ANIMAL BEHAVIOUR, 2006, 72, 781–789
doi:10.1016/j.anbehav.2005.11.030

Available online at www.sciencedirect.com
ScienceDirect

# Effects of hunting group size, snow depth and age on the success of wolves hunting moose

HÅKAN SAND*, CAMILLA WIKENROS*, PETTER WABAKKEN† & OLOF LIBERG*
*Grimsö Research Station, Swedish University of Agricultural Sciences
†Department of Forestry and Wildlife Management, Hedmark University College

*(Received 1 February 2005; initial acceptance 25 March 2005; final acceptance 20 December 2005; published online 23 August 2006; MS. number: 8455R)*

To study factors important to the success of wolves, *Canis lupus*, hunting moose, *Alces alces*, we analysed data from more than 4000 km of snow tracking of wolves during 1998–2003 in Scandinavia. We used two methods to estimate hunting success for 17 wolf territories from 185 observations of wolf attacks on moose. On average, hunting success was estimated at 45 and 64% for the two methods, respectively. We used a smaller data set ($N = 142$) to examine the effect of age of breeding wolves, hunting group size, snow depth and moose density on hunting success. Multiple logistic regression showed that age of breeding males was the only variable significantly related to hunting success, with maximum hunting success at 4.5–5.5+ years of age. We also studied prey selection of radiocollared adult wolves over successive winters in two wolf packs that lost one of the breeding wolves. Whereas the surviving adult female switched to prey on roe deer, *Capreolus capreolus*, the surviving adult male continued mainly to select moose. Our results suggest that the positive effect of male age on hunting success reflects both increased experience of attacking prey and possibly the greater size of adult male wolves (25–30%) compared to adult female wolves.



Early predator–prey theory predicted that per capita kill rate of the predator will depend exclusively on changes in prey density (Lotka 1925; Volterra 1926). Later it was recognized that other factors, including the behaviour of predators and prey, are important determinants of the per capita kill rate (Holling 1959; Taylor 1984). These developments of the theory have been supported by empirical studies, including studies of wolf–ungulate systems where large variation in per capita kill rates is found both within (Hayes et al. 2000; Vucetich et al. 2002) and between wolf, *Canis lupus*, populations (Messier 1994). Among wolf–moose populations across North America, interpopulation variation in per capita kill rate varied 10-fold, but only 53% could be attributed to variation in moose, *Alces alces*, density (Messier 1994). A long-term study at Isle Royale, Michigan, U.S.A., showed that one-third of the variation in wolf kill rates could be explained by predator density, or by predator:prey ratios, and another 10–15% by interannual variation in winter climate (Vucetich et al. 2002).

One important behavioural component of large carnivore kill rates is hunting success among individuals or groups of carnivores. Many prey-related factors may affect hunting success, such as prey species, age and sex structure of the prey population, and prey group size (Chrisler 1956; Van Orsdol 1984; Fanshawe & FitzGibbon 1993; Fuller & Kat 1993; Stander & Albon 1993; Funston et al. 2001; Mech & Peterson 2003). Environmental factors such as season, type of habitat and weather characteristics have also proved to be important for hunting success, and therefore for kill rates of carnivore species (Kruuk 1972; Stander & Albon 1993; Funston et al. 2001; Mech et al. 1971, 1991, 2001; Hebblewhite et al. 2002; Mech & Peterson 2004).

Hunting success may also be related to individual traits of the predator. According to Holekamp et al. (1997), hunting success increases with age in both males and females among spotted hyaenas, *Crocuta crocuta*, whereas hunting group size is important for hunting success in African lions, *Panthera leo* (Stander & Albon 1993; Funston et al. 2001) and in African wild dogs, *Lycaon pictus* (Fanshawe & FitzGibbon 1993; Creel & Creel 1995). Estimates of hunting success, and factors important to it,

*Correspondence: H. Sand, Grimsö Research Station, Swedish University of Agricultural Sciences, S-730 91 Riddarhyttan, Sweden (email: hakan.sand@nvb.slu.se). P. Wabakken is at the Department of Forestry and Wildlife Management, Hedmark University College, N-2480 Koppang, Norway.*


0003–3472/06/$30.00/0

have attracted much less attention than estimates of kill rates, probably because of the difficulties of observing and collecting data on hunting behaviour of forest-living carnivores such as the wolf. One explanation for the large intra- and interpack variation found in kill rates in wolf–moose systems could be variation in predator-related factors directly affecting hunting success, and ultimately kill rate, of the pack.

We used snow tracks during winter to estimate the success of Scandinavian wolves hunting moose, their main prey species, in terms of the number of successful and failed attacks. We examined the effects of individual, pack and environmental characteristics by correlating the age of the breeding pair, size of the hunting group, snow depth and moose density with variation in hunting success within and between wolf packs. We also compared prey selection in two wolf packs during successive winters, before and after they suffered the loss of one of the breeding wolves.

