Determinants of winter kill rates of wolves in Scandinavia

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Faktorer av betydelse för predationstakten på älg hos skandinaviska vargar

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Abstract

Winter wolf (*Canis lupus*) kill rates on moose (*Alces alces*) on the Scandinavian Peninsula are high and subject to strong variation, compared to other boreal wolf-moose systems. A more detailed understanding of factors influencing this variation is crucial for management and conservation of the Scandinavian wolf population. Although functional response models explain the relationship between prey density and kill rates, few studies quantify and investigate the predator-prey characteristics shaping the mechanisms of predation at a finer scale. I analysed 18 605 hourly GPS locations from 13 wolf packs during 2001-2010. There were 182 usable moose predation events from 17 winter study periods during this time span. With the GPS data I assessed patterns of wolf activity detecting consecutive kill-sites and reconstructing wolf hunting paths between predation events. I estimated two components of kill rate i.e., searching time (T_s) which is the time spent to detect, chase, and kill prey, and handling time (T_h), i.e., the time used to consume and process the prey for each predation event. I tested the difference between two different methods used for defining spatial criteria and evaluated a set of models to test factors potentially affecting T_s and T_h. These factors included prey age, pack size, winter period, moose density, and wolf density at two functional levels of scale. I demonstrate that the method used for defining T_s and T_h influenced their estimates and model selection. The majority of moose kills occurred during night time and wolves spent 75% of their total time away (>1km) from kill-sites. Wolf search time decreased with an increase in local moose density and pack size. At the pack level, T_h increased with pack size and decreased with the number of neighbouring packs highlighting the influence of territoriality and social interactions among wolf packs. Age of moose, i.e., calf (< 1 year), yearling (1 year) and adult ($\geq$ 2 year) moose, was an important variable for explaining variation in both T_s and T_h. This study shows the potential of a research approach using GPS data in time-to-event models and the effectiveness of these models to quantify mechanisms of predation and factors influencing wolf kill rates on moose.

Introduction

The ecological influence of a carnivore on a prey species has a relevant importance for conservation and management purposes (Sand et al. 2012). The knowledge of factors influencing the mechanisms of predation is crucial to understand prey-predator interactions. The relationship between kill rate and prey density defined as "functional response" in Solomon (1949) and reported in Holling's disc equation (1959), identified the components involved in the process of predation. The large number of studies implementing and reviewing this first predation model generated large variation in empirical functional response models (Jeschke et al. 2002). This encouraged the still open discussion about the nature of functional response and underlines the importance of empirical tests in order to improve our understanding of the processes (Abrams and Ginzburg 2000). In particular, Abrams, (1990) suggests how the three assumptions of Holling's disc equation (1959) i. e. : independency from prey density of: (i) the total time spent foraging and the costant capture rate;(ii) handling time and (iii) attack success rates, are seldom respected. Moreover Abrams, (1990) demonstrate how these dependencies could be integrated in a type 2 functional response. In addition to prey density, kill rates are influenced by various factors such as predator group size (Schmidt and Mech 1997, Sand et al. 2012), predator density (Vucetich et al. 2002), predator age (Metz et al. 2011), prey age distributions (Peterson et al. 1998, Sand et al. 2012), snow depth (Nelson and Mech 1986, Huggard 1993,

Jedrzejewski et al. 2002) and spatial heterogeneity (Kunkel and Pletscher 2000, Gorini et al. 2011).

The use of GPS technology allows one to investigate patterns of predation and to describe and quantify animal movements at a finer temporal and spatial scale than previous techniques (Nathan et al. 2008, Cagnacci et al. 2010). However, ensuring time scale correspondence between the real behaviour of an animal and the statistical approach used, is one of the major challenges in current research with GPS technology (Hebblewhite and Haydon 2010). GPS technology facilitates a more precise quantification of kill rates, reduces the number of carcasses missed (Anderson and Lindzey 2003, Sand et al. 2005, Zimmermann et al. 2007) and makes it possible to reconstruct the predator's hunting paths along consecutive kills. More precisely, it permits the partitioning of a movement sequence into groups of movement phases. Thereby GPS data enhances the possibility to understand the type of behaviour related to the hunting path and may allow investigation how those encapsulated behaviours are linked to the variation of kill rates (Nathan et al. 2008, Merrill et al. 2010, McPhee et al. 2012).

Each predation event included in hunting paths is spatially composed by two phases: the searching and handling for prey, defined in terms of time budgets and ecological behaviours as searching time (T_s) and handling time (T_h) (Webb et al. 2008, Knopff et al. 2010, Merrill et al. 2010, Mc Phee et al. 2012). This approach may allow for quantifying behavioural responses in terms of movement patterns that are able to increase our understanding of variation in kill rates (Merrill, et al. 2010, McPhee et al. 2012). Whereas T_s is behaviourally connected with prey encounter rate and hunting success, T_h is related to prey consumption and processing of prey biomass (Holling 1959, Eriksson 2003, Webb, et al. 2008, Merrill et al. 2010, Knopff et al. 2010, McPhee et al. 2012). T_s and T_h are fundamental factors of the functional response (Holling 1959, Merril et al. 2010, Mc Phee et al. 2012) and may allow for linking behavioural interactions of the predator to prey density, spatial heterogeneity, and other predator-prey population characteristics (Merrill et al. 2010, McPhee et al. 2012).

This study investigated a prey-predator system composed by moose (*Alces alces*) and wolf (*Canis lupus*). My first objective was to develop and test different decision rules to classify movements into T_s and T_h for estimation of time budget and the quantification of the functional response. My second objective was to quantify how T_s and T_h are functionally linked to moose density and how other factors such as prey age, pack size, wolf density, and time of winter interact with this main variable, at two spatial levels (kill site level, pack level, Figure 1).
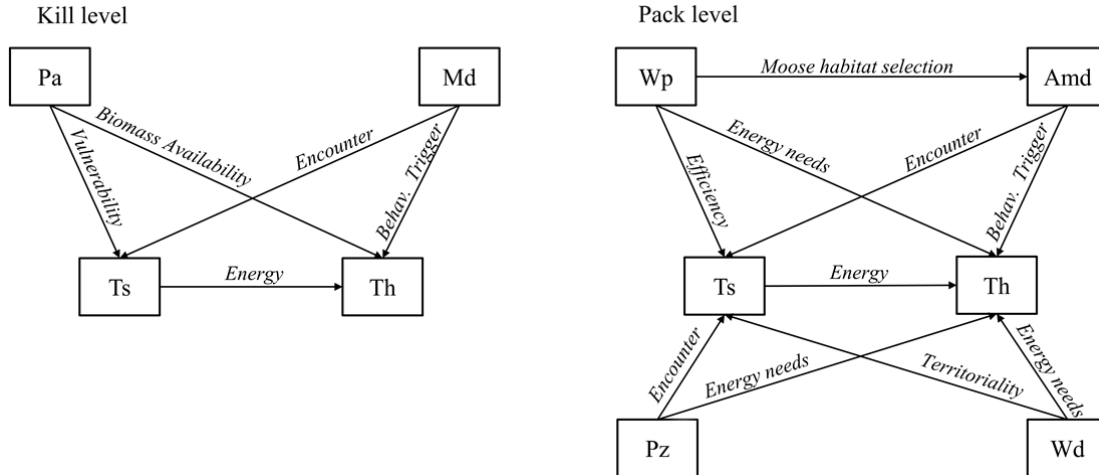
4

Kill level

Pa — Biomass Availability / Vulnerability → Ts — Energy → Th ← Encounter / Behav. Trigger — Md

Pack level

Wp — Moose habitat selection → Amd
Wp — Efficiency / Energy needs → Ts — Energy → Th ← Encounter / Behav. Trigger — Amd
Ts ← Encounter / Energy needs — Pz ; Th ← Territoriality / Energy needs — Wd

Figure 1. Conceptual hypothetic relationships between response and independent variables tested in this study at two functional levels. More specifically, every arrow shows the main ecological factor involved in the relationship. Response variables: T_s=*searching time*, T_h=*handling time*. Independent variable: Pa=*Prey age*, Md=*moose density at the kill-site*, Wp= *winter period*, Amd= *Average moose density in the pack home range*, Wd= *wolf densities-number of packs surrounding the considered one*, Pz=*Pack size*.

