$$

where  $m$  is the moose category (calf or adult),  $s$  is the proportion of moose in category  $m$  that were starving and were assumed not to have survived the winter, and  $p$  is the proportion of moose in category  $m$  that were killed (wolf or harvested).

### Analyses

Moose were pooled into three age classes (0, 1,  $\geq 2$ ) with males excluded in the oldest age class owing to small sample size. We arcsine-transformed the dependent variable (proportion marrow fat) to achieve a more normal distribution. Because we used data of harvested moose collected over a longer time period (18 years during 1990–2009) than data from wolf-killed moose (8 years during 1999–2009), and because 41% of this data were collected before the wolf study started, we initially tested for differences in MMF levels among the two time periods for harvested moose by including time period as a fixed effect (before or after the year of 1999) variable in a linear mixed model (LMM) while controlling for age class (fixed effect,  $n = 3$ ) and time of the year (Time) as a covariate. Inspection of residuals from a linear regression between time of the year and an arcsine-transformed marrow fat levels suggested that these two variables were linearly related. We also tested for differences in MFF between years while analyzing wolf-killed and harvested moose separately, controlling for age class and time of the year with and without year as a random factor. The results showed weaker support for models including year as a fixed or random factor for both harvested and wolf-killed moose (Table 1).

Because most wolf-killed moose were sampled from a larger area than harvested moose, we tested for an area effect of sampling by comparing a small subsample ( $n = 10$ ) of the wolf-killed moose, which matched geographically with that of the harvested moose, with that of the rest of the sample of wolf-killed moose ( $n = 113$ ). Using age class as fixed factor, we found no effect of area of sampling (entered as a fixed factor) on the adjusted MMF levels at 1 April (see below) (GLM:  $F_{[1,122]} = 0.019$ ,  $p = 0.89$ ).

For all moose, we initially tested for a linear effect of time (of kill) during winter and age class on MMF levels in the GLM model. We then estimated the effect of type of death (Type) including interactions with time (Time) and age (Age) using LMM both with and without the year of sampling (Year) as a random variable. Akaike's information criterion (AIC) with adjustment for small sample size (AIC<sub>c</sub>) was used for ranking the quality of each model. We considered the model with the lowest AIC<sub>c</sub> score as the best model, with models within 2 AIC<sub>c</sub> to be of similar quality (Burnham and Anderson 2002).

We used parameter estimates from the LMM model on the change in MMF levels with time during winter for both type moose and calculated the MMF levels for all moose at

**Table 1.** Model selection based on Akaike's information criterion (AIC) for variables affecting body condition (measured as mandibular marrow fat) of wolf (*Canis lupus*) killed and harvested moose (*Alces alces*) in Scandinavia.

<i>n</i>	Model	Model	<i>K</i>	$\Delta_i$	$w_i$
123	Wolf-killed	Time + Age	5	0	0.67
		Time + Age + Year	6	1.41	0.33
97	Harvested	Time + Age	5	0	0.70
		Time + Age + Year	6	1.72	0.30
97	Harvested	Age	4	0	0.38
		Time + Age	5	0.22	0.34
		Time + Age + Before/After	6	2.04	0.14
		Age + Before/After	5	2.11	0.13
		No effect	2	79.18	<0.001
		Before/After	3	79.75	<0.001
		Time	3	81.00	<0.001
		Time + Before/After	4	81.84	<0.001

**Note:** Models were performed with and without year of sampling as a random (Year) or fixed (Before/After) factor. The time during winter (Time) was calculated as the number of days from 1 July and the variable "Age" represents three age classes (calves, yearlings, and adult females).

1 April, assuming that this date represented the date with the lowest MMF levels reached during winter (Cederlund et al. 1989, 1991). We then tested for differences in the proportion of harvested and wolf-killed moose starving at 1 April with the Pearson  $\chi^2$  test.

Finally, we examined the relationship in two estimates of body condition (body mass and MMF) between mothers and their offspring using simple linear regression, whereas the relation between a mother's age and body condition of their calves was tested with Spearman's rank correlation. Parameter estimates of variables tested were considered significant at  $\alpha = 0.05$  and we refer to  $\alpha$  levels between 0.05 and 0.10 as showing a tendency to be significant. Analyses were done using SPSS version 19.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

## Results

Harvested moose ( $n = 97$ ) were killed earlier during the winter compared with wolf-killed moose ( $n = 123$ ,  $t = 8.59$ ,  $p < 0.0001$ ) and malnourished individuals (MMF < 20%) were found almost exclusively (94.7%,  $n = 19$ ) after 1 February (day no. 216; Fig. 1). Fat levels decreased with Time from 1 December (day no. 154; Fig. 1) for all age classes (LLM:  $b = 0.12$ ,  $SE = 0.03$ ,  $F_{[2,220]} = 63.03$ ,  $p < 0.001$ ) (Table 2, model A2; Figs. 1a–1c). The rate of decrease was 0.08%–0.10% per day depending on age class.

