# Predator-dependent functional response in wolves: from food limitation to surplus killing

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### Summary

**1.** The functional response of a predator describes the change in per capita kill rate to changes in prey density. This response can be influenced by predator densities, giving a predator-dependent functional response. In social carnivores which defend a territory, kill rates also depend on the individual energetic requirements of group members and their contribution to the kill rate.

**2.** This study aims to provide empirical data for the functional response of wolves *Canis lupus* to the highly managed moose *Alces alces* population in Scandinavia. We explored prey and predator dependence, and how the functional response relates to the energetic requirements of wolf packs.

**3.** Winter kill rates of GPS-collared wolves and densities of cervids were estimated for a total of 22 study periods in 15 wolf territories. The adult wolves were identified as the individuals responsible for providing kills to the wolf pack, while pups could be described as inept hunters.

**4.** The predator-dependent, asymptotic functional response models (i.e. Hassell–Varley type II and Crowley–Martin) performed best among a set of 23 competing linear, asymptotic and sigmoid models. Small wolf packs acquired $> 3$ times as much moose biomass as required to sustain their field metabolic rate (FMR), even at relatively low moose abundances. Large packs (6–9 wolves) acquired less biomass than required in territories with low moose abundance.

**5.** We suggest the surplus killing by small packs is a result of an optimal foraging strategy to consume only the most nutritious parts of easy accessible prey while avoiding the risk of being detected by humans. Food limitation may have a stabilizing effect on pack size in wolves, as supported by the observed negative relationship between body weight of pups and pack size.

**Key-words:** *Canis lupus*, faecal pellet group count, hunting success, kill-handling time, moose, numerical response, optimal foraging, predation, scavenging, social organization

## Introduction

The predator functional response was originally defined as the change in per capita kill rate in response to changing prey density (Solomon 1949; Holling 1959a). In its simplest form, the functional response model may be represented by a linear relationship between per capita kill rate and prey density. This type I response indicates that the time interval between consecutive kills decreases constantly with increasing access to prey (Lotka 1925; Volterra 1926). However, it might be expected that predators successively display saturation at higher prey densities, better described by an asymptotic relationship between per capita kill rate and prey density, that is, a type II functional response (Holling 1959b). Such a model becomes sigmoid (type III response) if, for example, predators switch to alternative prey species, or the focal prey species is less accessible due to surplus refuges, at low prey density (Holling 1959a).

As predator density increases, the number of prey animals available per predator decreases. The dependence of the per capita kill rate on per capita prey availability seems more realistic than dependence on absolute prey density. Such ratio-dependent models (RD) (Arditi & Ginzburg 1989) are the least mechanistic among different predator-dependent functional response models and suggest that attack rates will decrease and handling time will increase with increasing predator densities (Arditi *et al.* 2004). Potential mechanisms of predator dependence are (i) lowered individual encounter rates between predators and prey (Beddington 1975; Arditi & Ginzburg 1989); (ii) higher rates of unsuccessful individual attacks or prolonged individual prey handling time due to intraspecific interference (Hassell & Varley 1969; Beddington 1975; DeAngelis, Goldstein & O'Neill 1975; Arditi & Akçakaya 1990); and (iii) intensified antipredator behaviour of the prey (Crowley & Martin 1989; Skalski & Gilliam 2001; Lima 2009).

The strength of predator dependence is a function of the social organization of the predator species (Cosner *et al.* 1999). In solitary species, predator aggregation and interference are the most important factors shaping the adverse effect of predator dependence on per capita kill rate. In social predators, group size can have a positive effect on the attack rate through cooperative hunting behaviour (Packer & Ruttan 1988), as observed in wild dogs *Lycaon pictus* (Creel & Creel 1995), lions *Panthera leo* (Funston, Mills & Biggs 2001) and spotted hyenas *Crocuta crocuta* (Holekamp *et al.* 1997). A nonlinear relationship with per capita attack or consumption rates, peaking at intermediate group sizes of social predators, is most plausible. This is because so called 'free-riders' can take advantage of other group members in large groups, by letting them do the chase (with associated high energetic costs and risks) but still getting access to the kill (Scheel & Packer 1991; Carbone, DuToit & Gordon 1997; MacNulty *et al.* 2012).

Wolves *Canis lupus* L. are organized in territorial family groups (i.e. packs) that usually consist of a resident breeding pair and their offspring of the year, but often also include older offspring and sometimes other unrelated adult wolves (Mech & Boitani 2003). They are able to kill large, divisible prey. Time-series data from a wolf–moose *Alces alces* system and two wolf–elk *Cervus elaphus* systems supported predator-dependent rather than prey-dependent functional response models (Vucetich, Peterson & Schaefer 2002; Jost *et al.* 2005; Becker *et al.* 2008; Hebblewhite 2013), but the mechanisms behind this phenomenological description of predator–prey relations were not clear.

In the present study, we consider these mechanisms for wolves preying predominantly on moose in Scandinavia by assessing the role of the energetics and social organization of individual wolf packs. The average daily energy expenditure of an organism during its normal activities is called the field metabolic rate (FMR) (Ricklefs,

Konarzewski & Daan 1996) and has been measured for the wolf (Nagy 1994). Energy acquired in excess of the FMR is used for growth and reproduction (Nagy 2005). Consequently, the ratio of acquired to required energy directly links the numerical response of a predator to changes in prey density. By expressing kill rates not only as the number of animals killed per time unit, but also as the ratio of food acquired to that required to cover the daily energy needs of a pack, we aim to identify the prey abundance and predator group size that are crucial to the individual growth and survival of wolves. Our main predictions for wolves in Scandinavia are as follows: (1) Per capita kill rates are positively related to prey availability, estimated by density or abundance of moose within wolf territories; (2) This functional response is asymptotic (type II) or sigmoid (type III) rather than linear (type I); (3) The functional response is primarily driven by predator density (here: wolf pack size) or prey-predator ratio (here: moose/wolf ratio within wolf territories) rather than simple prey dependence; (4) The ratio of food acquired to food required to cover the FMR of a wolf pack is positively related to prey availability and negatively to pack size. We expect large wolf packs at low prey availability to kill just enough moose to cover the FMR of the pack, while small packs at high prey availability will exceed the FMR.