Study area

The study area which is in both Norway and Sweden, together are referred to as the Scandinavian Peninsula (60°N, 12° E), includes 13 wolf territories (Wabakken et al. 2001; 2010). The predominant habitat ranges from boreal coniferous forests to mixed-deciduous forests depending on the latitude and altitudinal gradient. The forest composition varies between mixtures of conifers, mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*) as wells as deciduous tree species, mainly white birch (*Betula pubescens),* silver birch *(Betula pendula)* and aspen (*Populus tremula*). Other, less common tree genera in the area are alder (*Alnus* spp.*)* and willow (*Salix* spp.). The main forest management regime consists of intensive clear cut logging, giving rise to a mosaic of forest stands at different age classes. An extensive road network, built mainly for forest logging, creates together with lakes, bogs and agricultural fields a heavily fragmented landscape. The average human population density between Norway and Sweden is 15.1 inhabitants/km^2 (Statistics Norway 2011; Statistics Sweden 2011). However, large areas within the main wolf range contain less than 1 inhabitant/km^2 (Swedish National Atlas 1991). Snow covers the study area 3-6 months each year with average snow depths between 20 to 60 cm, depending on altitude (Statistics Norway 2011; Statistics Sweden 2011).

The wolf population recolonized the Scandinavian peninsula in the late 1970's and the first pack reproduced in 1983 (Wabakken et al. 2001). In 2010, the wolf population consisted of approximately 250-290 individuals grouped in 52 packs with an average territory home range of 1000 km^2 and an average pack size of 4-5 individuals (Wabakken et al. 2010). Moose are the main prey for this wolf population and represent more than 95% of its winter diet biomass in Scandinavia (Sand et al. 2005). The rest of the diet includes smaller ungulates, i.e., roe deer (*Capreolus capreolus*), wild reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), small mammals like beaver (*Castor fiber*), badger (*Meles meles*), mountain hare (*Lepus timidus*), and birds, mainly black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*). During winter the moose density in the wolf pack territories

ranged from 0.8 to 3.4 moose/km^2 with an average of 1.42 ± 0.19 (SE) moose/km^2 (Sand et al. 2012). The moose population in all Sweden is annually harvested. Human hunting is the main cause of mortality in Sweden moose population (Rönnegård et al. 2008).

Methods

Dataset description

The GPS data locations span from 2001 to 2010 and are distributed on several winter study periods from December to April and different packs (Table 1). For all winter seasons, I used GPS locations sampled at one-hour intervals from one resident adult from each pack or pair except for the Gräsmark pack where I have used data from both the adult female and male because of a loss of contact with one of the collared wolves during the study period. For the Gråfjell pack, I used data from three consecutive winter studies whereas for the Uttersberg and Ulriksberg packs I used data from two winter studies (Table 1).

Table 1. Detailed description of the GPS datasets from wolves in Scandinavia used for this study, with study period, collared wolf id, fix rate, number of locations, total number of moose kills, and the number of moose kills used for each wolf pack. I excluded moose kills with missing searching or handling time or missing predictors effects.

Pack	Year	Study Period (month)	Study Period (days)	Collared wolf	Fix rate (%)	N° of Locations	Total N° of moose kills	N° of used moose kills
Gråfjell	2001	Feb.- Apr.	57.2	M0109	91.2	1254	16	12
Gråfjell	2002	Dec.- Apr.	121.6	M0110	87.1	2656	33	28
Tyngsjö	2002	Jan.- Apr.	79.0	M0204	91.2	1731	22	19
Bograngen	2003	Feb.- Apr.	45.0	M0009	92.8	1336	17	15
Gråfjell	2003	Feb.- Apr.	51.2	M0110	81.3	999	24	22
Hasselfors	2003	Feb.- Apr.	48.4	U0304	65.9	767	15	12
Djurskog	2004	Feb.- Mar.	45.2	M0306	92.8	896	13	10
Jangen	2004	Feb.- Mar.	52.7	M0404	65.4	823	13	10
Nyskoga	2004	Feb.- Mar.	27.0	M0007	94.0	610	11	3
Ulriksberg	2006	Feb.- Apr.	46.2	M0602	90.6	1007	9	7
Uttersberg	2006	Dec.- Jan.	44.9	M0506	90.8	980	8	4
Gräsmark	2007	Feb.- Apr.	46.2	M0610/11*	93.4	1037	19	17
Ulriksberg	2007	Jan.- Mar.	45.8	M0602	94.4	1089	10	6
Uttersberg	2007	Nov.- Dec.	31.1	M0601	74.8	561	4	2
Kloten	2008	Feb.- Mar.	45.5	M0910	95.9	1051	13	10
Fulufjället	2009	Feb.- Mar	43.6	M0904	99.0	1039	6	4
Tenskog	2010	Feb.- Apr	56.0	M1001	99.4	1340	6	1

*two wolves collared: M0610 and M0611

Wolves were captured from a helicopter with a CO_2 dart gun and equipped with a GPS collar following the procedure explained in detail in Sand et al. (2006). I defined position clusters as ≥ 2 GPS locations within a maximum distance of 200 m (Sand et al. 2005; 2006, Zimmerman 2007). All clusters were visited by field technicians, who verified and classified found carcasses into three categories: 1) wolf killed prey, 2) probable wolf killed prey and 3) other carcasses (Sand et al. 2005). I considered only moose of the first two categories for further analysis. Cluster survey and field procedures for the carcass search are explained in Sand et al. (2005). The research project, capture, handling and field protocols have been approved by the Swedish and Norwegian Agency of Animal Welfare (Sand et al. 2006). The GPS dataset has been analyzed with ESRI. 2009. ArcGIS 9.3.1.

Redlands, California, Environmental Systems Research Institute. All GPS locations were screened with ArcGIS 9.3.1 for coordinate errors that were subsequently removed in case of exceptionally high step distance lengths (>20 km) between two consecutives fixes or an unrealistic long movement distance outside the territory of the pack (Bjørneraas et al. 2010).

Wolf activity patterns

I used the distance between consecutive hourly locations as index of wolf activity patterns and distance from consecutive kill sites in order to describe wolf behaviour on kill-sites. I grouped those two indices in 3 classes: 0-200m, 201-1000m and >1000m. For an index of wolf activity pattern, I consider the first 2 classes reflecting handling behaviour like resting and consumption while the latter as searching behaviour. Net displacement from kill-sites was used to describe the proportion of time spent away from kill-sites versus wolf behaviour at and around carcasses.

Spatio-temporal methods for searching- and handling time

Predation movement patterns are composed by two main behaviours; searching and handling prey. They were first described in the Holling disc equation (Holling 1959), which defines T_s as the time or locations spent encountering, chasing and killing the prey and T_h as the time or locations spent consuming and processing the prey (Knopff et al. 2010, Merrill et al. 2010).

I defined the time of death of every wolf kill as the first location within 200 m of the carcass in the kill cluster. This time event was defined as the starting point of T_h for the wolf kill in consideration (Eriksson 2003, Knopff et al. 2010). T_s can be defined as the time between the last GPS locations belonging to T_h and the first location at the subsequent kill site (McPhee et al. 2012). For this reason, T_s in this study is the equivalent of the time to kill (T_k) defined in Merrill et al. (2010) and in McPhee et al. (2012). I calculated the inter-kill interval (IKI) as the time between the first location at consecutive kills for every winter predation period (Knopff et al. 2010). Based on those assumptions the IKI interval is composed by $T_{h(i)}$ of wolf kill i and the searching time ($T_{s(i+1)}$) for the next kill $i+1$.