# METHODS

## Study Area, Prey and Predator Populations

Sweden and Norway together constitute the 837 000-km$^2$ Scandinavian peninsula, hereafter referred to as Scandinavia (55°–72°N, 5°–31°E). Boreal coniferous forest and alpine areas cover more than 75% of the peninsula. Norway spruce, *Picea abies*, Scots pine, *Pinus silvestris*, birch, *Betula pubescens*, *B. pendula*, and aspen, *Populus tremula*, are the dominant tree species in various mixtures (Sweden 1991). Most of the forests are managed for a mosaic of different age class stands. The intensive forest management has also created an extensive network of forest roads. In the southern parts of Scandinavia large agricultural areas are common. Human population density averages 16/km$^2$, but large areas within the main wolf range, in south-central Scandinavia, have a density of less than 1/km$^2$ (Sweden 1991). Snow covers south-central Scandinavia for 3–6 months each year and snow depth in our study area commonly ranges between 30 and 60 cm in mid-winter (Sweden 1991). In south-central Scandinavia, moose are by far the most important wild prey for wolves, generally constituting more than 95% of the biomass ingested (Olsson et al. 1997; Sand et al. 2005) and at population densities of 0.5–1.5/km$^2$. In addition, roe deer, *Capreolus capreolus*, beaver, *Castor fiber*, and, in Norway, red deer *Cervus elaphus*, and wild reindeer, *Rangifer rangifer*, are also locally available. Average winter moose and roe deer densities within wolf territories, estimated by pellet group counts, were 1.2 moose/km$^2$ and 4.4 roe deer/km$^2$ (H. Sand, unpublished data). In two of the wolf territories (Leksand and Grangärde), where we investigated hunting success and prey choice in more detail, moose density was 0.85 and 1.11/km$^2$, respectively, and roe deer density was 0.01 and 0.20/km$^2$, respectively. Wolves successfully reproduced in south-central Scandinavia (Wabakken et al. 2001) for the first time in 1983, which was probably the first in more than 80 years (Lönnroth 1934; Haglund 1968). During the 1990s the wolf population increased in numbers and range and in the winter of 2003–2004 the total population size was estimated to be 101–120 wolves (Wabakken et al. 2004).

## Capture of Study Animals

For the purpose of this study we caught 10 wolves (nine adults and one 8-month-old pup) by darting from a helicopter in five territories, between December 1998 and February 2002. We used snow to search areas for tracks and to locate wolves for capture. When the approximate position of wolves was located, we called in a helicopter and a capture crew to track down the animals. Wolves were on average chased for 1–3 min (range 0.5–10 min), and if darting was not possible within 10 min the chase was terminated. Chasing distances were not measured regularly, but were estimated to average 1–2 km and never to exceed 5 km. This procedure with relatively short chasing times minimized stress of wolves during immobilization, and severe stress with physiological side-effects (hyperthermia) was not observed. We immobilized wolves from the air with a $CO_2$-powered dart gun and a dose of either 500 mg of tiletamine-zolazepam (Zoletil, Virbac, Carros, France), or a combination of 5 mg of medetomidine (Zalopine, Orion Pharma Animal Health, Sollentuna, Sweden) and 250 mg of ketamine (Narketan, Chassot, Dublin, Ireland). Other methods for capture, such as leg hold traps, were not considered because these were not permitted by the authorities. We measured, weighed and ear-tagged (25-mm-diameter plastic tags) all captured wolves. Blood ($4 \times 10$ ml) was sampled from the cephalic or femoral vein and tissue was taken from inside the ear by using a sterile 4-mm biopsy punch. Minor wounds from the lightweight darts, aseptic application of small plastic ear tags and aseptic tissue sampling from inside the ear were not treated, according to standard procedures for free-ranging wolves (Arnemo et al. 2004). We equipped wolves with either a GPS neck collar (Simplex, Televilt International, Lindesberg, Sweden; $N = 3$ in two territories, Gråfjell and Tyngsjö) or a conventional VHF radiocollar (Telonics Mod. 500, Mesa, Arizona, U.S.A.; $N = 7$ in three territories). The Telonics collar weighed 500 and the Televilt collar 650 equivalent to an average of 1.3% ($N = 5$, range 1.2–1.7%) and 1.1% ($N = 5$, range 1.0–1.3%) of the adult body weight of female and male wolves, respectively. Collar weights were therefore below, or well below, the maximum weight allowed (2%) by The Swedish Agency of Animal Welfare for fitting collars on wild animals, and which is believed not to impede or increase costs of locomotion. Collar neck size was adjusted to fit either males or females, using the adult neck size of collars for all ages. This was justified because in wolves 90% of the final neck size is completed at the age of 8–10 months. Minimum collar circumference used was 44.5 cm for females and 48.0 cm for males. All captured animals were observed by trained personnel until full recovery was evident, which was usually within 4–6 h. Wolves were in general recaptured every second year and the old collar were either removed or changed for a new one depending on the status of the wolf and the number of recapture events. No wolf was captured more than three times. Most wolves that were captured died later during the study period from human activities (legal and illegal killing) or from other reasons (disease, traffic accidents). For a more detailed description of capture and handling of immobilized wolves see Arnemo et al. (2004) and Kreeger et al. (2002). The research project, including capture and handling of animals, was evaluated and approved by The Swedish Agency of Animal Welfare and the Norwegian Agency of Animal Welfare.

## Radiotracking of Wolves

Wolves were radiotracked from the ground or from an aeroplane over an area of approximately 60 000 $km^2$. Ground tracking of traditional VHF collars was carried out at an average distance of 3 km (range 0.5−10 km) depending on topography and position of the wolves. Aerial tracking was normally carried out at 2000−4000 m elevation, but was sometimes done at 600 m elevation because of turbulent or misty weather at higher altitudes.

GPS collars were used on wolves in two territories. They were programmed for positioning at hourly intervals during the study periods and two to six positions per day for the rest of the year. Data were stored on the internal memory and included latitude and longitude (WGS 84), date, time and two quality estimates of each position taken (dilution of position, DOP) value and the number of satellites used for positioning: (two-dimensional or three-dimensional). Throughout the study periods, we downloaded data weekly at one territory, Gråfjell, and every second week at the other territory, Tyngsjö, from the ground. We downloaded data as VHF-coded signals using a VHF receiver and data logger (RX-900, Televilt International, Lindesberg, Sweden) and a hand-held antenna.

## Snow Tracking of Wolves

In the winters of 1998−2003 inclusive, both radio-collared and noncollared wolves ($N = 1−11$), were snow tracked on foot, on skis or occasionally by snow mobile. For all snow-tracking events, we recorded geographical location and length (km) of tracking route, name of territory and number of wolves. We also determined sex and social position by using wolves' scentmarking to distinguish residents from solitary, nonresident and subordinate wolves within packs. Thus, females were identified by the presence of vaginal blood in the urine before and during oestrus, and newly formed pairs and breeding wolves within packs were distinguished from other wolves by their scent-marking behaviour (Mech 1970; Peters & Mech 1975; Rothman & Mech 1979).