## Materials and methods

### STUDY AREA

The wolf breeding range in Scandinavia is limited to the central parts of Sweden and the adjacent areas in south-eastern Norway, at 59°–63° North and 11°–19° East (Fig. 1). The recolonizing wolf population (Wabakken *et al.* 2001) counted 60 wolf territories in winter 2011–2012, and there are still gaps between wolf territories, that is, the population is not saturated. The intercontinental climate is characterized by cold, dry winters with snow cover from November to April. The boreal forest zone of this area is dominated by Scots pine *Pinus sylvestris* L., Norway spruce *Picea abies* L. and birch *Betula* spp. intermixed with a few other deciduous tree species. Moose is the dominant wild cervid species, but we also find roe deer *Capreolus capreolus* L. at very low to intermediate densities in most parts of the study area, and red deer *Cervus elaphus* L. and fallow deer *Dama dama* L. at low densities in restricted parts of the area. More specific information about density and distribution of these cervid species is given in the results. Even though human population density averages 16 persons per $km^2$ throughout Scandinavia, vast areas within the wolf population range have fewer than 1 inhabitant per $km^2$ (Wabakken *et al.* 2001; Mattisson *et al.* 2013).

### ESTIMATION OF PREDATOR DENSITY, BIOMASS AND FMR

For this study, we used data from the winter season, here defined as the 7-month period from leaf fall in the beginning of October to the end of snow cover at the end of April. Our study included 15 wolf territories of the recolonizing Scandinavian wolf popula-
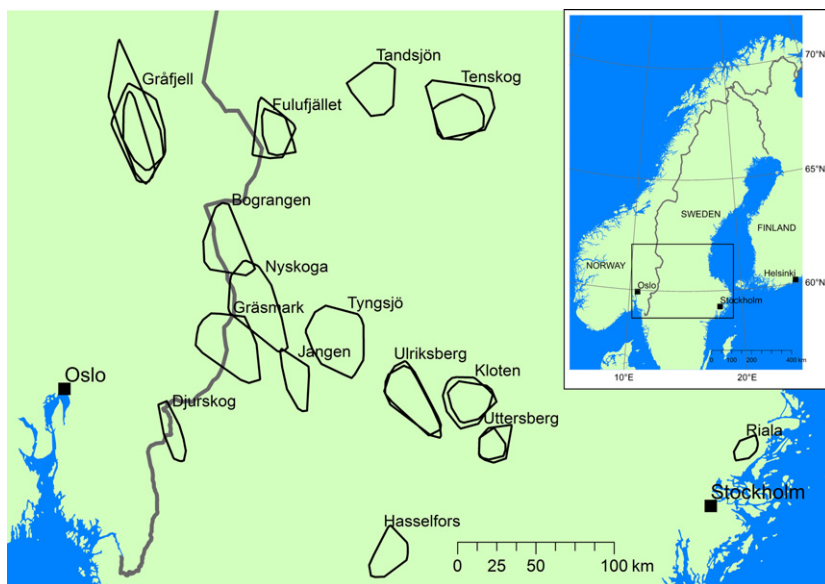
**Fig. 1.** Study area covering parts of Norway and Sweden on the Scandinavian Peninsula. The wolf territories included in this study are delineated in black, and territory names refer to Table S1 (Supporting information).

tion (Fig. 1, Table S1, Supporting information) (Wabakken *et al.* 2001; Sand *et al.* 2005). Six of the territories were sampled for more than one winter, yielding a total sample of 22 study periods (pack-winters) which have been treated as the statistical unit in this study (Table S1, Supporting information). The wolf territory covered by the wolves during the pack-winter was defined using the 100% minimum convex polygon (MCP) method.

Within these territories, adult wolves and occasionally pups (<1-year old) were collared with GPS devices [Simplex™ of Followit AB (Lindesberg, Sweden), or GPS plus of Vectronic (Berlin, Germany)]. Animal capture and handling techniques are described by Sand *et al.* (2006). The size and age structure of wolf packs was estimated by ground-tracking on snow (Wabakken *et al.* 2001) and in later years often supported by DNA identification of individual wolves (Liberg *et al.* 2012). Packs of two scent-marking adult wolves of opposite sexes without pups are hereafter called pairs, whereas family groups refer to packs consisting of more than two wolves. In our study, these were consistently the parents and their offspring of the year. Pack size is defined as the maximum number of pack members within the territory during the pack-winter.

Sex- and age-specific estimates of wolf body weight were based on measurement data from 89 adult wolves (>2 years of age) and 58 pups (<1 year) caught by the Scandinavian Wolf Research Pro-

ject during the winters of 1998–2013. On average, adult males (*n* = 51) weighed 46·8 ± 1·1 kg (2SE) and adult females (*n* = 38) weighed 38·3 ± 1·1 kg. Average pup weights were derived by modelling the observed weights with sex, age at capture date and litter size in a linear mixed model that included the birth territory of the pups as a random factor. Age at capture did not contribute to the most parsimonious model ($\Delta$AIC = 8·2), that is, weights did not increase during the capture period of 6 December to 21 March. Sex and sibling group size, however, were important predictors of pup weight: male pups were on average 1·23 times heavier than females and pup weights decreased with increasing litter size (pup weight (kg) = 35·394 (females) + 7·384 (males) − 0·742*litter size). The FMR of the wolf packs was estimated by adjusting the published FMR of 3·25 kg edible biomass for a wolf of 35 kg (Nagy 1994; Peterson & Ciucci 2003) to the estimated body weights of the Scandinavian wolves using the nonlinear function FMR ~ body weight$^{0.75}$ (Table 1) and is expressed in kg edible biomass per day. Pups were converted into adult metabolic rate equivalents using AE = pup weight$^{0.75}$/adult weight$^{0.75}$ (Metz *et al.* 2011) (Table 1).

