POPULATION ECOLOGY - ORIGINAL PAPER

Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates?

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Abstract So far the vast majority of studies on large carnivore predation, including kill rates and consumption, have been based on winter studies. Because large carnivores relying on ungulates as prey often show a preference for juveniles, kill rates may be both higher and more variable during the summer season than during the rest of the year leading to serious underestimates of the total annual predation rate. This study is the first to present detailed empirical data on kill rates and prey selection in a wolf–moose system during summer (June–September) as obtained by applying modern Global Positioning System-collar techniques on individual wolves (*Canis lupus*) in Scandinavia. Moose (*Alces alces*) was the dominant prey species both by number (74.4%) and biomass (95.6%); 89.9% of all moose killed were juveniles, representing 76.0% of the biomass consumed by wolves. Kill rate in terms of the kilogram biomass/kilogram wolf per day averaged 0.20 (range: 0.07–0.32) among wolf territories and was above, or well above, the daily minimum food requirements in most territories. The average number of days between moose kills across wolf territories and study periods was 1.71 days, but increased with time and size of growing moose calves during summer. Over the entire summer (June–September, 122 days), a group (from two to nine) of wolves killed a total of 66 (confidence interval 95%; 56–81) moose. Incorporation of body growth functions of moose calves and yearlings and wolf pups over the summer period showed that wolves adjusted their kill rate on moose, so the amount of biomass/kilogram wolf was relatively constant or increased. The kill rate was much higher (94–116%) than estimated from the winter period. As a consequence, projecting winter kill rates to obtain annual estimates of predation in similar predator–prey systems may result in a significant underestimation of the total number of prey killed.

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Introduction

Estimation of predator kill rates is important for gaining insights into predator–prey dynamics and management. The effects of predation have been studied within the concepts of numerical and functional response of the predator, i.e. changes in predator density and kill rate as a function of prey density (Solomon 1949). Prey-dependent models were later recognized as being limited with the notion that additional factors, such as the behaviour of predators and prey, are generally important determinants of the per capita kill rate (Holling 1959; Taylor 1984).

That the per capita kill rate is affected by a number of factors additional to prey density is supported by empirical 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 populations (Messier 1994; Eberhardt et al. 2003). Factors shown to be important for wolf kill rates include type of prey species, prey and predator density, prey and predator ratio (Vucetich et al. 2002), wolf group size (Schmidt and Mech 1997), age distribution of the prey population (Peterson et al. 1998), vulnerability of prey (Peterson and Allen 1974), availability of alternative prey (Dale et al. 1994), rate of scavenging (Promberger 1992; Hayes et al. 2000), time of winter (Mech 1977; Fritts and Mech 1981) snow cover (Huggard 1993; Jedrzejewski et al. 2002), habitat heterogeneity (Kunkel and Pletscher 2000), and the type of methods used to study the kill rate (Hebblewhite et al. 2003; Sand et al. 2005). However, most of the variation in wolf kill rates still remains unexplained (Messier 1994; Dale et al. 1995; Hayes et al. 2000; Vucetich et al. 2002).

So far the vast majority of studies on large- and medium-sized carnivore predation, including kill rates and consumption, in temperate regions have been based on winter studies, sometimes also projected to annual estimates of predation rate (Mech 1966, 1971; Kolenosky 1972; Fuller 1989; Ballard et al. 1997). Due to difficulties in finding and identifying killed prey during summer (Ballard et al. 1987), the predation patterns of wolves during this time of the year have been estimated primarily by scat analyses (Peterson and Ciucci 2003), but see Jedrzejewski et al. (2002) for an alternative approach. However, scat analyses do not provide data on kill rates in terms of the number of prey individuals killed (Mech and Peterson 2003), and estimates of summer kill rates may be especially important in temperate regions because wolves often show a preference for juveniles during this season (Mech 1966, 1988; Peterson 1977; Mech et al. 1998; Jedrzejewski et al. 2002).

Juvenile ungulates killed in summer rather than in winter offer a relatively small amount of biomass per kill, and body size increases rapidly during the vegetative growth period resulting in an increasing amount of biomass per kill. Therefore, kill rates measured in terms of the number of individual prey killed during summer may be both higher and more variable than during the rest of the year, and therefore may lead to serious underestimates of the total annual predation rate. In particular, if predation during summer is focused on the juvenile segment of their main prey, accurate estimates of kill rates may be especially difficult because individual prey may be almost completely consumed. To obtain correct estimates for the number and type of prey killed during the snow-free time of the year, Global Positioning System (GPS) techniques recently applied in studies of wildlife ecology may offer data of sufficiently high spatial and temporal resolution to study the predatory behaviour of large carnivores, including kill rates (Anderson and Lindzey 2003; Sand et al. 2005; Zimmermann et al. 2007).

We used detailed analyses of movements of GPS-collared wolves to examine kill rates and prey selection during summer in a wolf–ungulate system in southern-central Scandinavia where moose constitutes the main prey species in winter (Olsson et al. 1997; Sand et al. 2005). From the general extensive literature on feeding ecology of wolves we predicted that, during summer:

1. Wolves will show a preference for juvenile over adult moose.
2. Wolf kill rates should be negatively correlated with the size of their main prey.
3. The interval between wolf kills will increase with time during summer and should be adjusted to changes in the body size of both their main prey (juvenile moose) and the increasing food requirements of a reproducing wolf group.
4. As a result of the age/size-related selection of prey, wolf kill rates in terms of the number of prey individuals killed per time unit should be higher than during winter.