I calculated $T_{s(i)}$ for the wolf kill $P_{k(i)}$ by subtracting the previous $T_{h(i-1)}$ from the previous $IKI_{(i-1)}$ according to (Knopff et al. 2010) as:

$$T_{s(i)} = IKI_{(i-1)} - T_{h(i-1)} \hspace{4cm} (1.1)$$

For every wolf kill $P_{k(i)}$ I calculated the predation event $K_{e(i)}$ as the sum of $T_{s(i)}$ and $T_{h(i)}$:

$$K_{e(i)} = T_{s(i)} + T_{h(i)} \hspace{4cm} (1.2)$$

I assumed that T_s and T_h were mutually exclusive in time, i.e. that there was no overlap between these two behavioural stages. In contrast to herbivores whose search and handling time can overlap (Sparlinger and Hobbs 1992), carnivores partition the two behaviours when preying on large prey (Merrill et al. 2010). However, I estimated T_s and T_h following the consideration that some handling activity can be confounded by T_s (see McPhee et al. 2012 for further details). In particular field data suggest wolves in Scandinavia spent time digesting relatively far away from the kill-site. This suggests that a method based solely on spatial distance criteria for a "cluster" approach could underestimate T_h. A different

behaviour around kill sites seems to occur in the Scandinavian wolf population compared with North American studies, i. e., a different movement pattern and hunting success (Sand et al. 2005; 2006). Handling behaviour is characterized by a short time spent close (<200m) to the actual kill site, i.e., some of the moose kills were abandoned shortly after the time of kill and resting may occur at distances ≥ 2 km from the kill site (Sand et al. 2005). Although kill and resting sites may be spatially distant, they are closely connected behaviourally (Sand et al. 2005, Zimmermann et al. 2007). In order to consider this behaviour and to quantify the influence of decision rules on T_s and T_h, I developed two methods to estimate T_h:

1) Step Length Based (Slb)

This method is designed to include a proportion of resting sites far away from the kill site into T_h. It is founded on the distance of step length i.e., the straight-line distance or Euclidean distance between two consecutive locations reflecting the behavioural activity (Erickson 2003, Franke et al. 2006, Merrill et al. 2010). It includes all consecutive locations ≤200m around the kill and all the continuous locations with a step length of ≤1 km/h. For this method T_h ends when the step distance is >1 km/h, in combination with no return of the wolves back to the previous kill-site (≤200m from the kill site) or to another kill-site within the next 24 hours.

2) Radius Length Based (Rlb)

This method is spatially inspired by the concept of continuous and discontinuous handling time based on the distance from the cluster centre and considers the cluster as an indicator of activity behaviour (Webb et al. 2008). It is founded on the net displacement; i.e., the Euclidean distance between the kill-site and each wolf location (Webb et al. 2008). For this method all locations ≤ 1 km from the kill site within the first 10 days after the time of death are included to T_h.

Calculation of T_s for both methods is reported in equation 1.1. I considered revisits at kill sites (RT_h) as every location within 200m from the kill-site in a time range of 10 days after the time of death. RT_h occurs also for locations within 24 hours after the last T_h location of the kill-site or within 200m from an older kill-site belonging to a previous predation event. The total handling time for both methods is calculated according to:

$$T_{h\,(tot)} = T_h + RT_h \tag{1.3}$$

For predation events with double kills I divided the handling time into two singular events sharing equal proportions of the total T_h. For one of these kills, I assumed that search time was $T_s = 0$. If in a predation event the prey was assumed to be killed by a non-collared wolf of the same pack, I assumed that handling time was $T_s = 0$. In case a kill-site was found >200 meter from any location, I assumed handling time was $T_h = 0$. In the T_s and T_h time budget, I allocated one hour for every location. For missing locations between two different behavioural sequences (e.g. the last T_s and the first T_h locations), I allocated the missing location to the first one.

Statistical analysis

I did a paired *t*-test to verify differences in T_s and T_h estimated with the two methods Slb and Rlb and checked for correlation with Pearson's test. In case of a significant difference, I included T_s and T_h estimates from both methods as response in the model selection.

I used Wilcoxon test to check if T_s and T_h mean estimates differed for calf (<1 year), yearling (1 year) and adult (≥ 2 year) moose.

I analysed factors of wolf predation events at two spatial scales: the kill site and the pack level (Figure 1). For both levels I used a set of general linear mixed models with Gaussian errors and identity link (lme4, R package: Bates and Maechler 2009). I log-transformed (x+1) the response variable T_s and T_h in order to meet the assumption of normality for linear models.

At the kill site level I selected the following predictors: (1) prey age including calf, yearling and adult moose, (2) moose density at the kill site from interpolated pellet count data (ordinary Kriging, Spatial Analyst extension in ArcGIS 9.3) and expressed as the number of moose/10 km^2 (Sand et al. 2012). For T_h models I included T_s as a predictor. I used pack territory (Territory ID) as random factor for all models.

At the pack level, I included the following predictors: (1) average moose density in the pack territory, (2) winter period divided into early (Dec - Jan) and late (Feb - Apr) winter, (3) pack size, i.e. the number of wolves/pack, grouped in three categories: 2 wolves, 3-5 wolves, >5 wolves, and (4) wolf density, i.e. the number of territories of neighbouring wolf packs bordering the territory of interest. To evaluate wolf density, I used Minimum Convex Polygon (MCP) integrating GPS location (if available), snow tracking data and DNA analysis from collected scats, following the procedure reported in Wabakken et al. (2001; 2010). I created a buffer of 2 km around the territory for collared packs and a buffer of 5 km for non-collared pairs/packs in order to account for the underestimation of territory sizes.

I tested main effects and first-order interactions. I did not include higher-order interactions to avoid complex models of uncertain biological meaning. I included the following interaction terms as fixed factors; Moose density × prey age at all kill level models; average moose density × wolf density, average moose density× pack size, average moose density× winter period, wolf density × winter period, wolf density × pack size in all pack level models. The fixed factor searching time × moose density is exclusive for T_h kill level model set (Appendix 1-2).

I used Akaike's Information Criterion for small sample size (AIC$_C$) to rank model sets (Burnham and Anderson 2002). I calculated Δ_i AIC$_C$ between selected models and the model with the lowest AIC$_C$. From this I calculated AIC$_C$ weights (w$_i$) and evaluated parameter estimates with model averaging (Burnham and Anderson 2002). I reported exclusively models with Δ_i AIC$_C \leq 2$. To evaluate the relative importance of the predictor variables, as suggested in Arnold (2010), I estimated Cumulative Akaike's Information Criterion weight ($\sum$w$_i$) (Burnham and Anderson 2002:167-169).

I calculated R^2 of the selected models in order to evaluate how their regression lines fit with the dataset variance. I used the squared correlation value between the model fitted values and the log+1 response variables for every selected model (Baayen 2008). I back-transformed model results in order to present the response variable in the unit of hours. The statistical analysis was run in R (ver. 2.13.1 R Development Core Team 2011).

Results

Wolf predation and activity patterns

My analyses included 17 winter study periods of 13 packs, for a total of 887 days of studies and 19 176 locations at hourly intervals. The average fix rate success was 88.27% ± 2.51 (mean ± SE) and the average duration of predation studies was 52.1 ± 5.1 (mean ± SE) days (Table 1). Of the 239 moose kills found during all predation studies, I was able to include 182 for the calculation of searching and handling time, mainly due to missing values for some predictive variables. The 182 moose kills were composed of 71% calves, 12% yearlings and 17% adult moose including 42% females, 24% males and 34% of unknown sex. The majority (78%) of moose kills occurred in February and March. Most moose were killed during the night to early morning time (68%) from 21 pm to 8 am (Figure 2). In my dataset, only 2 moose were reported as killed in a multiple kill event.
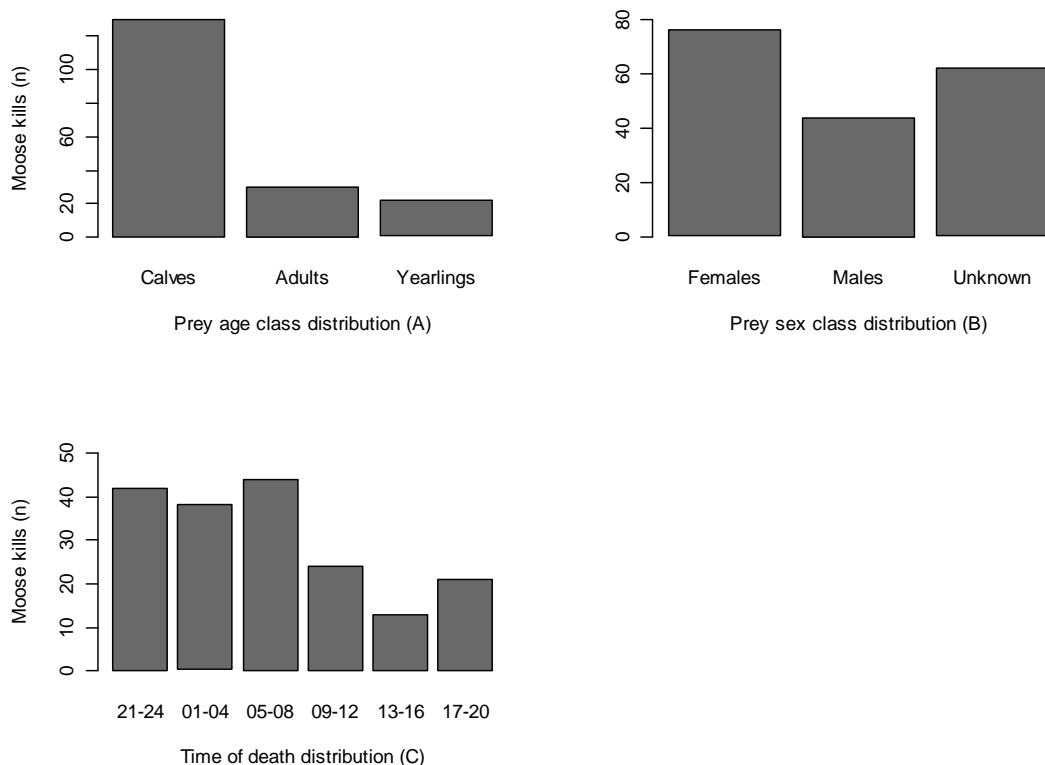