### ESTIMATION OF KILL RATES

The wolves were monitored with either a 1-h or 30-min positioning schedule for 30–132 days (Table S1, Supporting information).

**Table 1.** Estimates of pack-size-specific body mass (kg) and field metabolic rates (FMR) (kg edible biomass per day) for Scandinavian wolves assuming an equal sex-ratio between pups, and pack size expressed as adult equivalents (AE) when adjusted for pack-size-specific body mass and metabolic rate

| Pack size | Litter size | Wolf body mass (kg) | | | FMR (kg day$^{-1}$) | | | Pack size AE |
|---|---|---|---|---|---|---|---|---|
| | | Pup male | Pup female | Pack | Pup male | Pup female | Pack | |
| 2 | 0 | | | 85·1 | | | 7·5 | 2·0 |
| 3 | 1 | 42·0 | 34·7 | 123·4 | 3·7 | 3·2 | 11·0 | 2·9 |
| 4 | 2 | 41·3 | 33·9 | 160·3 | 3·7 | 3·2 | 14·4 | 3·8 |
| 5 | 3 | 40·6 | 33·2 | 195·7 | 3·6 | 3·1 | 17·6 | 4·7 |
| 6 | 4 | 39·8 | 32·4 | 229·6 | 3·6 | 3·1 | 20·8 | 5·5 |
| 7 | 5 | 39·1 | 31·7 | 262·0 | 3·5 | 3·0 | 23·9 | 6·4 |
| 8 | 6 | 38·3 | 30·9 | 292·9 | 3·5 | 3·0 | 26·8 | 7·1 |
| 9 | 7 | 37·6 | 30·2 | 322·3 | 3·4 | 2·9 | 29·7 | 7·9 |

Positions were retrieved for 92% of all 1-h positioning attempts. After weekly downloads of GPS data, clusters of positions were searched in the field for wolf-killed prey (Sand *et al.* 2005; Zimmermann *et al.* 2007). Kill rates were expressed as the number of moose killed per day per wolf. We estimated the edible biomass of all kills based on estimates of mean body mass of the different prey species and age classes, corrected for the species-specific edible proportion of the body mass (Table S2, Supporting information). This acquired biomass is the total edible biomass of all kills available to the pack and not necessarily the biomass actually consumed by the pack. The acquired biomass per pack per day divided by the daily FMR of the pack (Table 1) resulted in the ratio of acquired to required biomass.

Different individuals in the pack may have different roles in the killing process, for example, due to age or sex characteristics, which may create some underestimation of kill rates when only adults, or only one of the adults is radiocollared. However, of the 2924 simultaneous positions of both adult male and female partners in 14 pack-winters, 93% showed the adults were <1 km apart (range 74–100%). We therefore consider it highly unlikely that kills made by one un-collared adult alone would remain undetected. Data from six GPS-collared pups (Table S1, Supporting information) showed that the pups were more than 1 km from their parents on average 78% (range 55–99%) of the time. There was no evidence that pups killed cervids while travelling without their parents. The pups mainly fed on kills made by the adult wolves or on carcasses of unknown cause of death. One pup did not kill any prey at all during the pack-winter. The others were involved in one or two pup-killed small prey animals each. Based on these data, we conclude that the adult wolves were responsible for all cervid kills, and that our study design of following 1–2 collared adults was sufficient to estimate total predation during winter.

## ESTIMATION OF PREY DENSITY

To estimate the relative density of moose and other cervids, we carried out faecal pellet group (FPG) counts in each of the 15 territories (Rönnegård *et al.* 2008; McPhee, Webb & Merrill 2012). The sampling design consisted of 42–130 systematically distributed sampling squares of 1 × 1 km (Table S1, Supporting information). We established 40 circular sample plots along the 4 km perimeter of each square, with 10 evenly spaced plots on each side. All FPGs deposited on the leaf litter were counted in each 100 m$^2$ (10 m$^2$ for roe deer) plot immediately after snow melt. If no leaf litter was present, the position of the pellets in relation to the vegetation, the colour and consistency of the pellets, and the presence or absence of fungi, lichens and mosses on the pellet surface helped to distinguish winter pellets from older ones. We divided the density of FPGs found per plot by the winter length, resulting in a daily FPG deposition density (hereafter abbreviated to 'FPG density'). The average FPG density per sample square was interpolated across the total pellet count area using the Thiessen polygon method for a grid with a 30 m pixel size (ArcGIS 10.1; Esri, Redlands, CA, USA). Species-specific relative abundance, that is, the total number of FPGs deposited by each prey species per day in each wolf territory ('FPG abundance') was derived by multiplying the average FPG density by the territory area. Territory size varied greatly between packs (Fig. 1, Table S1, Supporting information) but was not correlated with the length of the pack-winter (Spearman's $\rho = 0.30$), moose

FPG density ($\rho = 0.24$), or pack size ($\rho = 0.17$). We therefore considered FPG abundance as a robust estimate of the relative number of moose and other cervids present in each wolf territory. To provide a rough estimate of absolute moose densities, FPG densities were divided by an average, low and high estimate of moose defecation rate of 14, 10 and 18 FPGs per day, respectively (Persson, Danell & Bergstrom 2000; Rönnegård *et al.* 2008).