To test the hypothesis that wolves expressed a stronger preference for moose in poor condition compared with hunters, we performed an analysis of model selection including the cause of death (Type) as potentially important variable. This analysis showed that a model including Type in addition to age class (Age), the time during winter (Time), and its interaction (Type  $\times$  Time) had most support (Table 2, model A1). This model had only slightly lower (0.85) AIC<sub>c</sub> value than the model without including Type (model A2), and model weights showed that this model (A1) had a 39% probability of being the best model compared with 26% for the model excluding the effect of Type.

Because data were collected over a number of years and year of sampling was only partially overlapping between the

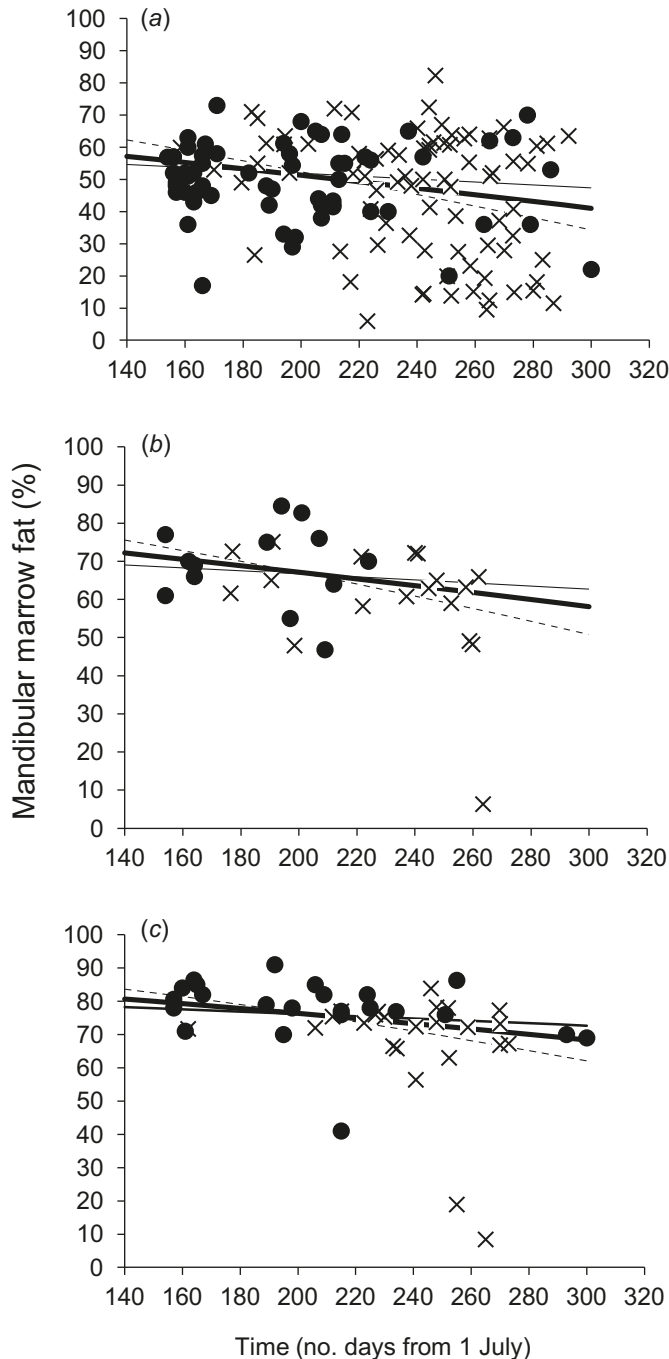
two causes of death and because annual variation in prey body condition may be an important confounding variable, we performed an analyses including the year (of sampling) as a random variable (Table 1, model B1–B9). This analysis showed that the model including Time, Age, and Year (B1) had the lowest AIC<sub>c</sub> value and the highest model weights of all candidate models (36%; Table 2). However, several of the models including Type and its interaction with Time were of similar quality according to the AIC<sub>c</sub>. This model selection analysis gave some support to the fact that a part of the variation found in MMF levels between wolf-killed and harvested moose may be attributed to variation between years and confounded by the fact that the year of sampling was only partially overlapping between the two causes of death.