Figure 2. Distribution of age and sex classes, month, and time of death of 182 wolf-killed moose during 2001 to 2010 from the 17 winter studies of predation. Prey age classes (A) are: calves (<1 year), yearlings (1 year) and adults (≥2 year). In the prey sex distribution (B), unknown class represents all moose kills where it was not possible to estimate the sex. The time of death was estimated as the first location within 200 m of the carcass. The time of death for each moose (C) was grouped in 4 hour intervals.

Of the 18 605 one-hour interval distances between consecutive locations the maximum distance was 11.4 km with 61% of those distances ranging between 0 and 200 meters, of which 36% in 0-20 m and 25% in 21-200 m. The remaining 39% ranged between 201 m and ≤11.4 km. (Figure 3A).

Wolves spent 75 % of their time at >1000 m from their kills, with a maximum value of 69.0 km. The remaining 25% of locations were distributed as 12% in 0-200 m and 13% in 201-1000 m, respectively (Figure 3B). The average daily wolf activity pattern showed two peaks with one in early morning and one late in the evening. Lowest activity occurred from midday to early afternoon (Figure 3C).
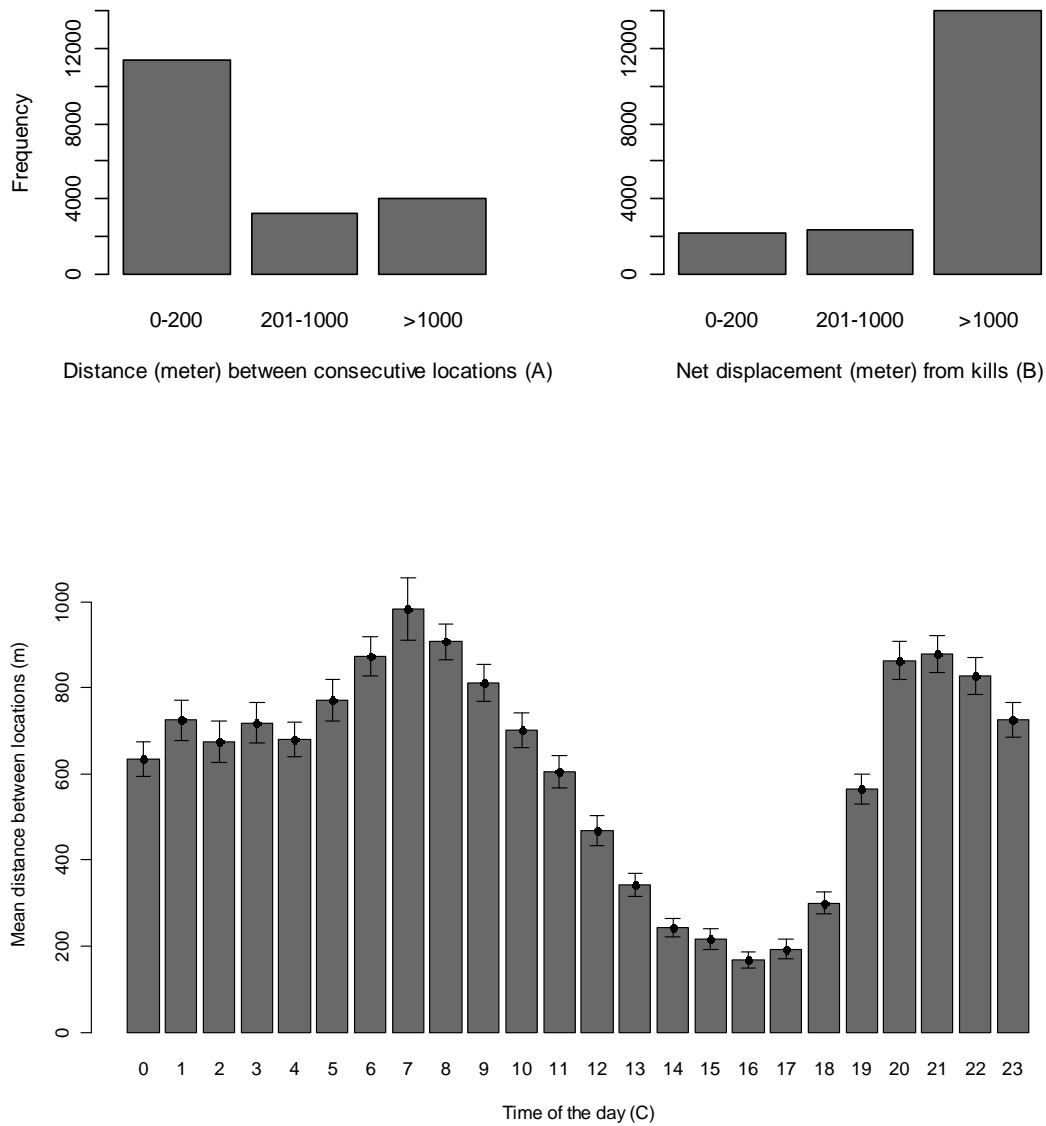

Figure 3. Frequency distribution of distance between consecutive locations (A) and net displacement from kills sites (B) for wolves in Scandinavia during winter. Diurnal activity pattern (C) expressed as mean distance ± SE between consecutive locations.

T_s and T_h estimates for two different methods

Time budgets estimated with the Slb method rendered generally shorter searching times ($t = -3.603$, $df = 181$, $P = 0.001$) and longer handling times ($t = 2.531$, $df = 181$, $P = 0.012$) as compared to the Rlb approach (Table. 2).

Table 2. T_s and T_h mean ± SE (hour) estimates by step length based (Slb) and radius length based (Rlb) methods: total average and prey age classes: calf (< 1 year), yearling (1 year) and adult (≥2 year). N° is the sample number for each class.

	T_s		T_h		N°
	Slb	Rlb	Slb	Rlb	
Total	67.68 ± 4.61	70.98 ± 4.41	25.88 ± 1.96	21.24 ±1.66	182
Calves	64.70 ± 5.50	68.41 ± 5.29	24.43 ± 2.26	19.58 ± 1.86	130
Yearlings	62.91 ± 9.02	75.64 ± 8.80	25.91 ± 5.45	22.32 ± 4.36	22
Adults	84.10 ± 12.91	78.73 ± 12.45	32.17 ± 5.55	27.63 ± 5.12	30