Materials and methods

Study area

Sweden and Norway together constitute the Scandinavian Peninsula, hereafter referred to as Scandinavia (55–72°N, 5–25°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, Betula pendula*) and aspen (*Populus tremula*) are the dominant tree species in various mixtures. 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 17 humans/km^2, but large areas within the main wolf range have less than 1 human/km^2 (Swedish National Atlas 1991; Statistics Norway 2003). Snow covers southern-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 (Swedish National Atlas 1991; Statistics Norway 2003). Important wild ungulate prey species for wolves include moose (approximately 1–2 moose/km^2 in summer), roe deer (*Capreolus capreolus*) and, in Norway, also red deer

(*Cervus elaphus*) and wild reindeer (*Rangifer rangifer*) may be locally available. Smaller prey consumed by wolves include beaver (*Castor fiber*), badger (*Meles meles*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), and mountain and European hares (*Lepus timidus, Lepus europeus*).

Wolves studied

Wolves were immobilized from the air according to standard procedures presented in Arnemo, Ahlqvist and Segerström (2004) and described in detail in Sand et al. (2006a). Wolves were equipped with GPS neck collars (GPS-Simplex; TVP International, Sweden or GPS-plus; Vectronic Aerospace, Germany). During 2002–2005 we investigated the pattern of summer (1 June–30 September; 122 days) predation during ten intensive studies of nine wolf territories for a total of 322 days (S1). The total study included 15 study periods, ranging between 9 and 44 days, when wolf movements were recorded intensively with a median study date of 14 July. Data was collected from 15 GPS-collared wolves including seven pairs of adult breeding wolves, two pairs of adult non-breeding wolves, and one lone 2-year-old wolf. One pair of breeding wolves (Gråfjell) was studied in two consecutive summers and treated as two separate observations in our dataset. Wolf group size, reproductive status, and the number of pups during summer were estimated from examination of combined data from: (1) pre- and post-reproduction intensive monitoring on snow, (2) movement patterns of adult GPS-collared wolves during the parturition period, (3) summer fieldwork by trained research personnel in the project, and (4) data on age-specific dispersal (Wabakken et al. 2001, 2006, unpublished data).

GPS technology

At least one of the adult breeding wolves, and in four of the ten intensive studies both the adult breeding wolves, was GPS-collared (S1). One or both of the GPS collars on the wolves in each group/territory were programmed for positioning at 30-min intervals throughout study periods (S1), except for the Gråfjell territory where a 60-min interval was used in both years. Data were stored in the internal memory and included latitude and longitude (WGS 84), date, time, and two quality estimates of each position taken (dilution of precision value and the number of satellites used for positioning: 2D/3D). Throughout study periods data were either remotely downloaded weekly or every second week from the ground using a VHF-receiver data logger (RX-900; Televilt International) and a hand-held antenna. Positioning data from Vectronic collars were automatically received as e-mail messages (Short Message Service) over the Global System for Mobile communications net to a computer and automatically stored in a database.

Clusters of GPS positions and search for wolf-killed prey

All GPS positions were plotted in a metric grid system using ArcView 3.2 (Environmental Systems Research Institute). Each position was buffered with a fixed radius of 50 or 100 m and overlapping buffers were unified and defined as clusters (i.e. minimum of two positions) with a unique cluster number and a maximum distance between positions of 200 m (Sand et al. 2005). This procedure was used to search for wolf-killed prey and was based on the assumption that wolves spend ≥1 h in the proximity of killed prey. This procedure was repeated with new data accumulating during the study period, and all new clusters, and enlarged clusters with new positions, were then intensively searched in the field for carcasses within a 50-m radius around positions using a hand-held GPS (Zimmermann et al. 2001). In addition, an average of 54% of all single positions in territories were randomly selected and searched in the field. The mean time elapsed between the time of GPS positions and field search for carcasses at the same positions was 8.3 days and ranged from 1 to 53 days (90% percentiles; 2–24, $n = 199$). No cluster was searched when wolves were within 2 km. For most of the time (>90%) the search team used one trained dog to facilitate the detection of carcass remains. Clusters and single positions were thoroughly searched for body parts, tracks, blood, wolf scats and other remains that could help determine the sex, age, condition of prey, time of death, 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 of adult moose were collected and used for age determination by counting cementum annuli in the first molar (Markgren 1969).

Age (i.e. duration since kill) of carcasses (i.e. time of death) were roughly estimated in the field on the basis of the proportion of the edible biomass consumed, state of decomposition of the carcass in relation to the site (sunny or shaded) and previous weather conditions, and was later compared with the exact locations of GPS-collared wolves. For those carcasses assessed as killed within the study period, the exact date and time of death was set to the time

of the first GPS position within 200 m from the location of the carcass that matched with the estimates of time of death made in the field.