Because of the above result, we performed analyses on a restricted data set including only years having both wolf-killed and harvested moose with and without Year as a random variable. Models including the type of death (Type), either as a single variable or in combination with other main variables, resulted in AIC<sub>c</sub> scores being 2.0–2.7 higher than the model excluding Type, and with model weights ranging from 14% to 20% compared with the best model including only Time and Age (55%; Table 2, C models). Models including Year as a random factor also did not support the inclusion of Type (Table 2, D models). Consequently, analyses of this restricted data set did not support the idea that wolves showed a stronger selection for moose in poor body condition compared with hunters. However, the analyses did not result in conclusive evidence of a difference in selection between the two mortality agents.

We also tested if the sex of moose would be an important character for the selection process between hunters and wolves by including this variable in another restricted data set ( $n = 144$ ), including only calves and yearlings of known sex (Table 3). This analysis neither supported sex as being an important variable to explain MMF, nor sex being important for evaluating the effect of type of death on MMF levels.

To estimate the proportion of both wolf-killed and harvested moose that were compensatory to assumed mortality from starvation, we calculated MMF levels for both wolf-

**Fig. 1.** (a–c) Mandibular marrow fat (MMF) of wolf (*Canis lupus*) killed (×) and harvested (●) moose (*Alces alces*) in relation to the date of kill from 1 July. Regression lines are parameters estimates of the slope  $b$  as derived from the GLM model A1 (Table 2) from wolf-killed (broken) and harvested (thin solid) lines. Thicker solid line represents the regression line from model B1 (Table 2), excluding the effect of the type of mortality while including year as a random variable. In the  $x$  axis, 1 December represents 154, 1 February represents 216, and 1 April represents 275, respectively.



killed and harvested moose at the time of year when this estimate of body condition is assumed to be at its lowest during the year. This was done by adjusting fat levels of moose to 1 April based on the mean reduction found with time during winter while including Age as a fixed effect and Year as a

random effect in the model (Table 2, model B1). Mean MMF levels of harvested and wolf-killed moose on 1 April were 42.0% (SE = 1.38%) calves, 58.0% (SE = 2.49%) yearlings, and 68.4% (SE = 2.15%) adult females. Using a 20% threshold for starvation, 12.0% of all (wolf-killed + harvested) calves, 3.2% of yearlings, and 4.3% of the adults had MMF levels below this level.

However, results from this analyses also showed that a significantly higher proportion of the wolf-killed moose calves, 15 out of 81 (18.5%), had adjusted MMF <20% compared with 2 out of 61 (3.3%) of the harvested moose calves (Pearson  $\chi^2 = 7.67$ ,  $p = 0.006$ ). For yearlings and adult females, 1 out of 18 (5.6%) and 2 out of 24 (8.3%) of the wolf-killed moose showed estimated MMF < 20%, compared with none of the same age classes among harvested moose (yearlings:  $n = 13$ ,  $\chi^2 = 0.75$ ,  $p = 0.39$ ; adults:  $n = 23$ ,  $\chi^2 = 2.0$ ,  $p = 0.16$ ).

As a result, the total proportion of wolf predation that should be compensatory (using a 20% MMF threshold for starvation) was 15.1% ((calves:  $0.185 \times 0.70$ ) + (yearlings and adult females:  $0.071 \times 0.30$ )), whereas only 1.6% of the harvested moose was classified as compensatory to starvation. If instead 10% and 30% MMF thresholds would have been used, then 3.2% and 22.9% of the wolf-killed and 0.1% and 5.7% of the harvested moose, respectively, would have died of starvation.

By assuming that only harvested moose were representative of the population and by applying 10%, 20%, and 30% MMF levels of starvation and accounting for the lower proportion of juveniles in the winter population (30%) compared with harvest (50%) resulted in 0%, 0.5%, and 1.7% of the moose population dying of starvation (in a population without wolves) in late winter, respectively. In contrast, if harvested and wolf-killed moose were equally representative of the moose population (i.e., differences between the two classes of mortality mainly because of yearly variation in MMF and an unbalanced sample design), 1.1%, 3.2%, and 5.0% of the moose population would die of starvation (in a population without wolves) in late winter, respectively.