The majority of T_s estimates were between 1 and 72 hours, while T_h estimates were between 1 to 24 hours. The majority (≥80%) of T_h estimates (both methods) occurred within 48 hours (Figure 4).
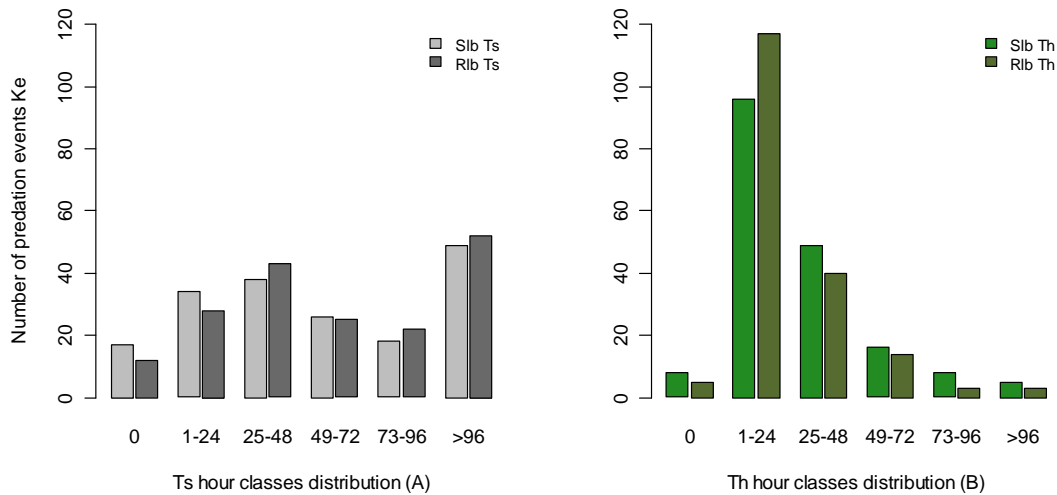

Figure 4. The distribution of searching- and handling time for different classes on the total number of predation events (K_e Tot=182). (A) search time and (B) handling time distribution estimated by the two methods: (A) Step length based (grey) and Radius length based (dim grey), (B) Step length based (forest green) and Radius length based (dark olive green) methods.

Searching time estimated with the Slb method was longer for adult than for calves and yearling moose classes (Wilcoxon test, $P = 0.021$) (Table, 2) whereas there were no significant differences between the other age classes for either of the methods or estimates of T_s and T_h.

A consistent part (13%) of all locations (n =18605) were classified differently according to the behaviour depending on the two (Slb-Rlb) spatio-temporal criteria used. There was no significant correlation between T_s and T_h estimates for either method: Slb r = 0.13 ($t = 1.803$, $df = 180$, $P = 0.072$) and Rlb r = 0.13 ($t = 1.783$, $df = 180$, $P = 0.076$). The average predation event length (average K_e) was almost 5 days (92.89 ± 5.12 hours, n° 182) as a result of the mean Slb and Rlb K_e estimates. There was no difference between the two

methods for Ke (log+1) estimates ($t = -0.433$, $df = 181$, $P = 0.665$). The mean inter-kill interval (IKI) of all $P_{k(tot)}$ IKI estimates was 93.71± 5.24 hours (n = 182).

T_s and T_h model selection

The methods used for estimating T_s and T_h (Slb vs Rlb) did not affect the model selection results for almost all functional response models except for T_h at the pack level (Table 4, 5), and therefore I report below only models results estimated by the Slb method.

T_s and T_h response variables were explained by several models with $\Delta_i AIC_c<2$, and for this reason I used AIC-weights to select the best one at both the kill and the pack level (Table 3, Table 4). The predictor variables' effect size was estimated with model averaging based on model weight (w_i) (Table 3, 5). The back transformed selected models at both the kill and pack level described a negative relationship for both T_s and T_h and the fixed effects of moose density and average moose density (Figure 5, 6).

Table 3. Model selection for fixed effect variables on the searching time (T_s) for 182 wolf-killed moose from 17 winter studies of wolf predation. GLMM models with T_s as response estimated by step length based (Slb) method, grouped in two spatial scales: kill level and pack level. Models are selected using Akaike information criteria corrected to finite sample size. I have presented only models with $\Delta_i \leq 2$ and the null model with no fixed effects. All models results with both methods are presented in Appendix 1,2.

Model Kill level	ΔAIC_i	w_i	R^2
Moose density	0.00	0.63	0.06
Moose density + Prey age	1.93	0.24	0.06
Null model	6.34	0.03	-
Model-Pack level			
Average moose density + Pack size + Average moose density × Pack size	0.00	0.63	0.09
Null model	5.29	0.05	-

Table 4. The effect size of the predictor variables reported with relative variable importance ($\sum w_i$) of all T_s model parameters estimated by the step length based method at kill and pack level.

Model parameter	$\sum w_i$
Model Kill level	
Moose density	0.96
Prey age	0.25
Model-Pack level	
Average moose density	0.74
Pack size	0.77
Wolves density	0.21
Winter period	0.12

At the kill-site scale, wolves spent less time searching for prey in high moose density areas (slope ± SE, -0.024 ± 0.007). Calves and yearlings required less time to be found and killed than did adult moose (mean searching time ± SE in hour for calves: 64.70 ± 5.50, yearling: 62.91 ± 9.02 and adults: 84.10 ± 12.91) (Figure 5A). Moose density was the main T_s predictor being almost four times as important as prey age (Table 3, 4).

13

At the pack scale, the type of relationship between T_s and average moose density was the same as at kill-site level (slope $\pm$ SE, -0.001 $\pm$ 0.017). Pairs (mean$\pm$ SE, 70.26 $\pm$ 6.27) and large packs (mean $\pm$ SE, 75.21 $\pm$ 9.56) had longer T_s compared to medium-sized packs (mean $\pm$ SE, 53.27 $\pm$ 8.73) (Figure 5B). On average moose density and pack size were the main predictors of T_s with an almost equal effect size whereas wolf density and winter period were not included in the best model of fixed effects (Table 3, 4).

Table 5. Model selection for fixed effects on handling time (T_h) for 17 winter studies of wolf predation. GLMM models with T_h as response estimated by step length based method (Slb), grouped in two functional level scales: kill level and pack level. At the pack level, I report both methods to show how different models were selected and their effect size. Models were selected using Akaike information criteria corrected for finite sample size. I have presented only models with $\Delta_i \leq 2$ and the null model with no fixed effects. The best model is selected with model averaging based on model weight (w_i).

Model-Kill level	Δ_i	w_i	R^2
Moose density + Searching time	0.00	0.32	0.08
Moose density + Searching time + Moose density × Searching time	1.29	0.17	0.08
Moose density	1.30	0.16	0.07
Moose density + Prey age + Searching time	1.50	0.15	0.08
Null model	3.58	0.00	-
Slb-Model-Pack level			
Average moose density	0.00	0.18	0.08
Average moose density + Wolves density	0.20	0.16	0.05
Average moose density + Winter period	1.23	0.10	0.04
Average moose density + Wolves density + Winter period	1.51	0.08	0.05
Wolves density	1.52	0.08	0.03
Null model	3.58	0.03	-
Rlb-Model-Pack level			
Average moose density + Wolves density	0.00	0.21	0.06
Wolves density	0.65	0.15	0.05
Wolves density + Pack size	1.29	0.11	0.07
Average moose density + Wolves density + Average moose density *Wolves density	1.48	0.10	0.07
Wolves density + Winter period + Pack size	1.66	0.09	0.07
Null model	8.49	0.00	-

Table 6. Relative variable importance ($\sum w_i$) of all T_h model parameters for both methods: step length based (Slb) and radius length based (Rlb) and grouped in two the functional level scales: kill level and pack level. Models were selected using Δ_i and w_i.

Model parameter	$\sum w_i$	
Model Kill level		
Moose density	0.97	
Prey age	0.34	
Searching time	0.66	
	Slb	Rlb
Model Pack level		
Average moose density	0.75	0.55
Pack size	0.16	0.27
Wolves density	0.36	0.91
Winter period	0.53	0.27

At the kill-site scale, moose density and searching time were the main T_h predictors with the highest effect size (Table 6). Wolves reduced T_h as moose density increased (slope ± SE, -0.01 ± 0.006) and T_h was proportional to the time wolves had used to search this particular prey (slope ± SE, 0.002 ± 0.001) and to prey age (slope ± SE, 0.09 ± 0.11) (Figure 6A, B).