All carcasses were classified into three different categories: (1) wolf-killed prey; (2) probably wolf-killed prey; and (3) other carcasses (other known causes of death or wolf-killed before the study period). For 140 moose and nine roe deer found during fieldwork, signs of fresh blood, the type of consumption of the carcass, scattering of prey remains, and the estimated time of death in relation to wolf presence according to GPS positions were criteria that in combination were used to classify prey as wolf-killed. For eight of the neonate moose and most of the prey smaller than ungulates, only small fragments of the carcass remained when found, thereby making decisions on the cause of death difficult. These carcasses were classified as probably wolf-killed if the condition of the carcass, and thus the estimated time of death, were within the study period, and matched temporally and spatially with GPS positions from adult GPS-collared wolves. In addition, carcasses of another 50 moose, six roe deer and 20 smaller prey were found during fieldwork but were not thought to have been killed by wolves within the study period. Nor were these carcasses believed to have offered any food biomass of importance to wolves during the study period because the estimated time of death was generally several months earlier compared to the date of detection, and during the summer decomposition is fast, leaving carcass remains consisting of dried skeletal bones and fur hairs.

Calculation of predator and prey biomass

To estimate the amount of biomass available from killed prey per kilogram wolf for each wolf group we calculated body growth of wolf pups from the assumed birth date according to the following growth equation:

$$y = -0.0098x^3 + 2.38935x^2 + 6.8725x + 600,$$

where y is the calculated body weight in grams at day x and mean birth weight is 600 g with a mean birth date of 5 May for pups (Alfredèen 2006). This equation was derived from fitting a third-order polynomial growth curve to weight estimates ($n = 320$) for wolf pups raised in captivity ($n = 7$) within their group during the first 150 days after birth, and showed a good fit ($r^2 = 0.996$) for estimating growth of captive wolves (M. Amundin, unpublished data). For adult wolves, we used the individual measured body weight during capture in winter, whereas the summer body weight of yearling wolves was assumed to be 40 kg. The total wolf biomass for each group during any time during summer was calculated as the sum of adult, yearling, and pup body weight.

Food availability was based on the number and size (age) of prey killed by wolves during study periods. Body mass of moose was estimated as a linear growth of calf moose according to: $y = 1.123x + 13$, where y is the estimated weight in kilogram at day x, assuming a birth weight of 13 kg on 1 June and a final weight of 150 kg on 1 October (Markgren 1969). Similarly, we assumed a linear growth of yearling moose: $y = 0.6863x + 135$, with a starting weight of 135 kg on 1 May and a final weight of 240 kg on 1 October (Markgren 1969; Cederlund and Sand 1991; Sand 1996). For other prey species, we assumed an average body weight of 25 and 10 kg for adult and juvenile roe deer respectively, 18 kg for beaver, 11 kg for badger, 2 kg for bird spp., 4 kg for hare, whereas for one calf of domestic cattle (Bos taurus) killed during the study period, we estimated that 5 kg biomass was consumed. For yearling moose, we assumed that the amount of edible biomass was equal to 65% of the total body weight whereas for moose calves, adult and juvenile roe deer 75% was used. For all other prey species, the amount of edible biomass was set to 90%. The proportion of the edible biomass consumed at the time of prey detection was visually estimated in the field to the nearest 5% of the edible parts of the carcass. For prey smaller than moose calves, all edible biomass was assumed to be wolf-consumed.

Estimates of wolf kill rate

We estimated wolf kill rates during the study period as: (1) the total number of prey killed/wolf group per day, (2) the number of prey killed/wolf per day, (3) the total kilogram biomass/wolf group per day, (4) the total kilogram biomass/wolf per day, and (5) the total kilogram biomass/kilogram wolf per day. For calculation of the kilogram biomass available from killed prey during study periods, we used time (date) specific estimates of prey (moose) biomass and the total wolf biomass estimated per wolf group during the median date of the study period (S2). We also calculated the total biomass consumed by wolves by incorporating the estimated proportion of biomass removed from each moose carcass at the day of detection. The consumption of biomass by wolves per day was calculated as: (1) per group, (2) per individual wolf, and (3) per kilogram wolf. Finally, kill rates and their variance were also calculated as the average estimated time interval in days between consecutive kills for both the total number of kills and for moose only.

Analyses

The relationship between different estimates of kill rate, proportion of prey types, and wolf pack size among wolf

territories ($n = 10$) was analysed by simple linear regression. The relationship between the time during the summer season (the number of days from 1 June) and the type of prey [moose yearlings vs. calves ($n = 148$) and moose vs. small prey ($n = 199$)] was analysed by logistic regression. We used a mixed-model logistic regression approach (SAS 9.1; Glimmix) to relate the degree of consumption of carcasses to the time during summer (number of days from 1 June), and to prey type (small prey, moose calf or moose yearling), using study period as the random factor. We also examined what factors affected summer kill rates, using a mixed-model linear regression (SAS 9.1, proc mixed) with territory as a random factor, and by relating time intervals between consecutive kills in all territories against type of previous prey killed, date of kill, group size, and reproductive status of wolf groups. The distribution of time intervals between consecutive kills showed that they were skewed towards shorter time intervals. Square root transformation resulted in a more normal distribution of estimates, and was therefore used in the analyses of GLM mixed effect models, whereas results of parameter estimates are presented as back-transformed estimates of time interval between consecutive kills. The total dataset consisted of 199 wolf-killed prey, but because of separate study periods in the field, the total data set resulted in 184 observations. The same type of analysis was performed on a subset of data that only included moose-killed, and yielded 133 time intervals. A stepwise forward procedure for including additional significant variables was chosen as the model-building strategy. Models were considered significant at an α-level of 0.05 and we refer to α-levels between 0.05 and 0.10 as showing a tendency to significance. For all analyses, we used either SAS version 9.1, (SAS Institute, Cary, N.C.) or SPSS version 14.0 for Windows (SPSS, Chicago, Ill.).