## Wolf Attacks on Moose

By using snow tracking of wolves, we were able to record all wolf attacks on moose. We identified a hunt where lengthening stride patterns for both wolves and moose indicated bounding gaits (fast running) and an attack where these tracks occurred together and where local snow conditions indicated that they had been made simultaneously (see also Murray et al. 1995 for a similar definition). An attack was considered successful if a wolf-killed moose was found near the site of lengthening stride pattern for both species and a failure if no carcass was found. Sometimes we could not distinguish this pattern of tracks in the snow near a moose carcass because of extensive wolf activity around the carcass. If fresh blood and/or bite marks were present on the carcass this was also classified as a successful wolf attack (Sand et al. 2005). For most attacks registered, we recorded additional information, such as the snow depth for moose tracks and the number of wolves and moose involved in the attack.

## Age Determination

We determined the age of breeding adult wolves by a combination of three methods: (1) known age of captured animals classified as pups by the presence of a growth zone in the tibia; (2) tooth wear of captured adults; and (3) construction of a population pedigree based on DNA analyses (Liberg et al. 2005). We used the population pedigree in combination with a complete set of data on the chronological order and geographical location of breeding packs in Scandinavia to identify the year of birth and, thus, current age for each wolf (Wabakken et al. 2001; Liberg et al. 2005). Samples for genetic analyses were derived from either blood or tissue from captured or dead wolves, scats or blood on snow from females in heat, collected during snow tracking of wolves. If the different methods estimated different ages for the same animal, we ranked the methods in order of accuracy as follows: capture of pups > pedigree construction of birth year > tooth wear of adult wolves. If results indicated that the birth year could have two or three alternatives, we used the lower or median age, respectively. For one of the 17 wolf territories (Tisjön) we had no age data for the adult wolves, and so this territory was excluded from further analyses.

## Calculation of Hunting Success

Data on wolf attacks on moose were collected in two different ways in different wolf territories, so we used two independent methods and data sets to calculate the rate of hunting success.

The first method involved collecting data from radio-collared breeding wolves in five territories during nine intensive study periods while estimating kill rates. In three of the five territories, we tracked intensively by radio, using a traditional VHF transmitter on one or both of the breeding wolves. All areas ($<5$ $km^2$) where wolves had been stationary for more than 24 h were searched for wolf-killed prey. In the other two territories we used the GPS-transmitters (Zimmermann et al. 2001). We used a GIS-based procedure for defining clusters of GPS positions, that is, two or more positions within 200 m, and these areas were then searched for wolf-killed prey within a week of data being downloaded (Sand et al. 2005).

We assumed that we found all wolf-killed moose during intensive study periods, but not all failed attacks since we did not follow entire paths of wolf movements between kills. Consequently, calculations using these data alone would have overestimated hunting success. Therefore, we used territory-specific kill rate, and average daily travel distance of radiocollared wolves, to calculate the total number of successful attacks during the number of wolf-days corresponding to the number of kilometres of tracks followed. We estimated kill rate as the average number of days between consecutive moose kills (Sand et al. 2005). Adult breeding wolves move on average 20.7 km/day ($N = 4$), according to preliminary data from Scandinavian wolves fitted with GPS-transmitters (programmed for positioning 24 or 48 GPS locations per day; H. Sand, unpublished data). In the five territories with intensive studies of radiocollared wolves (method 1), three wolves in two territories (Gråfjell, Tyngsjö) were equipped with GPS-collars. For these two territories we used the actual travel distance per day from GPS-data received (Gråfjell: 20.1 km; Tyngsjö: 22.3 km). For the other three territories where wolves were equipped with conventional VHF-collars we used an average estimate of travel distance based on four GPS-collared wolves from four different territories, two of which were included in this study of hunting success. Data from the additional two GPS-collared wolves in two other territories were included in this analysis only to give a more accurate estimate of travel distance and were not included in the analyses of hunting success. We then estimated hunting success for each territory and year from the calculated number of successful attacks and the actual number of failed attacks recorded during snow tracking according to the following model:

$$NS_{moose} = (ST_{dist}/WT_{dist})/KR_{interval}$$

and

$$WHS_{moose} = NS_{moose}/(NS_{moose} + NF_{moose})$$

where $NS_{moose}$ is the calculated number of successful attacks on moose, $ST_{dist}$ is the snow-tracked distance (km), $WT_{dist}$ is the average daily travelling distance of wolves in winter (km), $KR_{interval}$ is the kill rate calculated as the territory-specific interval in days between moose kills, $WHS_{moose}$ is the calculated hunting success on moose, and $NF_{moose}$ is the number of failed attacks on moose as registered during snow tracking.

The second method of calculating the rate of hunting success involved collecting data from 11 territories with noncollared wolves and five territories with radiocollared wolves, before or after intensive study periods of kill rate. Snow tracking was carried out whenever fresh wolf tracks were discovered and followed without actively searching for prey. These data may therefore be considered as random samples of attacks on moose by different wolf packs. We estimated hunting success from the actual number of successful and failed attacks recorded during snow tracking.

## Statistical Methods

We used a logistic regression to estimate the effect of age of breeding wolves, hunting group size and snow depth on hunting success between wolf territories and years. To control for temporal pseudoreplication (owing to repeated observations of the same wolf pack) we used a mixed-effect model with wolf territory included as a random factor. A successful attack was scored 1 and an unsuccessful attack 0. Breeding wolves were grouped into five age classes: 1.5, 2.5, 3.5, 4.5 and 5.5 years and older. Age was entered as both a continuous and a categorical variable to reveal nonlinear effects of age. Other variables included in the analyses were wolf hunting group size and the snow depth for moose during tracking. Because snow depth usually varied with topography and altitude it was grouped into two classes: 0–30 and >30 cm. Finally, we included the type of method used for estimating hunting success in the analyses. The total data set included 185 observations of wolf hunting attempts on moose using pooled data from both methods (Table 1). In the analyses evaluating the effects of individual and environmental variables on hunting success, we excluded 43 cases