## FUNCTIONAL RESPONSE MODELS

We compared the performance of 23 functional response models (Table 2), that is, models where the kill rate was constant and independent of prey and predator densities (CST), prey-dependent (density DD, abundance AD) and/or predator-dependent. The most basic predator-dependent model included pack status (pair or family group) as an interaction term in the constant (CST-S) and the prey-dependent models (DD-S, AD-S). Straightforward RD models (Arditi & Ginzburg 1989) imply that attack rates decrease linearly with an increasing number of predators as a result of the reduced per capita prey availability. The Hassel–Varley (HV) models (Hassell & Varley 1969) assume the attack rate will decrease exponentially with increasing predator density due to predator interference. The exponent *m* indicates the interference strength: If $m = 0$, the HV models become prey-abundance-dependent (AD). With $m = 1$, HV-models become RD models. If $m > 1$, the models indicate that predator interference affects attack rates more negatively than expected from per capita prey availability. We also applied a model that treats predators and their intraspecific interference as an additive effect to prey density, the DeAngelis–Beddington response (DB, Table 2) (Beddington 1975; DeAngelis, Goldstein & O'Neill 1975). Finally, the Crowley–Martin (CM) response (Crowley & Martin 1989) describes the interaction between the asymptotic prey-dependent model and the number of interfering predators (Table 2). It expects the functional response to changes in prey densities to be dependent on the density of the interfering predators. The parameter *b* in the DB and CM models is the interference constant. If $b = 0$, these models become ordinary AD models. If adequate, the performance of different types of prey-dependent models (linear type I, asymptotic type II and sigmoid type III) were compared (Table 2).

The nls function in R 3.0.0 (R Core Team 2013) was used to estimate model parameters, and observations were weighted by the length of the pack-winter (Table S1, Supporting information) to correct for sample size. Models were compared with AICc and $R^2$. Computation of $R^2$ in nonlinear modelling is questionable because the total sum-of-squares SST of a nonlinear model is not equal to the residual error sum-of-squares SSE plus the residual regression sum-of-squares SSR. Following Spiess & Neumeyer (2010), we therefore applied a quasi-$R^2$ to compare each model *i* to the CST model:

$$\text{Quasi } R_i^2 = 1 - \frac{\text{SSE}_i}{\text{SST}_{\text{CST}}}$$

Integrated functional response models account for continuous prey depletion during the pack-winters and should be considered if depletion is >5% (Jost *et al.* 2005). None of our predation studies resulted in predation rates >5%, and we therefore applied the simpler instantaneous models instead.

**Table 2.** Functional response models applied to winter predation data of wolves in Scandinavia, with number of parameters (K), form of dependence (linear type I, asymptotic type II or sigmoid type III) and model equations. The predictor $N$ is the prey availability in terms of either density or abundance (=density*territory size), $P$ is predator abundance (=wolf pack size) and $S$ describes the pack as either wolf pair or family group. The parameters $a$ (attack rate per day), $h$ (handling time), $m$ and $b$ (both predator interference terms) are constants. Model selection based on AICc and quasi-$R^2$ are given for models with the response (i) per capita moose kill rates, and (ii) ratio of edible moose biomass acquired to required to cover the field metabolic rate (FMR) of the wolf pack. For top models, model selection values are given in bold

| | | | | | Response variable | | | | | | | |
| | | | | | Number of moose killed per day per wolf | | | | Ratio moose biomass acquired/ required | | | |
| Model | K | Type | Equation | Predictor $N$ | AICc | ΔAICc | AICc weight | Quasi-$R^2$ | AICc | ΔAICc | AICc weight | Quasi-$R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Constant model | | | | | | | | | | | | |
| CST | 2 | 0 | $a$ | | 305·8 | 30·4 | | 0·00 | 374·4 | 16·8 | | 0·00 |
| Prey-dependent models | | | | | | | | | | | | |
| DD1[a] | 2 | I | $aN$ | Density | 308·0 | 32·6 | | 0·20 | 382·1 | 24·6 | | −0·01 |
| DD2[b] | 3 | II | $aN/(1 + ahN)$ | Density | 309·0 | 33·6 | | 0·22 | 379·9 | 22·4 | | 0·14 |
| DD3[b] | 3 | III | $aN^2/(1 + ahN^2)$ | Density | 308·5 | 33·1 | | 0·20 | 379·4 | 21·9 | | 0·14 |
| AD1 | 2 | I | $aN$ | Abundance | 298·8 | 23·4 | | 0·29 | 378·8 | 21·3 | | −0·05 |
| AD2 | 3 | II | $aN/(1 + ahN)$ | Abundance | 299·2 | 23·7 | | 0·40 | 375·5 | 18·0 | | 0·23 |
| AD3 | 3 | III | $aN^2/(1 + ahN^2)$ | Abundance | 302·4 | 27·0 | | 0·33 | 377·4 | 19·9 | | 0·18 |
| Pack (predator)-dependent models | | | | | | | | | | | | |
| CST-S | 3 | 0 | $a*S$ | | 294·5 | 19·1 | | 0·39 | 363·1 | 5·6 | 0·02 | 0·49 |
| DD-S1 | 3 | I | $(aN)*S$ | Density | 299·5 | 24·1 | | 0·41 | 378·8 | 21·3 | | 0·18 |
| DD-S2 | 5 | II | $(aN/(1 + ahN))*S$ | Density | 290·1 | 14·7 | | 0·58 | 364·0 | 6·5 | 0·01 | 0·62 |
| DD-S3 | 5 | III | $(aN^2/(1 + ahN^2))*S$ | Density | 287·7 | 12·3 | | 0·58 | 362·7 | 5·2 | 0·03 | 0·64 |
| AD-S1 | 3 | I | $(aN)*S$ | Abundance | 296·5 | 21·0 | | 0·37 | 380·7 | 23·2 | | −0·02 |
| AD-S2 | 5 | II | $(aN/(1 + ahN))*S$ | Abundance | 281·5 | 6·0 | 0·02 | 0·73 | 364·8 | 7·3 | 0·01 | 0·62 |
| AD-S3 | 5 | III | $(aN^2/(1 + ahN^2))*S$ | Abundance | 283·1 | 7·6 | 0·01 | 0·71 | 366·3 | 8·8 | | 0·59 |
| Predator-dependent models | | | | | | | | | | | | |
| PP1 | 2 | 0 | $a/P$ | | 290·7 | 15·2 | | 0·41 | 359·9 | 2·4 | 0·10 | 0·52 |
| PP2 | 3 | 0 | $a/(P + h)$ | | 293·5 | 18·0 | | 0·43 | 360·7 | 3·2 | 0·07 | 0·57 |
| RD1[c] | 2 | I | $\alpha(N/P)$ | Abundance | 297·1 | 21·7 | | 0·25 | 382·4 | 24·9 | | −0·29 |
| RD2 | 3 | II | $\alpha N/(P + \alpha hN)$ | Abundance | 276·4 | 1·0 | 0·23 | 0·75 | 360·2 | 2·7 | 0·09 | 0·62 |
| RD3 | 3 | III | $\alpha N^2/(P + \alpha hN^2)$ | Abundance | 291·0 | 15·5 | | 0·59 | 369·3 | 11·8 | | 0·45 |
| HV1[d] | 3 | I | $\alpha(N/P^m)$ | Abundance | 296·0 | 20·6 | | 0·39 | 380·5 | 23·0 | | −0·01 |
| HV2 | 4 | II | $\alpha N/(P^m + \alpha hN)$ | Abundance | 276·7 | 1·2 | 0·20 | 0·76 | **357·5** | **0·0** | **0·35** | **0·70** |
| DB[e] | 4 | II | $aN/(1 + ahN + b(P-1))$ | Abundance | 276·9 | 1·5 | 0·18 | 0·76 | 358·4 | 0·9 | 0·23 | 0·68 |
| CM[f] | 4 | II | $aN/(1 + ahN)(1 + b(P-1))$ | Abundance | **275·4** | **0·0** | **0·37** | **0·76** | 360·3 | 2·8 | 0·09 | 0·64 |