Finally, we tested the idea that body condition of moose calves is dependent on the body condition of mothers by examining the relationship between two physical traits for a number of harvested female moose and their offspring. We found no significant relationship between moose mothers and their calves for either body mass (linear regression:  $r = 0.15$ ,  $F_{[1,25]} = 0.57$ ,  $p = 0.46$ ) or MMF levels ( $r = 0.014$ ,  $F_{[1,17]} = 0.003$ ,  $p = 0.96$ ). The mother's age also was not important in explaining variation among individual calves with respect to these two traits (Spearman's rank correlation; body mass:  $n = 27$ ,  $r_s = -0.082$ ,  $p = 0.68$ ; MMF:  $n = 26$ ,  $r_s = 0.28$ ,  $p = 0.25$ ).

## Discussion

We did not find conclusive evidence to support the hypothesis that wolves showed a stronger selection for moose with lower body condition (here measured as MMF) compared with moose killed by hunters. The inability to identify, or rule out, such an effect was likely due to an unbalanced sample design over the years where moose of different mortality causes were sampled. To identify such an effect may be

**Table 2.** Model selection based on Akaike's information criterion (AIC) for variables affecting body condition (MMF, mandibular marrow fat) of wolf (*Canis lupus*) killed and harvested moose (*Alces alces*) (Type) in Scandinavia.

<i>n</i>	Model	Year included	Model	<i>K</i>	$\Delta_i$	$w_i$
220	A1	No	Time + Age + Type + Time $\times$ Type	7	0	0.39
	A2		Time + Age	5	0.85	0.26
	A3		Time + Age + Type	6	2.06	0.14
	A4		Time + Age + Type + Age $\times$ Type	8	2.30	0.12
	A5		Time + Age + Time $\times$ Age	7	3.06	0.09
	A6		Age	4	16.82	<0.001
	A7		Time	3	96.23	<0.001
	A8		Type	3	101.34	<0.001
	A9		No effect	2	106.86	<0.001
220	B1	Yes	Time + Age + Year	6	0	0.36
	B2		Time + Age + Year + Type + Time $\times$ Type	8	1.11	0.21
	B3		Time + Age + Year + Type	7	1.69	0.16
	B4		Time + Age + Year + Time $\times$ Age	8	1.86	0.14
	B5		Time + Age + Year + Type + Age $\times$ Type	9	2.01	0.13
	B6		Age + Year	5	9.79	0.003
	B7		Time + Year	4	100.25	<0.001
	B8		Type + Year	4	104.69	<0.001
	B9		Year	3	108.50	<0.001
157	C1	No	Time + Age	5	0	0.55
	C2		Time + Age + Type	6	1.96	0.20
	C3		Time + Age + Type + Time $\times$ Type	7	2.70	0.14
	C4		Time + Age + Time $\times$ Age	7	4.02	0.07
	C5		Time + Age + Type + Age $\times$ Type	8	5.51	0.03
	C6		Age	4	10.50	0.003
	C7		Time	3	48.89	<0.001
	C8		Type	3	55.89	<0.001
	C9		No effect	2	56.14	<0.001
157	D1	Yes	Time + Age + Year	6	0	0.58
	D2		Time + Age + Year + Type	7	2.14	0.20
	D3		Time + Age + Year + Time $\times$ Age	8	3.66	0.09
	D4		Time + Age + Year + Type + Time $\times$ Type	8	3.72	0.09
	D5		Time + Age + Year + Type + Age $\times$ Type	9	5.60	0.04
	D6		Age + Year	5	8.12	0.01
	D7		Time + Year	4	52.24	<0.001
	D8		Type + Year	4	58.54	<0.001
	D9		Year	3	59.12	<0.001

**Note:** The time during winter (Time) is equal the date of death calculated as the number of days from 1 July and the variable Age represents three age classes (calves, yearlings, and adult females). Year of sampling is included as a random variable in models B and D.

especially problematic if there exist annual variation in the response variable examined (MMF) and if years with better or worse condition are linked to years dominated by one source of mortality (harvest or wolves). We found no support for our response variable (MMF) being affected by year (of sampling) for either wolf-killed or harvested moose in our data set. Nevertheless, controlling statistically for the variable Year in our analyses seemed to result in less support for our working hypothesis that wolves showed a stronger selection for malnourished moose compared with hunters. However, if a preference among wolves for moose with low body condition does exist, then our data indicate that this selection is strongest in the youngest age class of moose (calves) and that the strength of this selection is dependent on time during winter (Fig. 1).