Results

The total study comprised 322 study days including 15 study periods averaging 21.5 days (range: 9–44) and distributed over ten wolf territories (S1). Wolf group size averaged 5.0 and ranged from one to nine individuals including a total of 50 wolves with reproduction occurring in seven of the ten territories. The number of GPS positions received/day during study periods averaged 36.2 (range: 19.3–66.7) among territories and of which 92% were used for search of killed prey in the field (S1).

Prey composition

In total, remains of 275 prey animals were found during fieldwork. Of these 199 were assessed as wolf-killed during the actual study period of 322 days, including 148 moose (74.4%), nine roe deer (4.5%), five beavers (2.5%), ten badgers (5.0%), six hares (3.0%), 20 birds (10.1%), and one calf (0.5%) of domestic cattle (S2). Among wolf-killed birds, capercaillie and black grouse were the dominating (81%) species, but one duck (*Anas* spp) and one crane (*Grus grus*) were also included.

In terms of prey biomass, moose constituted 95.6% of the total biomass from all prey killed during the study period whereas roe deer contributed 1.6%, and small prey 2.8%, respectively. Moose calves comprised 89.9% of all moose individuals killed during the study period and represented 76.0% of the moose biomass. Since no moose older than 1 year were killed during the study period, yearlings made up the remaining 10.1% of all moose killed and 24.0% of the moose biomass.

Small groups killed a larger proportion of small prey species compared to large groups ($r^2 = 0.34$, $P = 0.046$) and this relationship was significant, even after removing the data from the territory with only one wolf ($r^2 = 0.58$, $P = 0.017$). In contrast, there was no significant relation between the proportion of yearling moose killed (out of all moose) and group size ($r^2 = 0.04$, $P = 0.55$). Nor was there a significant pattern of change for the proportion of yearling moose in wolf-kills with the progress of the summer (day number from 1 June), irrespective of wolf group size (logistic regression: $df = 146$, $\chi^2 = 0.147$, $P = 0.70$). In contrast, the proportion of moose among prey individuals decreased significantly with time during the study period, and this relationship also remained negative when controlled for wolf group size (logistic regression: $df = 198$, $\chi^2 = 13.59$, $P = 0.001$). Across all territories, the proportion of non-moose prey during the 4 months June–September was 12.6, 34.0, 35.8 and 44.4%, respectively.

Kill rates

Across all territories wolves killed, on average, 0.60 prey animal/group per day (1 SE 0.05, range: 0.43–0.83) or 0.19 prey animal/wolf per day (1 SE 0.05, range: 0.05–0.52, S2). This corresponded to an average of 24.0 kg prey biomass/group per day (1 SE 3.03, range: 10.4–38.4) or 6.6 kg prey biomass/wolf per day (1 SE 1.28, range: 1.6–12.3) or 0.20 kg prey biomass/kg wolf per day (1 SE 0.02, range: 0.07–0.32) among territories. Assuming that all biomass estimated as consumed for each prey when found (and assumed to be killed by wolves) was obtained by wolves, they consumed on average 5.6 kg prey biomass/wolf per day (1 SE 1.11, range: 1.5–10.4) which was equivalent to 0.16 kg/kg wolf per day (1 SE 0.02, range: 0.07–0.25).

Kill rate, in terms of the number of prey killed/wolf per day among groups, was strongly negatively related to

group size ($r^2 = 0.71$, $P = 0.002$; Fig. 1b), to kilogram biomass/wolf per day ($r^2 = 0.74$, $P = 0.001$; Fig. 1d), and to kilogram biomass/kilogram wolf per day ($r^2 = 0.4$, $P = 0.045$; Fig. 1e). In contrast, group size was not related to the number of prey killed/group per day ($r^2 = 0.004$, $P = 0.86$; Fig. 1a) or to the kilogram biomass/group per day ($r^2 = 0.10$, $P = 0.36$; Fig. 1c). Thus, wolves in small groups killed approximately the same number of prey/day as compared to larger groups, but the per capita biomass/day was only 1.6–4.3 kg (approximately 35%) in large (equal to or greater than seven) groups compared to 4.7–12.0 kg in small (less than or equal to five) groups.

Factors affecting time interval between kills

We examined factors affecting kill rates, using the time interval (in days) between consecutive kills across all territories and study periods. The average time interval between consecutive kills across all territories and study periods was

1.35 days [95% confidence interval (CI); 1.12–1.61, range: 0.0–6.1, $n = 184$]. The time interval between consecutive wolf kills was significantly related to the type of prey previously killed (mixed model linear regression: $F_{2,171} = 6.46$, $P = 0.007$). Thus, the average interval to the next kill after killing small prey was 0.86 days (95% CI; 0.59–1.18, $n = 45$), whereas killing moose calves and yearlings resulted in an average interval of 1.48 days (95% CI; 1.26–1.73, $n = 124$) and 1.42 days (95% CI; 0.87–2.11, $n = 15$), respectively. The time interval between consecutive kills was, in addition to prey type, also significantly positively related to the date of kill measured as the number of days from 1 June (mixed model linear regression: $F_{1,171} = 14.2$, $P = 0.0002$, estimate $\pm$ SE = 0.0055 ± 0.0015). Neither wolf group size ($F_{1,171} = 1.73$, $P = 0.19$) nor reproductive status among wolf groups ($F_{1,171} = 0.2$, $P = 0.65$) could further significantly explain the variation in time interval between prey killed. Inclusion of the interaction term between prey type and date of kill did not significantly improve the model ($F_{2,169} = 2.21$, $P = 0.11$). Wolf