**Table 1.** Number of wolf attacks and hunting success (%) on moose per wolf territory and method of estimation in Scandinavia during winters 1998–2003

| Wolf territory | Method 1 | % Successful | Method 2 | % Successful | *N* total |
|---|---|---|---|---|---|
| Grangärde | 63 | 11 | 0 | | 63 |
| Gråfjell | 9 | 56 | 5 | 60 | 14 |
| Leksand | 17 | 53 | 11 | 45 | 28 |
| Nyskoga | 6 | 67 | 2 | 50 | 8 |
| Tyngsjö | 5 | 40 | 2 | 50 | 7 |
| Bograngen | 0 | | 3 | 33 | 3 |
| Filipstad | 0 | | 7 | 100 | 7 |
| Fredriksberg | 0 | | 1 | 100 | 1 |
| Furudal | 0 | | 29 | 65 | 29 |
| Glaskogen | 0 | | 1 | 100 | 1 |
| Gravendal | 0 | | 2 | 50 | 2 |
| Hagfors | 0 | | 5 | 40 | 5 |
| Hasselfors | 0 | | 4 | 25 | 4 |
| Ockelbo | 0 | | 8 | 75 | 8 |
| Tisjön | 0 | | 2 | 50 | 2 |
| Ulriksberg* | 0 | | 2 | 50 | 2 |
| Årjäng | 0 | | 1 | 100 | 1 |
| Total number of hunts | 100 | | 85 | | 185 |
| Total number of packs studied | 5 | | 16 | | 17 |
| Hunting success (%)† | 27 | | 61 | | 43 |
| Hunting success (%)‡ | 45 | | 64 | | 56 |
| Snow-tracked distance (km) | 2466 | | >1600 | | >4066 |

*Same breeding male (9804) as in the Grangärde territory.
†Mean of total number of attacks.
‡Unweighted mean between territories.

because of missing data for age of breeding wolves ($N = 2$) group size during hunting ($N = 13$) or absence of an intact breeding pair ($N = 28$). Thus, the data set used for building a model of significant individual and environmental variables was slightly reduced ($N = 142$; Table 2) compared to the total data set. In a further reduced data set ($N = 137$; Table 2), we also tested for the potential confounding effect of variation in moose density among territories. A stepwise forward procedure for including additional significant variables was chosen as the model-building strategy. A backward elimination procedure was also tested initially and yielded qualitatively similar results to the model-building strategy. Variables were considered significant at an alpha level <0.05. A chi-square one-group test was used to test for differences in prey selection (moose versus roe deer) between years in two wolf territories. For all analyses, we used SAS version 8.0 (SAS Institute Inc., Cary, NC, U.S.A.) and SPSS version 11.5 for Windows (SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

### Estimation of Wolf Hunting Success

The first method for estimating hunting success showed 73 failed attacks recorded in 2466 km of snow tracking in five territories (Table 1). Considering the average daily travel distances recorded for radiocollared wolves, the total distance of snow tracking was equal to 119 wolf-days distributed over five wolf territories. Applying territory-specific kill rates on moose to the total number of wolf-days resulted in an estimate of 27 moose being killed, and an average hunting success of 27% (Table 1). However, 635 km (25.8%) of the total 2466 km of snow tracking was carried out in one of the five territories (Grangärde) during two consecutive winters. In this territory 63 attacks on moose were recorded with only seven being successful (Table 1). Thus, a disproportionately low proportion (11%) of successful attacks on moose were recorded in the Grangärde territory, compared to the other four territories, where 20 of 37 (54%) attacks were successful. This resulted in a lower weighted mean hunting success (27%) for all territories compared to an unweighted mean of successful attacks in the five territories (45%).

**Table 2.** Individual and environmental variables used in the logistic regression analyses to estimate effects on wolf hunting success on moose in Scandinavia, during winters 1998–2003

| Variable | Mean±SD | Range | N |
|---|---|---|---|
| Male age (years) | 3.11±1.95 | 1–8 | 142 |
| Female age (years) | 6.20±2.42 | 2–12 | 142 |
| Male age (age classes) | 2.87±1.52 | 1–5 | 142 |
| Female age (age classes) | 4.65±0.80 | 2–5 | 142 |
| Snow depth (cm) | 28.00±12.60 | 2–70 | 142 |
| Hunting group size | 2.93±2.04 | 1–11 | 142 |
| Moose density (no./km$^2$) | 1.16±0.54 | 0.62–2.70 | 137 |

Statistics for age of breeding wolves are given for both the ungrouped variable and a variable grouped into five age classes (1.5, 2.5, 3.5, 4.5 and ≥5.5 years).

The second method used for estimating hunting success included data from 85 attacks distributed over 16 wolf territories and sampled during more than 1600 km of snow tracking (Table 1). In total, wolf-killed moose were encountered on 52 occasions (61%) and 33 failed attacks were recorded.

### Factors Affecting Hunting Success

The logistic regression analysis including each variable as single independent variables showed that age of breeding males was the only variable significantly related to hunting success (Table 3). The age of breeding females, hunting group size, snow depth and moose density were not significant predictors of variation in hunting success between wolf territories. We also tested for nonlinear effects of age among breeding wolves on hunting success by including age of breeding wolves as single categorical variables. As in the previous analyses male age was strongly significantly related to hunting success, whereas female age was not (Table 3, Fig. 1). According to the