[a]Lotka–Volterra models (Lotka 1925; Volterra 1926). [b]Holling models (Holling 1959b). [c]Ratio-dependent models (Arditi & Ginzburg 1989). [d]Hassell–Varley models (Hassell & Varley 1969). [e]DeAngelis–Beddington model (Beddington 1975; DeAngelis, Goldstein & O'Neill 1975). [f]Crowley–Martin model (Crowley & Martin 1989).

For prediction (4) regarding the prey and predator dependence of the ratio of moose biomass acquired to required, we used the same set of functional response models, but with the ratio as the response variable instead of per capita kill rate (Table 2). Two of the pack-winters were excluded from this analysis because roe deer dominated the prey individuals killed in those territories which had relatively high roe deer densities (Table S1, Supporting information).

## Results

### PREY AND KILL RATES

The relative moose densities across territories averaged 18·6 FPGs per day per km$^2$ (SE = 1·7, range 9·2–46·6, Fig. 2a). Given an average defecation rate of 14 moose FPGs per day (Persson, Danell & Bergstrom 2000;

Rönnegård *et al.* 2008), the average absolute density was 1·3 moose km$^{-2}$ (1·0 and 1·9 moose km$^{-2}$ for high (18) and low (10) estimates of defecation rates, respectively). Roe deer occurred at densities well below 1 roe deer per km$^2$ in 12 of the 15 territories (average FPG density 15·3 ± 6·5 day$^{-1}$ km$^{-2}$, range 0·0–128·4 day$^{-1}$ km$^{-2}$), given a defecation rate of 20 FPGs per day (Mitchell *et al.* 1985). Red deer occurred at low densities (0·35 FPGs day$^{-1}$ km$^{-2}$) in four territories, and fallow deer occurred only in one territory (5·5 FPGs day$^{-1}$ km$^{-2}$).

The main prey species was the moose, and on average, wolves killed 0·061 moose per wolf per day (range 0·012–0·135, Fig. 2). Kill rates estimated as the acquired edible biomass of moose averaged 7·6 ± 1·0 kg per wolf per day (range 1·2–16·1). Wolves killed roe deer in 12 of the 22 pack-winters, but they only made up a substantial part of the kills in two pack-winters (98% and 71% of all cervid
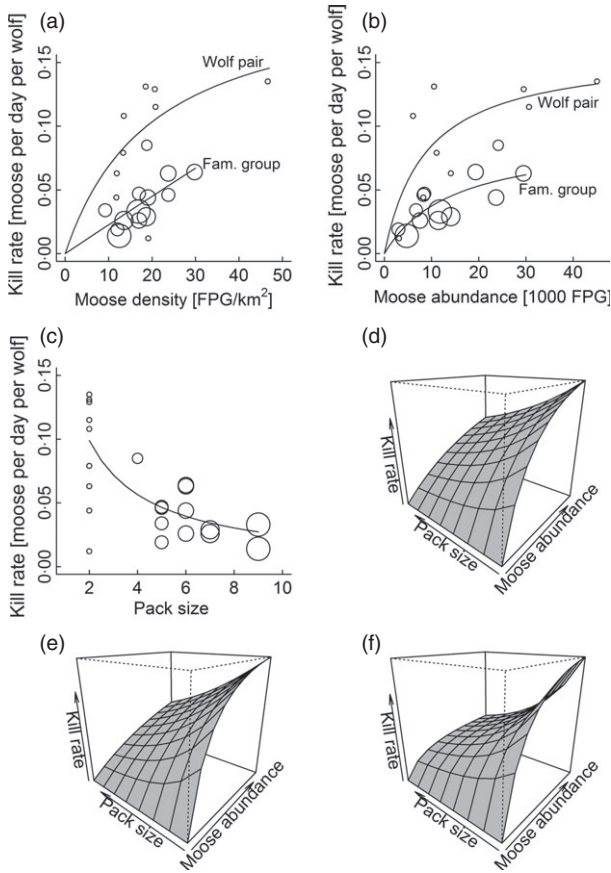
Fig. 2. Functional response models describing the number of moose killed per wolf per day in Scandinavia, in relation to relative moose density or abundance as estimated from faecal pellet group (FPG) counts, and wolf pack size. The models describe the dependence of the kill rates on (a) moose density DD-S2 (see Table 2); (b) moose abundance AD-S2; (c) wolf pack-size PP2; (d) ratio moose/wolf RD2; (e) ratio moose/wolf$^m$ with $m$ = interference parameter of the HV2 model; and (f) the additive effect of moose abundance and pack-size CM. Point size correlates with pack size.

carcasses). In all other pack-winters, roe deer constituted ≤40% of all cervid carcasses and <7% of the edible biomass of cervid kills. We found no wolf-killed red deer or fallow deer. Other smaller prey species, that is, tetraonids, hares *Lagopus* sp., beaver *Castor fiber* L., red squirrel *Sciurus vulgaris* L., badger *Meles meles* L. and red fox *Vulpes vulpes* L., made up only 6·8% of all prey items and 0·7% of the estimated acquired prey biomass. They were therefore omitted from the analyses.