Fig. 1 Kill rate estimated as the number of prey killed (**a**, **b**), and as kilogram biomass (**c**–**e**) per wolf group (*pack*), per individual wolf and per kilogram wolf, in relation to wolf group size (*Pack size*) among the ten wolf territories studied in Scandinavia during 2002–2005
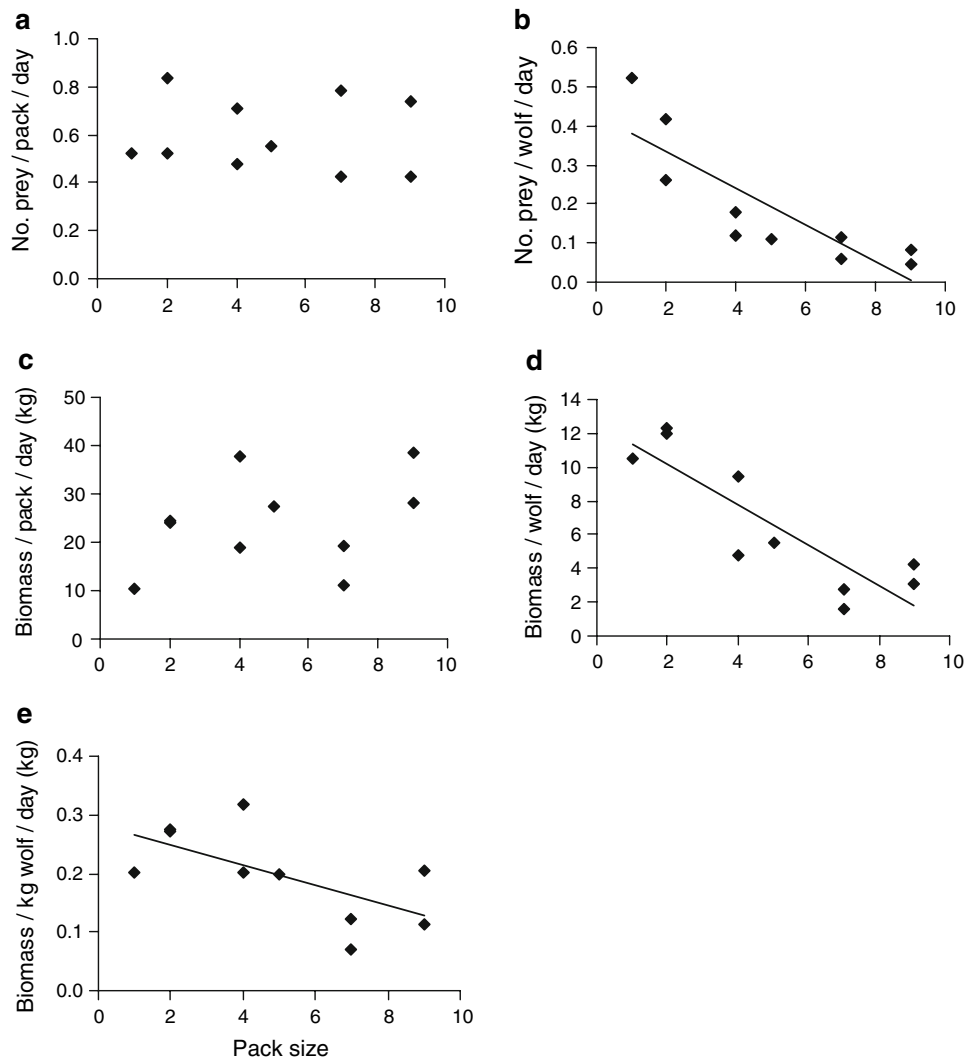
territory did not significantly explain any further variation in day interval between moose kills when included as a fixed effect in the model ($F_{9,171} = 1.20$, $P = 0.30$) in addition to time (date) during summer and type of prey. This means that kill rates did not differ significantly among wolf territories and that the effect of time (date) during summer on kill rate was apparent also at the intra-territory level ($F_{1,171} = 6.38$, $P = 0.01$), i.e. kill rates changed within wolf territories during the course of the summer.

The estimated degree of consumption of the edible portion of wolf-killed carcasses at the date of detection was not related to the time during summer (mixed model logistic regression: $F_{1,166} = 1.27$, $P = 0.26$) but differed significantly between small prey (95%), moose calves (91%) and yearling moose (69%) ($F_{2,166} = 6.87$, $P = 0.0014$).

Because moose was the main prey for wolves during summer in terms of both number and biomass, we further examined what factors affected summer kill rates on moose. The average time interval between moose kills across all territories and study periods was 1.71 days (95% CI; 1.36–2.10, range: 0.0–6.0, $n = 133$). The time interval between moose kills was significantly positively related to the time during summer (mixed model linear regression: $F_{1,122} = 18.99$, $P < 0.001$), measured as the number of days from 1 June [interval = $(0.0068 \times \text{day from 1st June} + 1.009)^2$]. The inclusion of wolf group size ($F_{1,122} = 0.54$, $P = 0.46$), age of the previous moose killed ($F_{1,121} = 0.16$, $P = 0.69$), or group reproductive status ($F_{1,122} = 0.12$, $P = 0.73$) did not improve the fit of the model. No interaction terms for any combination of time interval between moose kills and the other three explanatory variables improved the fit of the model.