**Table 3.** Logistic regression model testing the effects of different individual traits and environmental factors on wolf hunting success on moose in Scandinavia during the winters 1998–2003

| Variable | *F* | *df* | *P* |
|---|---|---|---|
| Constant + | | | |
| Age of males (continuous variable) | 13.09 | 1, 125 | <0.001 |
| Age of males (categorical variable) | 5.58 | 4, 123 | <0.001 |
| Age of females (continuous variable) | 0.00 | 1, 125 | 0.971 |
| Age of females (categorical variable) | 0.70 | 3, 123 | 0.554 |
| Snow depth | 2.79 | 1, 125 | 0.097 |
| Hunting group size | 2.56 | 1, 125 | 0.112 |
| Method of estimation | 0.79 | 1, 125 | 0.375 |
| Moose density | 0.21 | 1, 120 | 0.647 |
| Constant+Age of males (continuous variable) + | | | |
| Age of females (continuous variable) | 0.07 | 1, 124 | 0.787 |
| Snow depth | 2.09 | 1, 124 | 0.150 |
| Hunting group size | 0.40 | 1, 124 | 0.527 |
| Method | 0.66 | 1, 124 | 0.419 |
| Moose density | 0.60 | 1, 119 | 0.439 |
| Constant+Age of males (continuous variable) + | | | |
| Age of males (continuous variable) * Age of females (continuous variable) | 0.13 | 1, 123 | 0.721 |
| Age of males * Snow depth | 0.30 | 1, 123 | 0.585 |
| Age of males * Hunting group size | 0.21 | 1, 123 | 0.649 |
| Age of males * Method of estimation | 4.05 | 1, 23 | 0.046 |
| Age of males * Moose density | 0.15 | 1, 118 | 0.696 |

Male and female ages were grouped into five age classes (1.5, 2.5, 3.5, 4.5 and ≥5.5) and snow depth was grouped into two classes (0–30 and >30 cm).

*F* values, a better fit to the model predicting hunting success was achieved by using male age as a continuous variable and we therefore retained the continuous variable of male age in the following analyses.

A multiple logistic regression analysis including male age, in combination with each of the remaining independent variables, showed that no other variable was significant for predicting wolf hunting success (Table 3). Nor did any second-order term contribute significantly to the model, except that between male age and the type of method used. This interaction indicated that the effect of male age on hunting success was slightly stronger for data collected with method 1 than for method 2. Age of males alone correctly classified 70.4% of the 142 hunting attempts. For 1.5-year-old males, an average of 4.4% of the hunting attempts were successful, whereas 49% and 72% of the hunting attempts were successful for 3.5- and >5.5-year-old male wolves, respectively (Fig. 1). The logistic regression model of male age and hunting success was: $Y = (\exp(-2.43 + \text{male age} \times 0.69)) / (1 + \exp(-2.43 + \text{male age} \times 0.69))$.

On average, breeding females were older than breeding males in our subsample of 142 observations (Table 2). The age of breeding females was clearly skewed towards older age classes with no 1.5-year-old females and only 28 (20%) of the 142 observations distributed among the three youngest age classes (2.5, 3.5 and 4.5 years old). Male breeding wolves were more evenly distributed between age classes with 113 (79.6%) younger than 5 years (Table 2). Male age was also negatively correlated with female age (Pearson correlation: $r_{141} = -0.24$, $P = 0.004$) and positively with hunting group size ($r_{141} = 0.46$, $P = 0.0001$). Consequently, whereas the effect of age of breeding males on hunting success seems clear-cut in our data set, the true effect of female age might have been confounded by an unbalanced sample size between age classes, and possibly also the effect of hunting group size by covariation with male age.

## Prey Selection Among Single Adults

We documented a difference in prey selection in two territories consisting of a female and a male wolf before and after they each lost their adult partner. Female wolf number 9805 was the breeding female (4.5 years old) of a pack of eight when she lost her mate in February 1999. All 24 wolf-killed ungulates found in their territory the same winter were moose. The following winter this pack consisted of the adult female 9805 and two of her 1.5-year-old male offspring, weighing 49 and 52 kg, respectively, at capture the same winter. Of the 16 ungulates killed by this pack during this winter, all but one (94%) were moose (Fig. 2). The following winter both of the adult male offspring had dispersed, and the adult female was alone but still inhabited the same territory. This winter we found 10 ungulates killed by the female, but only two (20%) were moose (calves) and the rest were roe deer, which are six and 16 times smaller than juvenile and adult moose, respectively. In contrast, another male offspring (9804) of this female, a full sibling of the two previously mentioned males, dispersed at the age of 1 year and joined a 4-year-old female (0004) with an established territory (Grangärde) in the summer of 1999. During their first winter, moose made up 73% of the total number of ungulates found killed ($N = 22$). The pair reproduced during spring 2000, and in November the same year the female was probably killed illegally, and the male was the only adult (2.5 years old) in a pack of four wolves during the following winter (2001). In that winter, moose still dominated (75%) among the 32 ungulates found killed during the study period (Fig. 2). At least four of the 24 moose, and three of the eight roe deer, were killed by the adult male on his own. Prey selection (moose versus roe deer) changed significantly from year 2000 to 2001 in the Leksand territory (chi-square test: $\chi^2_1 = 14.8$, $P = 0.0002$, Fisher's exact *P* value) but not in the Grangärde territory ($\chi^2_1 = 0.035$, $P = 0.852$; Fig. 2).

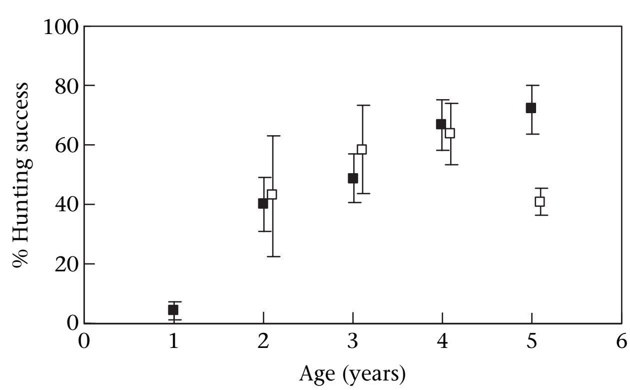


**Figure 1.** Effect of male (■) and female (□) age of breeding wolves on hunting success (mean % successful hunts ± SE) on moose in Scandinavia during winters 1998–2003. Data are based on the maximum number of observations for males ($N = 174$) and females ($N = 166$) in contrast to the reduced data set used in the logistic regression analyses ($N = 142$; both sexes).