### FUNCTIONAL RESPONSE MODELS

Our results supported the first prediction: per capita kill rates were positively related to prey availability (Fig. 2). Among the prey-dependent models, prey availability expressed as abundance (number of moose within the territory, AD) was a better predictor of per capita kill rates than moose density (DD), and model fit and parsimony improved when pack status, that is, pair or family group, was included in the model (DD-S, AD-S, Table 2, Fig. 2a,b). Our second prediction about the type of functional response was also supported: The asymptotic type II and sigmoid type III models performed better than the equivalent linear type I models. The asymptotic models resulted in higher parsimony than the corresponding sigmoid models (Table 2).

Consistent with our third prediction, predator-dependent models performed better than prey-dependent and constant models (Table 2). CM was the top model (Table 2), with a predator interference constant $b$ that was significantly >0 (Table 3). This indicates that the relationship between per capita kill rate and moose abundance per wolf pack depended on the number of interfering wolves in the pack (Fig. 2f). The CM model performed only slightly better than the other asymptotic predator-dependent models RD2, HV2 and DB (all

**Table 3.** Parameter estimates and *SE* of the most parsimonious functional response models described in Table 2 (ΔAICc <2 compared with the top-model CM), relating per capita kill rates of wolves (number of moose killed per wolf per day) to moose abundance and wolf pack size. Parameter $a$ (day$^{-1}$) is the attack rate, $h$ (days) is the handling time, $m$ is the strength of predator interference in Hassel–Varley (HV) models (see text), and $b$ is the interference constant in models that treat predator abundance as an additive or interacting factor (models DB and CM in Table 2). The first four columns relate to the abundance of moose faecal pellet groups (FPGs; in thousands), the fifth column to absolute moose abundances estimated by applying an average defecation rate of 14 FPGs per moose per day, and the last column reproduces estimates published by Jost *et al.* (2005)

| Parameters | Relative moose abundance | | | | Absolute moose abundance | |
|---|---|---|---|---|---|---|
| | Scandinavia | | | | Scandinavia HV2[a] | Isle Royale HV2 |
| | CM | RD2 | HV2 | DB | | |
| $a$ | 0·0248 ± 0·0087 | 0·0278 ± 0·0054 | 0·0505 ± 0·0267 | 0·1578 ± 0·5684 | 0·0007 ± 0·0004 | 0·0127 ± 0·0186 |
| $h$ | 4·35 ± 0·79 | 5·79 ± 0·84 | 6·45 ± 0·92 | 6·42 ± 0·93 | 6·45 ± 0·92 | 24·1 ± 1·94 |
| $m$ | | | 1·40 ± 0·32 | | 1·40 ± 0·32 | 1·85 ± 0·32 |
| $b$ | 0·42 ± 0·17 | | | 7·35 ± 27·82 | | |

[a]Applying a low (10 FPGs day$^{-1}$) or high (18) instead of average (14) defecation rate for the conversion from relative to absolute moose abundance per wolf pack did not change the estimates of parameters $h$ and $m$. Attack rate was 0·0005 ± 0·0002 and 0·0009 ± 0·0005 for moose density estimates based on defecation rates of 10 or 18 FPGs per day, respectively. CM, Crowley–Martin; DB, DeAngelis–Beddington.
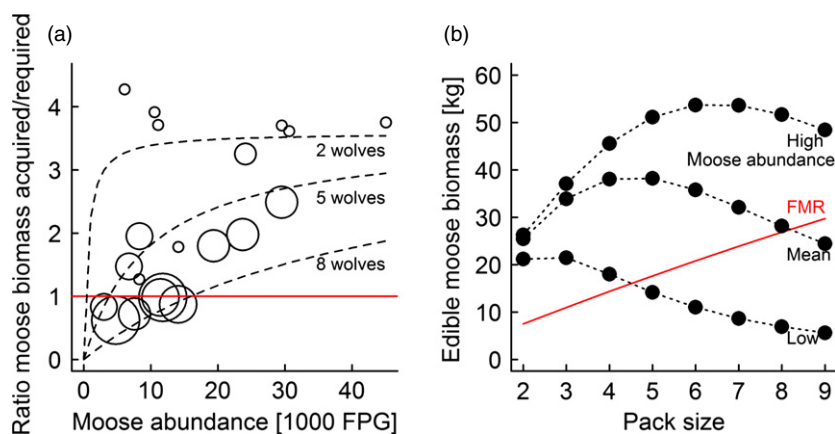
**Fig. 3.** Moose biomass acquired by wolf packs in Scandinavia in relation to biomass required to cover their field metabolic rate (FMR) (Table 1). (a) Ratio of acquired to required biomass in relation to relative moose abundance within the wolf territory. Point size relates to wolf pack size. Dotted lines are the predicted ratios based on the most parsimonious functional response model HV2 for different wolf pack sizes. If the ratio = 1 (solid line), the biomass of moose killed by a wolf pack equals the daily energetic needs of this pack; (b) Pack-size-dependent required biomass (solid line, FMR) and acquired moose biomass (dotted lines) for wolf packs predicted by model HV2 for low, mean, and high abundances of cervid biomass in the wolf territory. Low and high values correspond to minimum and maximum abundances recorded in this study.

$\Delta$AICc <1·6, Table 2). The estimate of the HV2-model parameter $m$ was >1 (Table 3), indicating that attack rates may decrease exponentially with increasing wolf pack size (Fig. 2e). However, as the confidence interval of this estimate included 1, per capita kill rates may simply depend on the per capita moose abundance (RD, Fig. 2d). The RD2-model was accordingly slightly more parsimonious than HV2 (Table 2). Even though the predator-dependent DB model was one of the top models, the interference parameter $b$ was not significantly different from 0 (Table 2), whereby it resembles the more parsimonious abundance-dependent model AD2.