Consequently, the time during summer was the only variable significantly explaining variation in kill rate of moose within and between groups and this variable accounted for 12.7% (adjusted r^2) of the total variation in time interval between moose kills (Fig. 2). On 1 June, the mean interval between moose kills was 1.02 days (95% CI; 0.75–1.33) and increased as the summer season progressed, so that the mean interval between moose kills by 30 September (day 122 from 1 June) was 3.39 (95% CI; 2.45–4.48) days. Over the entire summer period (1 June–30 September = 122 days) a group of wolves (i.e. two to nine individuals) was estimated to kill a total of 66 (95% CI; 56–81) moose.

Moose biomass

Model parameter estimates of time intervals between moose kills were combined with body growth functions of moose calves and yearlings, to calculate the amount of biomass available from moose kills during the summer
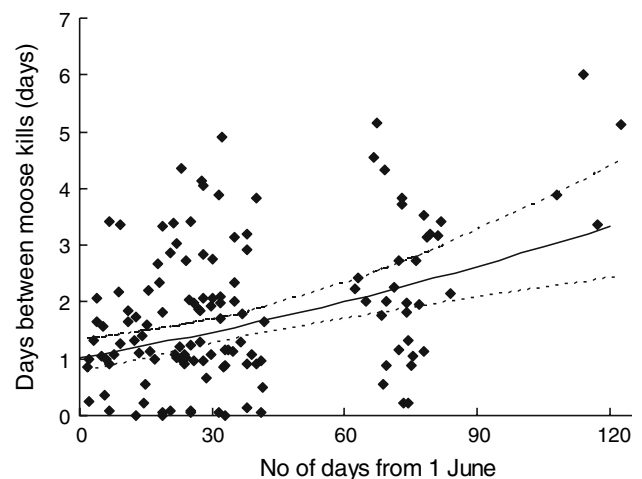

Fig. 2 Average kill rate, estimated as the time interval (in days) between consecutive moose kills, in relation to the time during summer (number of days from 1 June). Day interval between moose kills = $(0.0068 \times \text{day from 1 June} + 1.009)^2$. Data are pooled from the ten different wolf territories in Scandinavia, 2002–2005. *Dotted lines* indicate 95% confidence interval

period and to examine how the lowered kill rate by wolves balanced the growth in body mass of moose. Per capita moose biomass killed increased from June through September and, since this relationship was not affected by group size, this resulted in higher absolute estimates and a more pronounced increase for smaller groups than for larger ones (Fig. 3a). For a group of nine wolves (two adults, one yearling and six pups), the per capita moose biomass/day increased gradually from 2.2 to 3.8 kg during the 4-month period, whereas the same estimates for a pair of adult wolves were 9.7 and 17.3 kg.

To account for the smaller body size of wolf pups during summer, we also incorporated a body growth function for wolf pups into the calculation of the amount of per capita moose biomass/kilogram wolf. For groups of five and nine wolves, the amount of per capita moose biomass/kilogram wolf was relatively constant (0.21–0.27 and 0.13–0.17 respectively) throughout the summer, with a small peak in late June/early July (Fig. 3b). For a pair of adult wolves, the moose biomass/kilogram wolf increased from 0.22 to 0.39 kg during the same period. In summary, wolves continuously adjusted their kill rate on moose in accordance with both the body growth of their own pups and their main prey, so that the amount of moose biomass/kilogram wolf was high and relatively constant throughout the summer period.

Discussion

The majority of studies of wolf predation have exclusively focused on the situation in winter, mainly because of

a

b
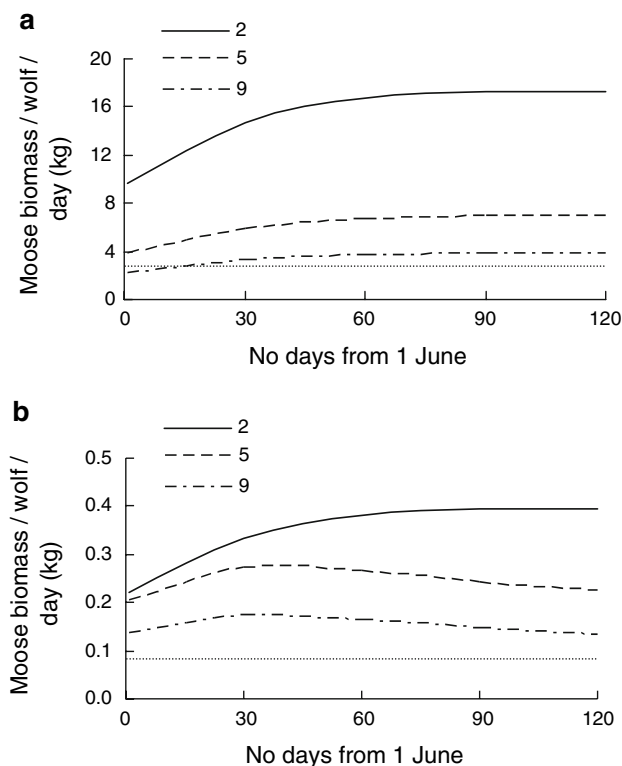
Fig. 3 Moose biomass (kg) obtained/capita per day (**a**) and per kilogram wolf per day (**b**) for wolf groups consisting of two (adults), five (two adults and three pups), and nine (two adults, one yearling and six pups) during 1 June–30 September in Scandinavia. Estimates of kilogram biomass obtained accounted for the variable interval between moose kills, the body mass growth of calf and yearling moose during summer, and the body growth of wolf pups during summer. *Dotted line* indicates the estimated minimum daily food requirements for wild wolves