At the pack scale, T_h decreased with an increase in average moose density (slope ± SE, -0.03 ± 0.01) and wolf density (slope ± SE, -0.19 ± 0.12) (Figure 6C). T_h was higher in the first part of the winter (slope ± SE, 3.60 ± 0.34) compared to the second part (slope ± SE, -0.35 ± 0.30) (Figure 6D). Pack size was selected only in the Rlb method models set: T_h depended on pack size: pairs (mean ± SE, 20.45 ± 2.50), packs between 3-5 individuals (mean± SE, 21.65 ± 2.65), and packs bigger than 5 individuals (mean ± SE, 22.07 ± 3.24) (Figure 6E). The main variables' effect size depended on the method used: average moose density and winter period were most important for Slb-models, whereas wolf density and average moose density were most important for Rlb-models.
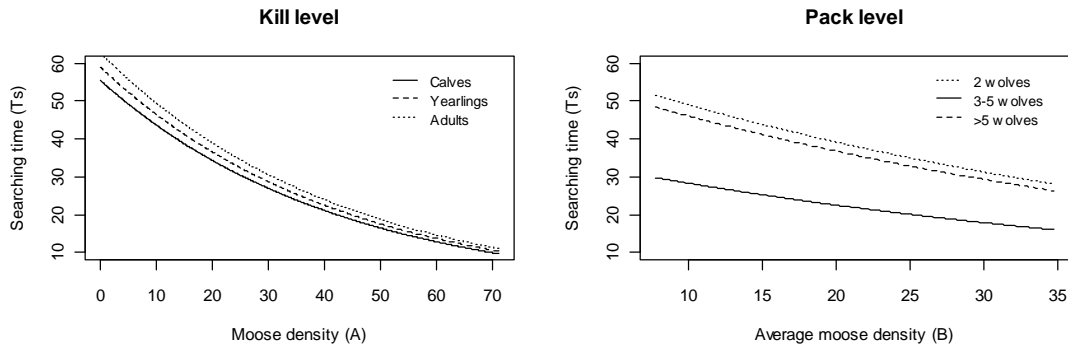

Figure 5. Functional response of back transformed selected models at kill level and pack level for T_s searching time. Influence of explanatory variables: (A) moose density (no moose/10 km^2), prey age: calves (<1 year), yearlings (1year) and adult (≥2 year), (B) average moose density (no moose/10 km^2), pack size as number of wolves in the pack: 2 wolves, 3-5 wolves and >5 wolves. All models predictors reported are estimated with Step length based method.
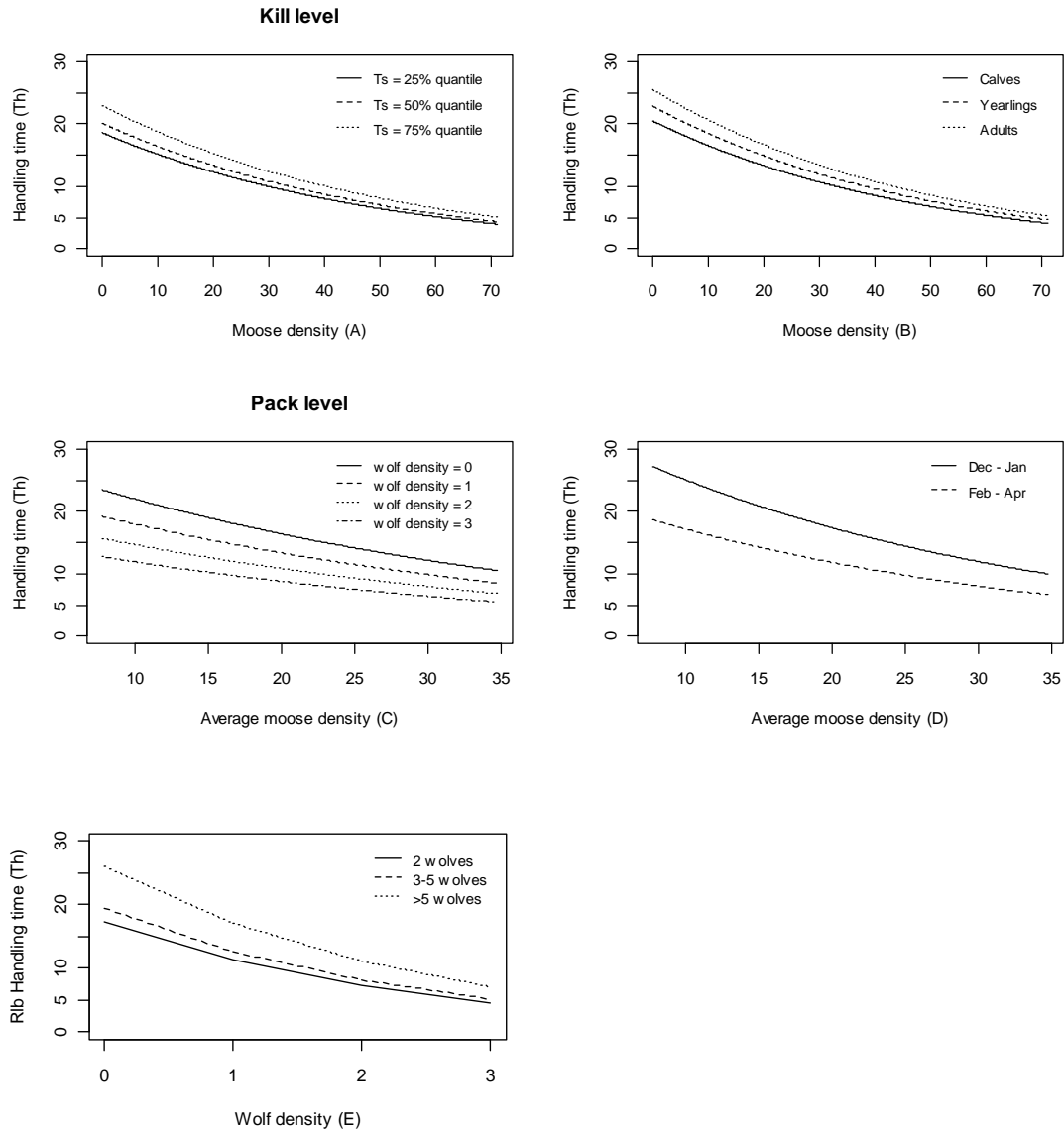
Figure 6. Functional response of back transformed selected models at kill level and pack level for T_h handling time. All model predictors reported are estimated with Step length based method except for figure 6E which is estimated with Radius length based method (Rlb). Influence of explanatory variables: (A) moose density (no moose/10 km^2) and T_s where T_s is used as explanatory variable expressed respectively with the 25, 50, 75 % of the predictor quartile, (B) prey age: calves (<1 year), yearlings (1year) and adult ($\geq$2 year), average moose density (no moose/10 km^2), (C) wolf density (number of wolves home-ranges) surrounding the pack, (D) average moose density and winter period (early Dec - Jan and late Feb - Apr winter) and (E) pack size as number of wolves in the pack: 2 wolves, 3-5 wolves and >5 wolves.

Discussion

This study produced three main results that significantly contribute to our understanding of the mechanisms of predation influencing wolf winter kill rates on moose in Scandinavia.

First, the number of studied packs in different years and the large number of total predation events analysed improves the inference made at the population level giving a robust description of wolf activity patterns of the Scandinavian wolf population. Second, in a strictly methodological perspective, this study evaluates the influence of different methods on time budgets of T_s and T_h and their relative contribution to predation functional response as suggested in Merrill et al. (2010). This study improves the understanding of the predator effects on shaping prey population due to the size and precision of GPS wolf predation events documented over a decade. Third, it highlights, at a finer spatial and temporal scale, how the combination of prey density, wolf-related or other prey related factors interact to explain complex mechanisms of predation in a multi-scale perspective. This study directly confirms the multi-causality of variation in kill rates suggested by Sand et al. (2012) and the effectiveness of studies based on discrete movement paths suggested in Merrill et al. (2010), McPhee et al. (2012) and DeCesare (2012).

Estimates of predation behaviour such as T_s, T_h, K_e and IKI, confirmed the high moose kill rates shown in the Scandinavian wolf population (Sand et al. 2012). Searching time mean value was almost half of the time to kill (126.2 ± 18.46 h) reported for large prey in McPhee et al. (2012) in Alberta study. Handling time showed values close to an average of the 30 hours reported in Sand et al. (2005). The lower values of handling time found in my study is in line with the 75% of the total wolf time budget spent far away from the kill-sites confirming similar kill-site behaviour as described in Sand et al. (2005). Similar to Zimmermann et al. (2007), wolves spent 61 % of their time budget in a low activity mode (0-200m), thus indicating that 53% of the total cluster set were at bed sites. The time of death for moose, (mainly during night time), combined with wolf activity patterns and the consistent distance of wolves away from the kill-site, reflect a behavioural pattern similar to populations of southern Europe who have been exposed to a high degree of human disturbance (Vilà et al. 1995, Ciucci et al.1997).