### PACK SIZE AND ENERGETIC REQUIREMENTS

In the functional response models above, pack size was expressed as the number of wolves regardless of their size or energetic requirements. One might argue that pups have a lower FMR due to their lower body weight, and that this difference would be important in explaining the negative relationship between per capita kill rate and pack size. However, if pups are converted into adult equivalents (AE) based on metabolic rate, the estimated AE pack size is only reduced slightly (Table 1). For large packs of nine wolves, an adjustment to AE corresponds to a pack-size reduction of 1·1 wolves, and for packs of five wolves, the reduction is 0·3 wolves.

Concordant with prediction (4) and as a result of the observed predator-dependent functional response, the ratio of food acquired to required to cover the FMR of the pack (Table 1) was positively related to prey abundance and negatively to pack size (Fig. 3a). This relationship was best described by an HV2-model (Table 2) and was stronger than expected. In six of 20 pack-winters (30%), the adults killed moose prey at lower rates than

required to cover the total FMR of their pack. These packs included the four largest packs of seven and nine wolves, plus two packs with intermediate pack sizes but low moose abundance in their territories (Fig. 3a). The HV2 model predicts that with an average moose abundance in their territory, a non-breeding pair of wolves would kill 25·6 kg edible moose biomass per pair per day and thereby exceed their FMR 3·4-fold; family groups with three pups would exceed their FMR 2·2-fold, while family groups with seven pups would only cover 89% of their total FMR (Fig. 3b). Predicted total pack kill rates were nonlinearly related to pack size, with a peak at packs of five wolves at average prey abundance, at 2–3 wolves at low moose abundance, and at packs of seven wolves at high moose abundance (Fig. 3b).

## Discussion

Our long-term study on GPS-collared wolves in Scandinavia showed a clear positive relationship between per capita kill rates and prey availability for individual wolf packs during winter (prediction 1). Our study adds to a handful of empirical studies that describe functional responses for large predators in the wild; the wolf–moose system of Isle Royale (Vucetich, Peterson & Schaefer 2002), a wolf–caribou system in Alaska (Dale, Adams & Bowyer 1994), two wolf–elk systems in Yellowstone and Banff National Parks (Becker *et al.* 2008; Hebblewhite 2013), a Eurasian lynx–roe deer system in Scandinavia (Nilsen *et al.* 2009), and lions in the Serengeti (Fryxell *et al.* 2007). However, a study of the wolf–moose system in the Yukon with low moose densities (<0·50 moose km$^{-2}$) failed to fit functional response models (Hayes & Harestad 2000). Lake *et al.* (2013) found kill rates comparable with the Yukon study at even lower
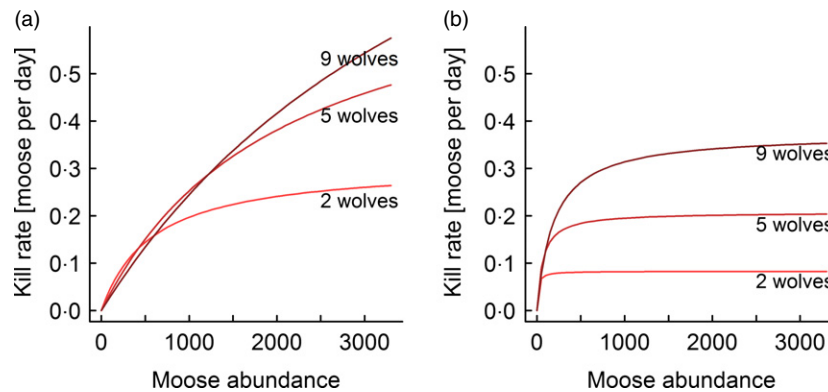
**Fig. 4.** Predicted kill rates of wolf packs from predator-dependent functional response model HV2 (see Table 2) for the wolf–moose systems (a) in Scandinavia and (b) on Isle Royale. Parameter estimates of the Isle Royale models are from Jost *et al.* (2005) (see Table 3). Absolute moose abundance in Scandinavia was estimated by applying an average defecation rate of 14 faecal pellet groups (FPGs) per day.

moose densities in Alaska (average 0·11 moose km$^{-2}$) and suggested that wolves responded numerically rather than functionally at such low prey densities.

Per capita kill rates of the Scandinavian wolves increased with increasing prey availability, but levelled off above a threshold (prediction 2). This type II functional response is typical in predator–prey systems where predators need to spend considerable time handling large kills, in contrast to, for example, filter feeders which feed on miniscule prey compared with their own body size (Jeschke, Kopp & Tollrian 2004). The sigmoid type III models did not perform as well as type II models. To detect significant differences between type II and type III functional responses, we would probably need more observations at low moose densities (Marshal & Boutin 1999). Prey switching is unlikely in most Scandinavian wolf territories due to the relatively high moose densities and low densities of alternative prey.

Territory size, and consequently, the abundance of prey at a given prey density vary between wolf packs. By replacing prey densities with the prey abundance per wolf pack, we introduced a predator component into the functional response models. The abundance models AD are therefore a first approximation to RD models. Model fit and parsimony improved successively when strengthening the predator dependence from purely prey-dependent models DD to AD models, to AD models that distinguished pairs and packs of wolves AD-S, to RD models and finally to the strongly predator-dependent models HV, DB and CM. This means that even though prey density influenced per capita kill rates to some extent, territory size, predator density and the interference between predators were factors of great importance for wolf kill rates.