methodological problems of finding and identifying killed prey during the snow-free time of the year (Mech and Peterson 2003). In the present study, by using intensive GPS data on adult wolves, we were able to overcome much of the difficulty with finding prey during summer, and to provide detailed estimates on wolf predation in terms of prey choice, and prey-specific estimates of kill rate. Our results confirmed our four predictions although the second prediction (2) was only partly confirmed:

1. Wolves showed a strong preference for juvenile over adult moose.
2. The time interval between kills was longer after a wolves killed moose compared to small prey, but there was no difference with respect to juvenile and adult moose.
3. Kill rates changed during the course of the summer and were adjusted to the ontogenetic development of both the main prey and wolf pups.
4. Kill rates measured as individual moose killed/unit of time were 94–116% higher than those found during winter (Sand et al. 2005).

Accuracy of the results

Although some of the prey found, and assumed to have been wolf-killed, may have been the result of scavenging rather than predation, we are confident that the method used for finding wolf-killed prey in this study did not overestimate the true kill rates. Survival among juvenile moose during summer is high (>95%) in areas of low or zero density of large predators in southern-central Scandinavia (Saether et al. 1996; Solberg et al. 2003; H. Sand, unpublished data). Therefore, scavenging by wolves on moose calves that died of other causes is not likely to occur frequently, and mortality of moose calves due to wolf predation during summer is likely to be mainly additive to other sources of mortality, including predation in early June, when calves are newborn. Moreover, our study area was mainly outside the range of the only other predator on moose, the brown bear (*Ursus arctos*) (Swenson et al. 1998), and most (92%) predation by brown bears on moose calves is known to occur up to the age of 1 month (Swenson et al. 2006). Consequently, predation by other large carnivores and concomitant scavenging by wolves is unlikely to occur frequently.

More likely, our estimates of kill rates of both moose and small prey were underestimates (P. Wabakken et al., unpublished data). This was because:

1. In most groups only one of the adult breeding wolves was radio-collared and, in territories where both breeding wolves were collared, they occasionally hunted moose separately.
2. We did not search all single GPS positions and some prey (20% of small prey and 4% of the moose) were found at, or close to, single positions indicating that another two or three moose and four or five small prey should have been found if all single positions had been searched, a pattern also found during winter (Sand et al. 2005).
3. We did not consistently use dogs during fieldwork during the first years of the study and some moose calves and small prey found were likely not to have been found without the use of dogs searching upwind over the cluster area.
4. For prey smaller than moose it is not likely that all kills were found, due to the total consumption of individual prey.

Analyses of wolf scats (*n* = 794) collected during summer (May–September) from ten wolf territories (some of them the same as in this study) in this population, showed that moose biomass constituted 88.9–93.0% of the total mammalian biomass consumed (Müller 2006; Knappwost 2006), depending on the model used for converting scats to biomass (e.g. Floyd et al. 1978; Weaver 1993;

Rühe et al. 2003). In our study, moose constituted 95.6% of the total mammalian biomass consumed. By assuming that scat analyses (Müller 2006; Knappwost 2006) represent the true proportion of the total biomass of small prey killed (and available) to wolves, the actual number of small prey killed would have been 1.6–2.5 times higher than that found in this study (assuming a similar proportion among small prey species).

Summer versus winter kill rates

In most previous studies on wolf–prey interactions and predation rate, it was not possible to estimate the total annual take-out by wolves due to the absence of kill rate data from non-winter periods (Mech and Peterson 2003). Ballard et al. (1987), using aerial location of radio-collared wolves and their killed prey during summer, concluded that kill rates were comparable to winter estimates but that some kills were undoubtedly undetected, and actual summer predation rates therefore underestimated. Peterson et al. (1984) argued that most of the occurrence of adult moose in wolf summer scats resulted from scavenging of moose killed during the previous winter, as they rarely observed wolves feeding on freshly killed adult moose in summer.

Annual kill rates have sometimes been estimated by projecting data from the winter period to represent the rest of the year (Mech 1966, 1971; Kolenosky 1972; Fuller 1989; Ballard et al. 1997). However, it has been suggested that this approach produces overestimates because ungulates are generally in poorer condition and therefore easier to kill in winter (Mech and Peterson 2003). This assumption has been supported by the results from studies that made monthly comparisons over the winter period (Mech 1977; Fritts and Mech 1981; Dale et al. 1995; Jedrzejewski et al. 2002; Smith et al. 2004), which showed that kill rates generally peaked during February and March. Although kill rates may be highest during late winter in terms of kilogram biomass available (and consumed), the results from this study show that estimates of summer kill rates may be much higher than those in winter in terms of the number of individual prey killed. Projecting winter kill rates from our area (Sand et al. 2005) over the summer period (122 days) would have resulted in a 48–54% lower estimate of the total number of moose killed. As a consequence, total annual predation of moose would have been underestimated by 24–28% if we had projected winter kill rates to the rest of the year. From a management perspective our results may lead to annual harvest quotas being set higher than the actual sustainable yield leading to negative growth of the local moose population.