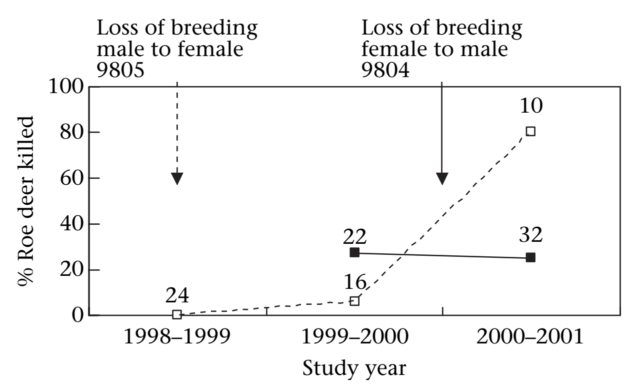


**Figure 2.** Prey species composition, measured as the percentage of roe deer killed of the total number of moose and roe deer found killed in two wolf territories during two and three study winters 1999–2001. In the Leksand territory (□) the breeding female (9805) lost her mate in February 1999, whereas in the Grangärde territory (■) the breeding male (9804) lost his mate during autumn 2000. Sample sizes of the total number of ungulates found killed by the wolves during the study period are given above each point.

## DISCUSSION

### Variation Between Methods

The results for hunting success differed between the two methods used in our study (Table 1). The method based on radiocollared wolves involved an unbalanced sample size between territories with the majority (77%) of the unsuccessful attacks recorded in one territory (Grangärde), resulting in a relatively low hunting success rate (11%) compared to the other four territories (54%). The low hunting success for wolves in the Grangärde territory, especially in the winter of 2000, may be explained by the fact that this was a newly formed pair, including a 1.5-year-old male, in their first winter. Sixteen moose were found killed in that winter during a 111-day period, whereas 49 failed hunting attacks on moose were recorded during 275 km of snow tracking (assumed to equal 11–12% of their total moving path). In the second winter of study (2001) in this territory, the adult male, either alone or together with his three pups, was tracked for 360 km during a 96-day period (approximately equal to 18% of total moving path); there were 24 successful attacks on moose but only eight failed attacks recorded. Therefore, kill rate almost doubled (7.4 versus 4.2 days/kill) and the number of failed attacks per tracked km was reduced by a factor of eight compared to the previous year (0.022 versus 0.18). Consequently, the low overall hunting success rate shown by the first method was mainly caused by a disproportionate impact from one territory in one winter season, inhabited by a young and inexperienced male wolf. Excluding this territory resulted in an estimate of hunting success shown by the first method of 54% and use of an unweighted mean between territories resulted in a hunting success of 45%. Both figures were now closer to the estimates produced by the second method (61%). This conclusion is also supported by the fact that the type of method was not a significant variable in the logistic regression analyses, either as a single variable or in addition to male age.

### Hunting Group Size

Hunting group size has a positive effect on the hunting success of several African group-living species including lions (Stander & Albon 1993; Funston et al. 2001), spotted hyaenas (Holekamp et al. 1997) and African wild dogs (Fanshawe & Fitzgibbon 1993; Creel & Creel 1995). In contrast, we found no evidence that hunting group size was an important factor affecting hunting success of another group-living carnivore, the wolf, even on large prey such as moose. Two factors may have distorted our interpretation of the results. First, because we used tracking of wolves in snow as the method for estimating the number of wolves involved in an attack we were not able to identify the actual number and type of individuals involved in the killing of the moose. Second, although hunting group size was positively correlated with hunting success in our data set, it was also positively correlated with the main predictor of hunting success, age of breeding males. However, if hunting group size in wolves is of no, or minor, importance to hunting success this may be because, in most cases, wolf packs are family groups comprising a breeding pair and their offspring of the previous years (Mech 1999). In Scandinavia, most pups disperse during their first or second year (O. Liberg & P. Wabakken, unpublished data), so most wolf packs during winter consist of a breeding pair and their pups of the year. Correspondingly, Mech (1966, 1988) observed that it was the animals at the head of the pack, usually the breeders that led the attack on moose and muskoxen, *Ovibos moschatus*. Our results therefore support the general view that the breeding pair are the active animals during attacks on prey, and that pups do not contribute significantly to the outcome of hunts (Mech 1966; Haber 1977; Mech & Peterson 2003). The importance of the composition of the group for the outcome of hunting success is supported in a study of lions in South Africa, where female groups with subadults and/or large cubs were less successful on medium-sized prey than a similar group size consisting of adult females only (Funston et al. 2001). For wolf packs, the presence of >2-year-old offspring, or inclusion of adult unrelated wolves, may be far more important for hunting success than group size per se.

### Snow Depth

Studies investigating the effects of snow on predatory behaviour of wolves show that deeper snow generally increases hunting success (Kolenosky 1972; Peterson & Allen 1974; Haber 1977) and kill rate (Nelson & Mech 1986; Huggard 1993). In contrast, we found no evidence that snow depth affected the success of Scandinavian wolves hunting moose. However, the average snow depth in this study was only 28 cm and most of the observations (99%) were made at snow depths of less than 60 cm. Moose are more vulnerable to predation by wolves at snow depths greater than 75 cm (Peterson 1977). Snow depth may be an important factor affecting the outcome of wolf attacks on moose in deep snow or under certain snow conditions (Mech et al. 1987, 1998; Post et al. 1999), but this was clearly not the case in our study area.

### Age and Sex

We did find support for the hypothesis that age affects individual or pack variation in wolf hunting success. Age may be important in at least two ways for a relatively long-lived species such as the wolf. First, learning and thus experience will increase with age, leading to the prediction that increased age would be equally important in both sexes. Alternatively, or in addition, increased age will reflect increased body size of individual wolves, a physical characteristic that may be important for wolves preying on large ungulates such as moose. In this case we may predict that male age would be more important than female age since adult males are 25–30% heavier than female wolves (Wabakken et al. 2001; Mech & Peterson 2003; H. Sand, unpublished data). Our results showed that male age, but not female age, of breeding wolves, was a significant predictor of hunting success on moose, and that hunting success increased in packs after the age of maximum body size of breeding males (1.5–2.5 years). This supports the prediction that the positive effect of age on hunting success reflects both increased experience of attacking prey and the effect of greater size of individual male than female wolves. Our finding is also supported by observations from other wolf–moose systems. In Alaska, Murie (1944) and Haber (1977) documented that high-ranking males tended to lead and press the attack on moose and Ballard et al. (1987) found that adult males in particular led hunts on moose. Haber (1977) also reported that during an attack breeding males typically grab the nose of the moose while other wolves in the pack attack and bite at the rear end.

