Hedmark University College

Faculty of Applied Ecology and Agricultural Sciences

Barbara Zimmermann

PhD-thesis

Predatory behaviour of wolves in Scandinavia

PhD in Applied Ecology

2014

Samtykker til utlån hos høgskolebiblioteket   JA ☒   NEI ☐

Samtykker til tilgjengeliggjøring i digitalt arkiv Brage   JA ☒   NEI ☐

Ola Jons GPS-cluster song: Barbra

Ref.: Barbra Zimmermann
Kom og ta meg i land
Barbra

Barbra, du gir meg cluster
Men jeg vet ikke hvor de er
I Afghanistan?
Jeg sliter.

Ref.

Barbra har gitt meg cluster
Men jeg ser ikke skog for trær
Nå vil jeg hjem igjen
Jeg sliter.

Ref.

Barbra, du har meg godt på gli
Koordinat i Afghanistan
Det kan bli tungt på ski
Til Afghanistan.

Ref.

Front page illustration: Sari Elena Dötterer

Preface

Wolves engage. They engage because they kill. Not just tiny prey, but animals ten times their own size. They engage because they live in strong family bonds. They engage because they remind us of our best friend, the dog, and of scary fairytales about piglets, goat kids and red riding hood. They engage because they have become a symbol for wilderness, devastation, power and politics all at that same time. My engagement towards the wolf is through research, and I feel much privileged to have been given the opportunity to work with wild wolves.

I deeply acknowledge Petter Wabakken who introduced me to the world of wolves in the Scandinavian environment, the human dimension of large carnivore recovery, and to magnificent Evenstad. Thank you for giving me so much trust and pushing me forward! I am looking forward to working with you for many years to come! I am also deeply indebted to Håkan Sand, my external supervisor at Grimsö who has been so patient with me, and who was always helpful and responded quickly when I needed some advice. Wonderful comments to manuscripts and always a good smile! Håkan and Petter are two of the heads behind the Scandinavian Wolf Research Project SKANDULV, so was Hans Christian Pedersen of NINA for many years, and the head of the heads has for all those years been Olof Liberg, now replaced by Johan Månsson. Camilla Wikenros did her excellent PhD-thesis with SKANDULV. Thank you all for inspiring meetings and feedback!

Harry Andreassen, my internal supervisor for the last two years, my boss and Dean of Evenstad, made my dreams come true: To get a position at the truly best place on Earth, to work with whatever I like to do, to finish up this thesis and defend it at Evenstad, and to visit the amazing ecosystem of the Chobe River in Botswana. Harry is the key to the incredible development of Evenstad during the past 12 years. Harry, I am so deeply indebted to you for all you have done for me and the environment at Evenstad. You are just amazing! I also want to thank Torstein Storaas for giving me the opportunity to do a PhD at Evenstad and to become a member of the moose team a long time back. The wolves tore me off, sorry! Although Harry is the head of Evenstad, you are the soul: always positive and creative! Many thanks also to all my friends and colleagues at Evenstad - you are just such great people!

Contents

Abstract

The study of predatory behaviour is essential for understanding the interactions that may affect the behaviour and population dynamics of the species involved and consequent cascading ecosystem effects. In the case of large carnivores feeding on large ungulate prey, predation is strongly impacted by humans who alter the habitat of both predators and their prey, control population sizes, and compete with large carnivores for the same prey species.

The objectives of this thesis were to 1) establish a robust method to estimate kill rates of wolves (*Canis lupus*); 2) estimate kill rates during both summer and winter; 3) relate kill rates to prey availability in winter (functional response) and to the energetic requirements of the wolf packs; and 4) to study the impact of roads on predatory and other behaviour of wolves. To meet these objectives, the Scandinavian Wolf Research Project (SKANDULV) fitted wolves with Global Positioning System (GPS) collars and searched for kill remains on clusters of GPS-positions during defined time periods in winter and summer. Winter prey densities of cervids were assessed by spring counts of faecal pellet groups.

High variation in the spatio-temporal movement pattern of wolves in relation to kill sites made it difficult to predictably identify kill sites along the wolf trajectory without fieldwork. Consequently, field personnel checked all clusters, and in addition some single positions, to obtain robust estimates of kill rate. Human disturbance at kill sites may be one possible reason for the high variation in the handling of kills, with a relatively short handling time associated with kills located in areas with a high potential for human disturbance. During summer, wolves preferred to be at intermediate distances to roads while handling prey. This was probably the result of a trade-off between avoidance of human presence and the preference for roads while traveling.

In most wolf territories, moose (*Alces alces*) was the pre-dominant prey species during both summer and winter. Kill rates, measured as the acquired edible biomass per pack, did not differ between summer (mean $\pm$ SE = 24.0 $\pm$ 3.0 kg/day/pack) and winter (28.2 $\pm$ 2.3 kg/day/pack), but wolves killed twice as many moose per unit time in summer (0.60 $\pm$ 0.05 moose/day/pack) as during winter (0.31 $\pm$ 0.04 moose/day/pack). This difference occurred because wolves selected for moose calves and in summer these provided significantly less biomass per moose kill than in winter. In both seasons, per capita kill rates were negatively

associated with wolf pack size. This negative association, combined with a positive association between kill rate and prey availability, resulted in a predator-dependent functional response in winter. Small wolf packs (2 – 4 wolves) acquired more than three times as much biomass as required to cover the energetic needs of the pack, while large packs (7 – 9 wolves) in territories with low to intermediate prey abundance seemed to be food-limited during winter.