Even if the precision of GPS wolf datasets can in detail describe discrete behavioural patterns, the number of locations for every pack and the number of packs are essential for inferences at the population level (Hebblewhite and Haydon, 2010). Furthermore, using 1 hour fix interval and 200m cluster radius were sufficient to locate the 87 % of carcass potentially detected and the intensive field work included in the location survey protocol can significantly reduce missing moose carcasses (Sand et al. 2005) and generally improve detection of all prey killed (Webb et al. 2008). However, this approach can produce an underestimation of wolf movement especially when movements are measured using an Euclidean distance between consecutives locations and when movements are of a non-linear type of hunting path (Mills et al. 2006). For this reason, it is strongly suggested to use a fix interval of ≤ 30min interval to improve predation event movement accuracy (Mills et al. 2006, Zimmermann, et al. 2007), and implemented with activity sensor GPS data (Cagnacci, et al. 2010) to enhance T_s and T_h estimates.

The statistical difference between Slb and Rlb methods in terms of time budgets with the 13% percent of total locations differently allocated to T_s and T_h and the different results reported for T_h model selection, demonstrate the strong impact of assumptions based on

movement rules as suggested in Merrill et al. (2010). Moreover, this suggests that the different methods can result in variable effect sizes for single predictor variables.

This is the first time that different approaches to estimate T_s and T_h are compared. However, both methods showed a relatively low R^2, which likely is a result of model set design and the exclusion of landscape variables (Gorini et al. 2011). Habitat heterogeneity can reduce the proportion of prey accessible to predator and so affect kill rates. If this is not accounted for the results may have some source of bias (Nachmann, 2006).

This study showed that both T_s and T_h were negatively related to moose density at two functional scales and confirmed the violation of independency for searching time and handling time reported by Abrams (1990). T_s has a similar relationship with time to kill (T_k) as shown in Merrill (2010) and McPhee (2012) from reviewing of the Holling's (1959) disk equation (Figure 5A, B). In those studies, the search for prey takes longer time at a low prey density along the hunting path. Those studies also confirmed the hypothesis that an increase in prey density is directly related with prey encounter rate (Hebblewhite et al. 2005 Merrill et al. 2010, McPhee et al. 2012).

Here I demonstrate how T_h is negatively related to moose density while it is positively related to (Ts) searching time (Figure 6A). High moose density at kill sites can indirectly influence encounter rates with other potential moose prey (McPhee, et al. 2012). This factor combined with winter moose habitat selection based on migration in winter browsing ranges (Gundersen, et al. 2004) and the lack of moose response to wolf predation risk area (Milleret, 2012), may trigger predation behaviour of surplus killing (DelGiudice, et al. 1998). Therefore, this could disturb the handling of the present kill. In addition, it could also increase encounters with other potential prey and so to produce an overlap of T_s and T_h behaviour. Moreover, human disturbance can be an additional relevant stochastic factor explaining the short time spent at a kill site by wolves (Sand, et al. 2005) and may displace large carnivores so that they reduce their home range overlap with prey (Muhly, et al. 2011). Handling time response to Ts at constant moose density, (Figure 6A) can be explained by the proportional relationship between time to kill and prey size shown by small and large prey in a multi-prey system (McPhee et al. 2012).

The winter period was only important for the Slb T_h model sets. This relationship suggests that the influence of winter severity is stronger during the later part of the predation study period (Hebblewhite 2005) or indirectly on wolf behaviour due to intra-pack wolf interactions i.e., pack breeding season (Harrington and Mech 1979).

The effect of prey age on T_s and T_h confirms the important role of prey population age structure to shape predation dynamics (Sand, et al. 2012). The significant difference of T_s estimates between predation events with calves and yearlings compared with adult moose kills, may further contribute to the wolf preference for calves in the Scandinavian wolf population (Sand et al. 2005). Moreover a longer T_h for adult moose kills, confirms the relation between T_h and body size of the prey.

Pack size interactions with T_s (Figure 5C), contrasts with Sand et al. (2006) who found that group size did not influence hunting success. MacNulty et al. (2011) found no group size effect on time to complete the predatory task. These contradictory findings could be a result of the different spatial scales used for the analysis and therefore, medium-pack size could indirectly reduce the encounter rate more than the hunting success and so indirectly reduce T_s in terms of the time budget.

Wolf density was negatively related to T_h (Figure 6C, E), but was not selected as significant variable for T_s. Moreover, the effect size of this variable on T_h was dependent on the method used (Table 5). This result suggests an influence of territoriality between neighbouring packs on behaviour time budget. Pack territoriality can be a cause of wolf mortality (Packard, 2003) when intra-pack interactions occur in overlap zones of different neighbouring packs (Mech and Boitani, 2003). Moreover, territorial behaviour can be relevant during pack breeding season (Harrington and Mech 1979) having a role in the behavioural time budget. In particular, the model selected using the Rlb method to estimate T_h (Figure 6, F), suggests an interaction between wolf density and pack size, i.e., pairs can have a different territorial behaviour compared to larger packs and so change their behaviour around kill-sites in order to reduce interactions with other packs.

Conclusions

The advent and development of GPS technology improve the understanding of the mechanisms and scales important to study animal behaviour (Morales, et al. 2010, Cagnacci, et al. 2010, Merrill et al 2010). The availability of long terms datasets based on GPS data facilitates spatiotemporal analyses of movements (Nathan, et al. 2008, Cagnacci et al. 2010) and the ability to investigate mechanisms of predation. The spatial and temporal scale of analysis used could mask different environmental factors directly correlated with moose density not tested at this functional level. Moreover, the confounding or conflicting results could be influenced by behavioural alteration of wolves during breeding season, i. e., packs hunting behaviour can change due to influence of the alpha couple breeding season in the second part of the winter.

My analysis does not include environmental or habitat variables. I suggest future analysis include kill-site habitat descriptions to decompose factors affecting attack efficiency rates and prey vulnerability as reported in DeCesare (2012). Moreover, future studies should consider that wolves may not increase search rates to compensate for low prey density as reported in McPhee (2012). In a future research perspective, I suggest to decompose searching time and handling time in more specific nested behaviour and relate them with predator-prey specific habitat heterogeneity variables including secondary prey kills. Finally, an improvement of knowledge on territorial wolf behaviour and intra-pack aggregation dynamics could improve our understanding of the mechanisms important for territoriality and its influence on wolf predatory behaviour.

This study reports the complexity of the mechanisms and the validity of individual based movement studies to explain variation in wolf winter movement and kill-rates. Additionally, this study highlights the influence of decision rules that define spatial behaviours and the resulting influence on functional response.

Acknowledgements

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Appendix

Appendix1. AICc and AICc weight values of all models used at kill level. Response variables: T_s=*searching time*, T_h=*handling time*. Independent variable: Pa=*Prey age*, Md=*moose density at the kill-site*, Wp= *winter period*, Amd= *Average moose density in the pack home range*, Wd= *wolf densities-number of packs surrounding the considered one*, Pz=*Pack size*, Ts=*Searching time as independent variable.*

Kill Level Models

Ts-Step length based	AICc	AICc weight
Md+(1|Territory)	649.28	0.63
Pa+Md+(1|Territory)	651.21	0.24
Pa+Md+Pa*Md+(1|Territory)	653.26	0.09
1+(1|Territory)	655.62	0.03
Pa+(1|Territory)	656.95	0.01
Ts-Radius length based		
Md+(1|Territory)	619.22	0.63
Pa+Md+(1|Territory)	621.33	0.22
Pa+Md+Pa*Md+(1|Territory)	622.54	0.12
1+(1|Territory)	626.71	0.01
Pa+(1|Territory)	628.40	0.01
Th-Step length based		
Ts1+Md+(1|Territory)	584.89	0.32
Ts1+Md+Ts1*Md+(1|Territory)	586.18	0.17
Md+(1|Territory)	586.19	0.16
Pa+Md+Ts1+(1|Territory)	586.39	0.15
Pa+Md+Pa*Md+(1|Territory)	587.45	0.09
Pa+Md+(1|Territory)	587.54	0.08
Ts1+Pa+Ts1*Pa+(1|Territory)	591.37	0.01
Ts1+(1|Territory)	591.79	0.01
Ts1+Pa+(1|Territory)	592.34	0.01
1+(1|Territory)	595.20	0.00
Pa+(1|Territory)	595.22	0.00
Th -Radius length based		
Ts1+Md+Ts1*Md+(1|Territory)	571.91	0.38
Ts1+Md+(1|Territory)	573.60	0.16
Md+(1|Territory)	574.09	0.13
Pa+Md+Pa*Md+(1|Territory)	574.23	0.12
Pa+Md+Ts1+(1|Territory)	574.77	0.09
Pa+Md+(1|Territory)	575.25	0.07
Ts1+Pa+(1|Territory)	578.47	0.01
Ts1+Pa+Ts1*Pa+(1|Territory)	578.89	0.01
Ts1+(1|Territory)	579.11	0.01
Pa+(1|Territory)	581.17	0.00
1+(1|Territory)	582.29	0.00