Another potentially confounding factor in our analyses may have been the data from wolf-killed moose were collected over a much larger area than the data from harvested

moose. However, two findings support the view that a spatially unbalanced sample design was not important for the results found in this study. First, there was no difference in MMF levels between a subsample of wolf-killed moose overlapping with harvested moose and the rest of the wolf-killed moose. Second, previous sampling of moose fitness traits from a large number of moose populations in Sweden showed that moose from the Grimsö population (harvest sample) generally had equal or lower body mass and fecundity than other populations in central and southern Sweden (Sand 1996).

For predators that kill large-sized prey species such as moose and bison (*Bison bison* (L., 1758)), juveniles are easier to kill than adult individuals and there should therefore be less selection for weak or malnourished individuals within this age class relative to that of adult animals (cf. Temple 1987). From this, we predicted that selection for moose with poor body condition by wolves would be most pronounced

**Table 3.** Model selection based on Akaike's information criterion (AIC) for variables affecting body condition (MMF, mandibular marrow fat) of wolf (*Canis lupus*) killed and harvested moose (*Alces alces*) (effect of Type) in Scandinavia ( $n = 144$ ).

Model	Year included	Model	$K$	$\Delta_i$	$w_i$
E1	No	Time + Age + Type + Time x Type	6	0	0.47
E2		Time + Age	4	1.887	0.18
E3		Time + Age + Type + Sex + Time x Type	7	1.937	0.18
E4		Time + Age + Time x Age	5	3.145	0.1
E5		Time + Age + Type	5	3.88	0.07
E6		Time + Age + Type + Age x Type	6	5.358	0.03
E7		Time + Age + Type + Sex	6	5.789	0.03
E8		Age	3	12.364	<0.001
E9		Time	3	25.196	<0.001
E10		Type	3	34.702	<0.001
E11		No effect	2	36.365	<0.001
F1	Yes	Time + Age + Year	5	0	0.35
F2		Time + Age + Year + Type + Time x Type	7	0.55	0.27
F3		Time + Age + Year + Time x Age	6	1.545	0.16
F4		Time + Age + Year + Type	6	2.101	0.12
F5		Time + Age + Year + Type + Sex + Time x Type	8	2.587	0.1
F6		Time + Age + Year + Type + Age x Type	7	3.74	0.05
F7		Time + Age + Year + Type + Sex	7	4.174	0.04
F8		Age + Year	4	7.136	0.001
F9		Time + Year	4	25.481	<0.001
F10		Type + Year	4	34.528	<0.001
F11		Year	3	35.578	<0.001

**Note:** Models were performed with and without year (Year) of sampling as a random factor, time during winter (Time), age class (Age; divided into calves, yearlings, and adult females), and sex.

among adults. In this respect, our results were contrary to our prediction. However, the success of an attack on (and preference for) juveniles of these large prey species may be ultimately dependent on the physical status of the mother (Mech 1970) or on other group members for social species such as bison (Carbyn 2003) because offspring may be actively defended and (or) the escape facilitated by older animals. If correct, selection for malnourished juveniles would be expected if body condition of juveniles were closely related to the physical status of the mother, which in turn would affect her ability to protect offspring from predation. Although we had no data on the true physical status of the mother of wolf-killed juvenile moose, data from harvested moose in the Grimsö population where harvested juveniles and their mothers could be linked to each other did not reveal such a relationship with regard to either body mass or MMF level. Age of the mother also was not an important factor explaining variation in body condition of their calves. Our data therefore did not support the idea that low body condition of wolf-killed calves actually reflected body condition of their mother.

Interestingly, a study of radio-collared moose and their offspring in northern Sweden demonstrated that juveniles with older mothers suffered higher harvest mortality rate compared with those with prime-aged mothers (Ericsson et al. 2001). It is possible that the same pattern of selection may occur for both harvested and wolf-killed juveniles in our study. If true, then the real preference by wolves for sub-optimal individuals (old females with calves) in the population would be even larger than found in our comparison with harvested animals because under this scenario harvested indi-

viduals should not constitute a representative sample of the standing population. Instead, if the same pattern shown in the study by Ericsson et al. (2001) applies to our data, then both wolf predation and human harvest of moose calves may actually result from an over-representation of calves produced by older females relative to their fraction in the population.