Thus, for large carnivore–ungulate systems in temperate regions where birth synchrony in ungulates is high and the body growth of juveniles (and adults) is restricted to the summer season, the ontogenetic development of juvenile prey may be the proximate factor governing the season-specific kill rates. This result is partly supported by a study of another wolf–ungulate system in Poland, where wolf kill rates of wild boar were higher in spring–summer (140%), when piglets were present, than during autumn–winter, although the opposite pattern was true for the major prey species, red deer (Jedrzejewski et al. 2002).

Daily energy requirements

In seven of the ten groups the amount of biomass per wolf was above, or well above, the minimum daily food requirements (3.25 kg/wolf per day or 0.09 kg/kg wolf, i.e. 5 x basal metabolic rate) estimated for wild wolves (Peterson and Ciucci 2003). For 18 studies in North America, average estimated daily food consumption (available) in winter was 5.4 kg/wolf per day (minimum 2.0 kg, maximum 11.4 kg) (Peterson and Ciucci 2003), which was similar to an estimate of food consumption in eastern Poland of 5.6 kg/wolf per day (Jedrzejewski et al. 2002). Thus, our estimate of wolf food available (6.6 kg) or consumed (5.6 kg) during summer corresponded well with estimates of wolf consumption during winter from other wolf–ungulate systems, and with preliminary estimates of winter kill rates in Scandinavia (Sand et al. 2005; H. Sand et al., unpublished data).

Kill rates, group size and type of prey

For wolves, kill rates in terms of the number of prey killed/wolf group per day usually show a positive relationship to group size (Messier and Crete 1985; Ballard et al. 1987; Dale et al. 1995; Hayes et al. 2000; Jedrzejewski et al. 2002) whereas the per capita kill rate, in terms of kilogram biomass, is generally negatively related to group size over a broad range of studies (Thurber and Peterson 1993; Dale et al. 1995; Schmidt and Mech 1997; Hayes et al. 2000). Our results were not in accordance with the former trend, but they supported the latter, i.e. a reduced per capita kill rate with increasing group size. This resulted in a surplus of food available for smaller wolf groups, whereas larger groups were closer to the minimum daily food requirements. On a finer temporal scale, this study also showed that kill rates of moose during summer were adjusted to the growth in body size of both juvenile moose and wolf pups. Biomass from killed prey during the first weeks of the summer was well above food requirements, and supply of

food thereafter either increased progressively with time (pairs) or was relatively constant throughout the summer (groups).

Although different type of prey offer various amounts of biomass to wolves, the time interval between kills was largely variable and not solely dependent on prey size, especially in early summer. Thus, although wolves seem to be able to adjust the interval between moose kills in relation to the growth of calves throughout the summer period, and to the type of prey (small vs. moose), an instant variation in the size of killed moose (e.g. juvenile vs. adult) did not automatically result in predictive foraging behaviour, i.e. an increased time interval to the next kill. This result was surprising, as we estimate that a yearling moose on average may provide a crude biomass (120 kg) for up to 1 week, and it differs from studies of multi-prey systems where the time to next kill markedly increased with the size of most recent prey killed (Jedrzejwski et al. 2002; Dale et al. 2005).

Selection for juveniles

Strong selection for juvenile ungulates is generally typical for wolves, both in summer (Nelson and Mech 1981; Mech 1988; Kunkel and Mech 1994; Mech et al. 1998; Tremblay et al. 2001; Peterson and Ciucci 2003; Wam and Hjeljord 2003) and in winter (Mech 1966; Peterson 1977; Peterson et al. 1984; Nelson and Mech 1986; Huggard 1993; Olsson et al. 1997; Mech et al. 1998; Hayes et al. 2000; Smith et al. 2004; Sand et al. 2005). However, the proportion of moose calves killed in Scandinavia seems to constitute an extreme compared to most other studies of wolf–moose systems (Mech 1966; 36%; Peterson et al. 1984; 47%; Ballard et al. 1987; 40%; Mech et al. 1998; 36%; Hayes et al. 2000; 31%). This is true for the winter season (68%; Sand et al. 2005), but especially so for the summer. In this study, calves comprised 89.9% of the total number of moose killed during summer, whereas their proportion in the summer population is estimated to range between 25 and 30% (Solberg et al. 2003, 2005).

We suggest that the high proportion of juvenile moose killed by wolves in Scandinavia, and the lack of a relationship between the size of moose killed and the time interval to next kill, are linked and a combined effect of at least two factors. Firstly, a high abundance of moose calves due to a high (relative to other studies) population density, productivity, and ratio of moose to wolf within wolf territories (Solberg et al. 2003, 2005), results in a short search time for this type of prey. The relative abundance of moose calves during summer is estimated to be >50% higher than the number of yearlings (Solberg et al. 2005). Secondly, poor defence of juvenile offspring by female moose is

likely to be the case in Scandinavia, as has been indicated by the significantly higher rate of success (4–5 times) for wolves in hunting moose, compared to populations in North America, and is ultimately likely to result from relaxed anti-predatory behaviour in Scandinavian moose, due to the long-term absence (>120 years) of large predators (Sand et al. 2006b). Therefore, selecting moose calves over yearlings per se, and making new kills instead of re-visiting previously killed moose (i.e. yearlings), may be an optimal foraging strategy in the present Scandinavian wolf population.

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