Our results also concur with those of Holekamp et al. (1997) on the spotted hyaena showing that young individuals are generally inefficient predators and reach adult competency levels after several years of hunting practice. However, in contrast to our results their study found no gender differences in hunting success between adult (>5–6 years) hyaenas but group hunting was more common than solo hunting for large prey species such as zebra, *Equus burchelli*, buffalo, *Syncerus caffer*, and giraffe, *Giraffa camelopardalis*.

### Sex Dimorphism and Age Effects

The consequences of sex dimorphism for the pattern of predation in wolves were demonstrated in this study by the difference in prey selection of a female and a male wolf before and after each of them lost their breeding partner. Whereas the adult female switched to a smaller prey species (roe deer) once alone, the male continued to kill moose, both calves and adults, when he became the only adult wolf in his pack.

The sex dimorphism of the predator and its consequences for hunting success has not been addressed for wolves, but is important for lions where males have greater hunting success on larger prey such as buffalo, while females are more successful hunting medium-sized ungulates such as zebra and wildebeest, *Connochaetes taurinus* (Funston et al. 1998, 2001). For a pack-living species such as the wolf, where the breeding pair, working cooperatively, is responsible for most hunting on larger prey during winter, the importance of adult body size for hunting success may differ according to the prey. Consequently, experienced males may be more important for hunting success on large prey such as moose and bison, *Bison bison*, whereas both adult animals may be equally important for smaller prey species such as deer and other small mammals.

### Potential Mechanisms

Although we found evidence for the importance of a predator-related character for hunting success, we were not able to control fully for confounding prey-related factors other than population density. It is possible that the lower hunting success of younger wolves in our study resulted from less experience and skills to handle similar moose categories. Alternatively, the lower hunting success may have resulted from a lower ability by young wolves to select prey individuals more vulnerable than average. Although we obtained basic demographic data (age, sex, condition) on most of those moose that were killed, we had no data on those moose that were able to escape the attacks by wolves. Thus, the proximate mechanism for a change in hunting success with age in wolves remains unknown and should be addressed in future studies.

## Acknowledgments

Many people helped with tracking of wolves, especially Daniel Palm, Kjell Johansson, Åke Aronson, Mats Rapp, Sture Nordlund, Ole Knut Steinset, Per Larsson, Per Johansson, Håvard Rønning, Jörgen Johansson, Bertil Broman, Göran Jansson, Runa Skyrud, Jan Perjons, Mikael Sandström, Börje Dalèn. Harry P. Andreassen supported us by logistic regression analysis, recalculated in SAS and Lars Rönnegård provided other statistical advice on the analyses. Leslie Walke improved the language. The study was supported by the Swedish Environmental Protection Agency, The Association for Hunting and Wildlife Management, World Wildlife Fund for Nature (WWF, Sweden), Swedish University of Agricultural Sciences, Norwegian Directorate for Nature Management, Norwegian Research Council, Norwegian Institute for Nature Research, Hedmark University College, County Governor of Hedmark, Borregaard Skoger AS, Glommen Skogeierforening, Olle and Signhild Engkvists Stiftelser, Carl Tryggers Stiftelse, Swedish Carnivore Association, and Stor-Elvdal, Åmot and Trysil Municipalities.

## References

**Arnemo, J. M., Ahlqvist, P. & Segerström, P.** 2004. Biomedical Protocol for Free-ranging Wolves (*Canis lupus*): Capture, Anaesthesia, Surgery, Tagging, Sampling and Necropsy Procedures. http://skandulv.nina.no/skandulv%20new/Publikasjoner/publikasjoner.htm.

**Ballard, W. B., Whitman, J. S. & Gardner, C. L.** 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monograph*, **98**, 1–54.

**Chrisler, L.** 1956. Observations of wolves hunting caribou. *Journal of Mammalogy*, **37**, 337–346.

**Creel, S. & Creel, N. M.** 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **50**, 1325–1339.

**Fanshawe, J. H. & FitzGibbon, C. D.** 1993. Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, **45**, 479–490.

**Fuller, T. K. & Kat, P. W.** 1993. Hunting success of African wild dogs in southeastern Kenya. *Journal of Mammalogy*, **74**, 464–467.

**Funston, P. J., Mills, M. G. L., Biggs, H. C. & Richardson, P. R. K.** 1998. Hunting by male lions: ecological influences and socio-ecological implications. *Animal Behaviour*, **56**, 1333–1345.

**Funston, P. J., Mills, M. G. L. & Biggs, H. C.** 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, **253**, 419–431.

**Haber, G. C.** 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. thesis, University of British Columbia, Vancouver.

**Haglund, B.** 1968. De stora rovdjurens vintervanor II. *Swedish Wildlife Research*, **5**, 213–361.

**Hayes, R. D., Baer, A. M., Wotschikowsky, U. & Harestad, A. S.** 2000. Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology*, **78**, 49–59.

**Hebblewhite, M., Pletscher, D. H. & Paquet, P. C.** 2002. Elk population dynamics in areas with and without predation by re-colonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.

**Holekamp, K. E., Smale, L., Berg, R. & Cooper, S. M.** 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology*, **242**, 1–15.

**Holling, C. S.** 1959. The components of predation as revealed by a study of small-mammal predation of the European sawfly. *Canadian Entomology*, **91**, 293–320.

**Huggard, D. J.** 1993. Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management*, **57**, 382–388.

**Kolenosky, G. B.** 1972. Wolf predation on wintering deer in east-central Ontario. *Journal of Wildlife Management*, **36**, 357–369.