### Marrow fat and starvation mortality

Mech and DelGiudice (1985) cautioned that high MMF levels do not automatically mean that animals are in good condition because other somatic fat deposits will be depleted long before the marrow fat content is affected. In adult moose, marrow fat levels <50% may indicate starvation (Ballard et al. 1987). Because fat in the bone marrow is the last fat source to be metabolized, it is most useful as an indicator of severe starvation (Dauphine 1971; Hanks 1981; Caughley and Sinclair 1994). Marrow fat levels <20%–30% have been suggested to indicate severe starvation (Franzmann and Arneson 1976; Mech and DelGiudice 1985; Ballard 1995; Murray et al. 2006) and some studies reported that moose calves dying from starvation had marrow fat levels close to 10% (Franzmann and Arneson 1976; Ballard et al. 1987). Although there is no absolute level of marrow fat content that can be used to predict when the “point of no return” is reached, i.e., below which individuals will die from starvation, the bulk of the literature suggest that this occurs within a range of 10%–30%. Accordingly, estimates based on moose harvested during 1 December through April in our study (using a 10%–30% MMF threshold) indicated that 0%–1.7% would die annually from starvation in a population without large predators. Alternatively, if both harvested and wolf-

killed moose were representative of the standing population, then 1.1%–5.0% would die annually from starvation.

Our results may be viewed in light of data on nonharvest mortality from radio-collared moose ( $n = 192$ ) in the Grimsö moose population before wolf establishment (Rönnegård et al. 2008). These data showed that 6%–7% of the winter population died annually owing to causes other than human harvest. Of this mortality,  $\geq 50\%$  is typically due to traffic accidents (Cederlund and Sand 1991; Ericsson and Wallin 2001; Broman et al. 2002). Consequently, about 3%–4% of the moose in the population annually suffers from mortality other than harvest and traffic accidents, and of which starvation (and starvation-linked diseases) may constitute an unknown proportion.

### Comparison between populations

Wolf-killed moose calves in our population had marrow fat levels similar to, or higher than, wolf-killed calves in other studies performed in winter (Ballard et al. 1987; Mech et al. 1995; Hayes et al. 2000). However, our results partly (i.e., calves) support results from other predation studies involving wolves (Mech 1970; Mech et al. 1995; Huggard 1993; Śmiećana 2005) and other group-hunting large carnivores (Pole et al. 2003) where predator-killed prey generally was in less good condition in terms of marrow fat than harvested or accidentally killed animals.

Two factors are likely important for the relatively weak (or absent) selective pattern of malnourished moose found for wolves in our study. First, in contrast to many North American moose populations (Franzmann and Schwartz 1998), the Scandinavian moose population has been exposed to an intense annual harvest pressure during the last 30–40 years (Solberg et al. 2002; Lavsund et al. 2003), generally constituting  $>90\%$  of the total mortality in the population (Stubsjøen et al. 2000; Ericsson and Wallin 2001; Rönnegård et al. 2008) and is of a magnitude that causes a numerical population turnover within 3–5 years (Solberg et al. 2000, 2002; Sæther et al. 2001; Lavsund et al. 2003). This intensive harvest regime likely has provided small opportunities for density-dependent food limitation during the last 20 years and has resulted in a moose population consisting of individuals in generally good body condition with high fecundity and relatively low rates of nonharvest mortality (Ericsson et al. 2001; Rönnegård et al. 2008). Secondly, in our study area, winter severity may be considered moderate to mild compared with some of the studies in which larger differences in body condition between predator-killed and other animals has been reported (e.g., Mech et al. 1995; Hayes et al. 2000).

The results from our study, that the majority of wolf predation on moose in Scandinavia is additive (i.e., 77%–97%; depending on the level of MMF used for starvation mortality), is consistent with the idea that extensive compensatory mortality most likely occurs in populations near  $K$ , where population densities and mortality rates are high (McCullough 1979; Bartmann et al. 1992; Gasaway et al. 1992). Our results may also indicate that the selection pattern of prey by large predators is dependent on the general nutritional status of the prey population with the intensity of selection increasing with the magnitude of resource limitation and with in-

creased differences in the nutritional status among individuals.

We conclude that the majority of wolf predation on Scandinavian moose in winter is additive to starvation mortality and that the proportion of malnourished calves killed by wolves was approximately 5–6 times higher (using a 20% MMF level for starvation mortality) than for human harvest. This difference in the body condition of killed prey between the two predators may be reflective of an ability among wolves to test and identify malnourished individuals even within age and sex classes vulnerable to wolf predation, whereas human harvest is nonselective, or at least, less selective.

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