As in our study, predator dependence gained more support than pure prey-dependence in all wolf studies where these models were compared (e.g. Becker *et al.* 2008). In the wolf–elk system of Banff National Park (Hebblewhite 2013) and the wolf–moose system on Isle Royale (Vuce-

tich, Peterson & Schaefer 2002), the RD model was superior to HV models. In contrast to our study across 15 wolf territories with a total area of >12 000 km$^2$, these studies were longitudinal time series conducted in limited study areas of 310–544 km$^2$ that roamed parts of or entire wolf territories, but never more than 1–5 wolf packs at the same time. The role of the scale in functional response modelling was exemplified with the reanalysis of the Isle Royale data (Jost *et al.* 2005). If kill rates and prey abundance were assessed across packs at the island scale, or if kill rates were at the pack scale and prey abundance at the island scale (initial analysis), RD2 performed best. But if both kill rates and prey abundance were assessed at the pack scale, as in our study, HV2 was the most parsimonious model. In Scandinavia, the attack rate *a* of the HV2 model was lower than on Isle Royale (Table 3), probably due to larger territory sizes and therefore a higher abundance of moose per wolf pack; the handling time *h* was shorter, and predator interference *m* was slightly weaker. Whereas the attack rate and the predator interference do not affect the form of the functional response curve significantly for a given pack size, the 3·7 times shorter handling time in Scandinavia flattens the initial slope and strongly increases the asymptote (Fig. 4). Interestingly, this difference in handling time is most likely due to a higher proportion of calves killed by wolves in Scandinavia, which in turn relates to the higher proportion of calves present in the moose population as compared to Isle Royale (Sand *et al.* 2012).

The predator dependence observed in Scandinavian wolves cannot be explained by an adjustment of kill rates to the lower energetic requirements of wolf pups in larger packs, as wolf pups in their first winter are close to adult size and have only a slightly lower FMR than adults (Table 1). We suggest that the unequal individual contribution of pack members to pack kill rates is the main factor influencing predator interference in our study. If all group members in social carnivores had the same ability to hunt and kill prey, group kill rate would relate more

linearly to group size. Hunting success is dependent on the age of the predator (Holekamp *et al.* 1997; Sand *et al.* 2006; MacNulty *et al.* 2009). Killing moose, a prey species much larger than wolves and able to successfully defend itself, is a behaviourally complex and risky skill which requires learning (Peterson & Ciucci 2003). The wolf pups in our study did not kill cervids while travelling without their parents, and they have been described elsewhere as inept hunters (MacNulty *et al.* 2012). They are simply scavengers or free riders within the social predator group, as observed in other carnivore species (Scheel & Packer 1991; Carbone, DuToit & Gordon 1997).

The functional response of a predator to changes in prey density is the underlying mechanism of the numerical response. As per capita kill rates increase with increasing prey density, energy acquired in excess of the FMR of an individual can be invested into growth and reproduction. At low prey densities, energy deficiency decreases reproductive output and survival. In our study, more than a quarter of the studied wolf packs, among those the four largest packs, killed less moose biomass than needed to cover their daily energetic needs. We are aware that the measurement of the FMR of one individual wolf published by Nagy (1994) and our estimates of prey body size and proportion of edible biomass per prey are crude estimates. The idea that large packs in Scandinavia suffer food limitation and that it is mainly pups that are affected is however supported by the analysis of the body weight data from marked pups. Pups did not increase in weight during winter, and body weight was inversely related to pack size (Table 1). This may in turn be an important stabilizing factor for litter size in wolves.

Our models predicted that non-breeding wolf pairs kill more than three times as many moose as needed to sustain their daily energy needs, even at relatively low moose abundances (Fig. 3). With an average moose abundance in their territory, non-breeding pairs killed about the same amount of moose biomass as packs with seven pups. The surplus-killing behaviour of small packs may be an optimal foraging strategy, that is, if finding a new food patch comes at a relatively low cost, it is favourable to consume only the most nutritious parts of the food patch. Partial prey consumption has been suggested as an optimal foraging strategy for wolves on Isle Royale (Vucetich, Vucetich & Peterson 2012), and we may expect the same mechanism to be important for the predator-dependent kill rates in Scandinavia.

Another plausible explanation of the observed surplus killing is inverse pack-size-dependent losses to scavengers because small packs are more exposed to kleptoparasitism (Carbone, DuToit & Gordon 1997; Hayes *et al.* 2000; Vucetich, Peterson & Waite 2004). Interestingly, in Scandinavia, adult wolf pairs did not exhibit any specific guarding behaviour, but rather chose day beds far away from kill sites (Zimmermann *et al.* 2007). Guarding prey may even be considered risky for wolves because it will increase the rate of detection by humans, the main cause of mortality for wolves in Scandinavia for centuries. As optimal foragers and risk minimizers, the wolves may reduce the risk of detection by humans by reducing the time spent at new kills after devouring the most nutritious parts of a carcass (Stahler, Smith & Guernsey 2006).

The theoretical background of functional response models roots in predator–prey dynamics. A positive correlation between per capita kill rate and prey density, especially if combined with a consequential numerical response, may result in density-dependent predation rates for the prey. We have not analysed the predation rates in this study, but we consider wolf predation on moose as being limiting rather than regulatory, despite the observed functional response. This is because the moose population is highly managed by hunting, and the overwhelming mortality factor is human harvesting (Solberg *et al.* 2000; Rönnegård *et al.* 2008). Wolf predation is to a high degree compensatory to hunting because managers often adjust hunting quotas to wolf presence (Jonzén *et al.* 2013). Nonetheless, wolf predation of moose is an important cause of conflict because hunters have to share some of the sustainable off-take with the wolf. Predator control both as licensed hunting and selective removal by managers has already been implemented in both Sweden and Norway and will probably gain more importance as the wolf population grows. Within the core of the wolf population range, reduction of pack size has often been considered an appropriate tool to dampen conflicts. Here, we show that removing two wolf pups from a pack is likely to have a minor effect on wolf predation compared with removing a non-breeding pair. In fact, reducing large packs to intermediate sizes may even have an adverse effect on pack kill rates (Fig. 3b).

## Data accessibility

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.9g2p2 (Zimmermann *et al.* 2014).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Wolf territories included in the study, with pack size, home range area, time and length of pack-winters, and sample size of faecal pellet counts.

**Table S2.** Estimates of body mass of prey species killed by wolves in Scandinavia and the proportions assumed to be edible.