Appendix 2. AICc and AICc weight values of all T_s and T_h models used at pack level

Pack Level Models

Ts-Step length based	AICc	AICc weight
Pz+Amd+Pz*Amd+(1|Territory)	650.33	0.63
Wd+(1|Territory)	655.34	0.05
Wd+Pz+(1|Territory)	655.57	0.05
1+(1|Territory)	655.62	0.05
Ws+(1|Territory)	656.63	0.03
Wd+Ws+(1|Territory)	656.83	0.02
Amd+(1|Territory)	657.09	0.02
Wd+Ws+Pz+(1|Territory)	657.37	0.02
Wd+Amd+(1|Territory)	657.42	0.02
Pz+(1|Territory)	657.56	0.02
Wd+Pz+Amd+(1|Territory)	657.70	0.02
Ws+Amd+(1|Territory)	658.32	0.01
Pz+Amd+(1|Territory)	658.68	0.01
Wd+Pz+Wd*Pz+(1|Territory)	658.68	0.01
Ws+Pz+(1|Territory)	658.74	0.01
Wd+Ws+Wd*Ws+(1|Territory)	658.83	0.01
Wd+Ws+Amd+(1|Territory)	658.95	0.01
Wd+Amd+Wd*Amd+(1|Territory)	659.07	0.01
Ws+Amd+Ws*Amd+(1|Territory)	659.39	0.01
Ws+Pz+Amd+(1|Territory)	660.07	0.00
Ws+Pz+Ws*Pz+(1|Territory)	661.20	0.00

Ts-Radius length based		
Pz+Amd+Pz*Amd+(1|Territory)	621.94	0.51
Ws+(1|Territory)	626.34	0.06
Wd+Pz+(1|Territory)	626.40	0.05
Wd+(1|Territory)	626.58	0.05
1+(1|Territory)	626.71	0.05
Wd+Ws+(1|Territory)	626.87	0.04
Wd+Ws+Pz+(1|Territory)	627.50	0.03
Ws+Pz+(1|Territory)	628.05	0.02
Ws+Amd+(1|Territory)	628.28	0.02
Amd+(1|Territory)	628.38	0.02
Pz+(1|Territory)	628.43	0.02
Wd+Pz+Amd+(1|Territory)	628.56	0.02
Wd+Amd+(1|Territory)	628.69	0.02
Wd+Pz+Wd*Pz+(1|Territory)	628.99	0.01
Wd+Ws+Amd+(1|Territory)	629.00	0.01
Wd+Ws+Wd*Ws+(1|Territory)	629.01	0.01
Ws+Pz+Amd+(1|Territory)	629.59	0.01
Pz+Amd+(1|Territory)	629.66	0.01
Ws+Amd+Ws*Amd+(1|Territory)	629.80	0.01
Wd+Amd+Wd*Amd+(1|Territory)	630.45	0.01
Ws+Pz+Ws*Pz+(1|Territory)	630.52	0.01

Pack Level Models

Th-Step length based	AICc	AICc weight
Amd+(1|Territory)	591.62	0.18
Wd+Amd+(1|Territory)	591.82	0.16
Ws+Amd+(1|Territory)	592.85	0.10
Wd+Ws+Amd+(1|Territory)	593.13	0.08
Wd+(1|Territory)	593.13	0.08
Wd+Amd+Wd*Amd+(1|Territory)	593.76	0.06
Wd+Ws+(1|Territory)	594.27	0.05
Pz+Amd+(1|Territory)	594.31	0.05
Wd+Ws+Wd*Ws+(1|Territory)	594.81	0.04
Ws+Amd+Ws*Amd+(1|Territory)	594.95	0.03
Wd+Pz+Amd+(1|Territory)	595.18	0.03
1+(1|Territory)	595.20	0.03
Ws+Pz+Amd+(1|Territory)	595.20	0.03
Pz+Amd+Pz*Amd+(1|Territory)	595.47	0.03
Ws+(1|Territory)	595.88	0.02
Wd+Pz+(1|Territory)	597.32	0.01
Wd+Ws+Pz+(1|Territory)	598.55	0.01
Pz+(1|Territory)	599.36	0.00
Wd+Pz+Wd*Pz+(1|Territory)	600.16	0.00
Ws+Pz+(1|Territory)	600.36	0.00
Ws+Pz+Ws*Pz+(1|Territory)	601.21	0.00

Th-Radius length based		
Wd+Amd+(1|Territory)	573.80	0.21
Wd+(1|Territory)	574.45	0.15
Wd+Pz+(1|Territory)	575.09	0.11
Wd+Amd+Wd*Amd+(1|Territory)	575.28	0.10
Wd+Ws+Amd+(1|Territory)	575.46	0.09
Wd+Ws+(1|Territory)	575.98	0.07
Wd+Pz+Amd+(1|Territory)	576.22	0.06
Wd+Ws+Pz+(1|Territory)	576.83	0.05
Amd+(1|Territory)	576.93	0.04
Wd+Pz+Wd*Pz+(1|Territory)	577.71	0.03
Wd+Ws+Wd*Ws+(1|Territory)	577.75	0.03
Ws+Amd+Ws*Amd+(1|Territory)	578.53	0.02
Pz+Amd+(1|Territory)	580.86	0.01
Ws+Pz+Amd+(1|Territory)	581.71	0.00
Pz+Amd+Pz*Amd+(1|Territory)	581.97	0.00
1+(1|Territory)	582.29	0.00
Ws+(1|Territory)	582.47	0.00
Ws+Pz+(1|Territory)	584.60	0.00
Pz+(1|Territory)	584.64	0.00
Ws+Pz+Ws*Pz+(1|Territory)	585.95	0.00
Ws+Amd+(1|Territory)	592.85	0.00

SENASTE UTGIVNA NUMMER

2013:3 Predicting spawning bed erosion and longevity: a case study in tributaries to river Vindelälven, northern Sweden.
Författare: Viktor Tylstedt

2013:4 Passage efficiency and migration behavior for adult Atlantic salmon at a Half-Ice Harbor fish ladder.
Författare: Robert Karlsson

2013:5 Will Atlantic salmon (Salmo salar L.) colonize restored tributaries in the river Vindelälven, northern Sweden?
Författare: Erik Mellgren

2013:6 The influence of forestry stands treatments on brown bears (*Ursus arctos*) habitat selection in Sweden – an option for Alberta forestry?
Författare: Anna Maria Petré

2013:7 The effects of Gotland pony grazing on forest composition and structure in Lojsta hed, south eastern Sweden.
Författare: Emma Andersson

2013:8 Social and economic consequences of wolf (Canis lupus) establishments in Sweden.
Författare: Emma Kvastegård

2013:9 Manipulations of feed ration and rearing density: effects on river migration performance of Atlantic salmon smolt.
Författare: Mansour Royan

2013:10 Winter feeding site choice of ungulates in relation to food quality.
Författare: Philipp Otto

2013:11 Tidningen Dagens Nyheters uppfattning om vildsvinen (Sus scrofa)? – En innehålls-analys av en rikstäckande nyhetstidning.
Författare: Mariellé Månsson

2013:12 Effects of African elephant (*Loxodonta africana*) on forage opportunities for local ungulates through pushing over trees.
Författare: Janson Wong

2013:13 Relationship between moose (*Alces alces*) home range size and crossing wildlife fences.
Författare: Jerk Sjöberg

2013:14 Effekt av habitat på täthetsdynamik mellan stensimpa och ung öring I svenska vattendrag.
Författare: Olof Tellström

2013:15 Effects of brown bear (*Ursus arctos*) odour on the patch choice and behaviour of different ungulate species.
Författare: Sonja Noell