**Kreeger, T. J., Arnemo, J. M. & Raath, J. P.** 2002. *Handbook of Wildlife Chemical Immobilization*. Fort Collins, Colorado: Wildlife Pharmaceuticals Inc.

**Kruuk, H.** 1972. *The Spotted Hyena*. Chicago: University of Chicago Press.

**Liberg, O., Andrén, H., Pedersen, H.-C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M. & Bensch, S.** 2005. Severe inbreeding depression in a wild wolf *Canis lupus* population. *Biology Letters*, **1**, 17–20.

**Lotka, A. J.** 1925. *Elements of Physical Biology*. Baltimore: Williams & Wilkins.

**Lönnroth, E.** 1934. Bidrag till vargens historia i Sverige. *Kungliga Vetenskapsakademins Skrifter i Naturskyddsärenden*, **26**, 1–33.

**Mech, L. D.** 1966. *The Wolves of Isle Royale*. Washington, D.C.: U.S. Goverment Printing Office.

**Mech, L. D.** 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. Garden City, New York: Doubleday/Natural History Press.

**Mech, L. D.** 1988. *The Arctic Wolf: Living with the Pack*. Stillwater, Minnesota: Voyageur Press.

**Mech, L. D.** 1999. Alpha status, dominance, and division of labor in wolf packs. *Canadian Journal of Zoology*, **77**, 1196–1203.

**Mech, L. D. & Peterson, R. O.** 2003. Wolf–prey relations. In: *Wolves: Behavior, Ecology and Conservation* (Ed. by L. D. Mech & L. Boitani), pp. 131–160. Chicago: University of Chicago Press.

**Mech, L. D., Frenzel, L. D., Jr & Karns, P. D.** 1971. The effect of snow conditions on the ability of wolves to capture deer. In: *Ecological Studies of the Timber Wolf in Minnesota* (Ed. by L. D. Mech & L. D. Frenzel, Jr), pp. 51–59. St Paul, Minnesota: USDA Forest Service.

**Mech, L. D., McRoberts, R. E., Peterson, R. O. & Page, R. E.** 1987. Relationship of deer and moose populations to previous winters' snow. *Journal of Animal Ecology*, **56**, 615–627.

**Mech, L. D., Nelson, M. E. & MacRoberts, R. E.** 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. *Journal of Mammalogy*, **72**, 146–151.

**Mech, L. D., Adams, L. G., Meier, T. J., Burch, J. W. & Dale, B. W.** 1998. *The Wolves of Denali*. Minneapolis: University of Minnesota Press.

**Mech, L. D., Smith, D. W., Murphy, K. M. & MacNulty, D. R.** 2001. Winter severeity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management*, **64**, 998–1003.

**Messier, F.** 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology*, **75**, 478–488.

**Murie, A.** 1944. *The Wolves of Mount McKinley*. Washington, D.C.: U.S. Government Printing Office.

**Murray, D., Boutin, S., O'Donoghue, M. & Nams, V.-O.** 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Animal Behaviour*, **50**, 1203–1210.

**Nelson, M. E. & Mech, L. D.** 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *Journal of Wildlife Management*, **50**, 471–474.

**Olsson, O., Wirtberg, J., Andersson, M. & Wirtberg, I.** 1997. Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. *Wildlife Biology*, **3**, 13–25.

**Peters, R. P. & Mech, L. D.** 1975. Behavioural and intellectual adaptations of selected mammalian predators to the problem of hunting large animals. In: *Socioecology and Psychology of Primates* (Ed. by R. H. Tuttle), pp. 279–300. Paris: Mouton Publishers.

**Peterson, R. O.** 1977. Wolf ecology and prey relationships on Isle Royale. *U.S. Naturalist Park Service Science Monographs*, **11**, 1–210.

**Peterson, R. O. & Allen, D. L.** 1974. Snow conditions as a parameter in moose-wolf relationships. *Canadian Naturalist*, **101**, 481–492.

**Post, E. S., Peterson, R. O., Stenseth, N.-C. & McLaren, B. E.** 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.

**Rothman, R. J. & Mech, L. D.** 1979. Scent-marking in lone wolves and newly formed pairs. *Animal Behaviour*, **27**, 750–760.

**Sand, H., Zimmermann, B., Wabakken, P. & Andrén, H.** 2005. Using GPS-technology and GIS-cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, **33**, 914–925.

**Stander, P. E. & Albon, S. D.** 1993. Hunting success of lions in a semi-arid environment. *Symposia of the Zoological Society of London*, **65**, 127–143.

**Sweden.** 1991. *Swedish National Atlas*. Stockholm: SNA Förlag.

**Taylor, R. J.** 1984. *Predation*. New York: Chapman & Hall.

**Van Orsdol, K. G.** 1984. Foraging behavior and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, **22**, 79–99.

**Volterra, V.** 1926. Fluctuations in the abundance of a species considered mathematically. *Nature*, **118**, 558–560.

**Vucetich, J. A., Peterson, R. O. & Schaefer, C. L.** 2002. The effect of prey and predator densities on wolf predation. *Ecology*, **83**, 3003–3013.

**Wabakken, P., Sand, H., Liberg, O. & Bjärvall, A.** 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. *Canadian Journal of Zoology*, **79**, 710–725.

**Wabakken, P., Aronson, Å., Sand, H., Strømseth, T. & Kojola, I.** 2004. *The Wolf in Scandinavia: Status Report of the 2003–2004 Winter*. Elverum, Norway: Högskolen i Hedmark.

**Zimmermann, B., Storaas, T., Wabakken, P., Nicolaysen, K., Steinset, O. K., Dötterer, M., Gundersen, H. & Andreassen, H. P.** 2001. GPS collars with remote download facilities, for studying the economics of moose hunting and moose–wolf interactions. In: *Tracking Animals with GPS* (Ed. by A. M. Sibbald & I. J. Gordon), pp. 33–38. Aberdeen: The Macaulay Institute.