The average annual kill rate was estimated at 120 moose per wolf pack (95% CI 100 – 144) in territories where moose accounted for the majority of the kills. Predation rates during winter, i.e. the proportion of the moose population killed by predators, were not related to wolf pack size or kill rates, but were negatively correlated with the abundance of moose or the moose-to-wolf ratio within the wolf territory. Wolves did not regulate, but rather limited, the highly managed moose population in Scandinavia, with wolf-induced mortality being mainly additive to other sources of mortality. If the wolf population is to be controlled as a measure to reduce predation on moose, the removal of non-breeding pairs and small family groups will likely have a stronger effect on moose kill rates than a reduction in the number of wolves in larger packs.

Author's address: Barbara Zimmermann, Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, N-2480 Koppang, Norway.

E-mail: barbara.zimmermann@hihm.no

Sammendrag (Norwegian summary)

Gjennom predasjon påvirker rovdyr og byttedyr hverandres atferd og populasjonsdynamikk, noe som kan føre til kaskadeeffekter i økologiske samfunn. Studien av rovdyrenes predasjonsatferd er viktig for å kunne forstå interaksjoner mellom ulike arter. Hos store rovdyr som lever av store byttedyr er predasjon sterkt påvirket av menneskene gjennom habitatsforandringer, målrettet artsforvaltning og konkurranse med rovdyrene om felles byttedyr.

Målsetningene med denne avhandlingen var å 1) utarbeide en robust metode for estimering av drapsrate hos ulv (*Canis lupus*); 2) estimere drapsrater for både vinter og sommer; 3) relatere drapsratene til tilgang til byttedyr vinterstid (funksjonell respons) og til ulvenes energibehov; og 4) studere effekten av veier på predasjonsatferd og annen atferd hos ulv. Det Skandinaviske Ulveforskningsprosjektet SKANDULV har for dette formålet merket ulv med GPS-halsbånd. Områder med flere GPS-posisjoner (cluster) ble oppsøkt i felt for å lete etter ulvedrepte byttedyr i løpet av en avgrenset studieperiode. Vintertetthet av hjortevilt i ulverevir ble estimert ved hjelp av møkktellinger om våren.

Ulvenes forflytningsmønster rundt drapsstedene varierte mye i tid og rom, og det var derfor vanskelig å estimere antall ulvedrepte byttedyr kun basert på ulvenes forflytninger, uten å kombinere det med feltarbeid. For å oppnå et robust estimat av drapsraten ble derfor alle GPS-clustere og i tillegg en del enkeltpunkter sjekket i felt. Menneskelig forstyrrelse kan ha vært en av årsakene til den store variasjonen i ulvenes forflytningsmønster, med kortere håndteringstid av kadavre som var plassert i områder med høy risiko for menneskelig forstyrrelse. Sommerstid foretrakk ulvene mellomstore avstander til nærmeste vei når de håndterte bytte. Dette var sannsynligvis et resultat av en avveining mellom å unngå mennesker og å bruke veier for effektiv forflytning.

I de fleste ulverevir dominerte elg (*Alces alces*) som byttedyr både om sommeren og vinterstid. Drapsratene målt som spiselig biomasse per flokk var sammenlignbare for sommer (gjennomsnitt ± standardfeil = 24.0 ± 3.0 kg/døgn/ulveflokk) og vinter (28.2 ± 2.3 kg/døgn/flokk), men ulvene drepte dobbelt så mange elger per tidsenhet om sommeren (0.60 ± 0.05 elg/døgn/flokk) som om vinteren (0.31 ± 0.04 elg/døgn/flokk). Denne forskjellen var et resultat av at ulvene foretrakk å drepe elgkalver, og at biomassen til kalvene var atskillig

mindre om sommeren enn vinterstid. I begge sesongene var det en negativ sammenheng mellom antall byttedyr drept per døgn per ulv (per capita drapsrate) og ulvenes flokkstørrelse. Denne negative sammenhengen kombinert med en positiv sammenheng mellom drapsrate og byttedyrtilgang resulterte i en predator-avhengig funksjonell respons. Små ulveflokker (2 – 4 ulver) la ned tre ganger så mye biomasse som deres energibehov skulle tilsi, mens store flokker (7 – 9 ulver) i ulverevir med lav til mellomstor byttedyrtilgang holdt seg under den samlete flokkens energibehov.

Den årlige drapsraten ble estimert til 120 elger per ulveflokk i ulverevir der elg var hovedføde (95% konfidensintervall 100 – 144 elger). Andelen av elgbestanden i et ulverevir som blir drept av ulv kalles predasjonsrate. Det var ingen sammenheng mellom predasjonsraten vinterstid og ulveflokkenes størrelse eller drapsraten, men det var en negativ sammenheng mellom predasjonsraten og antallet elg i ulverevir, eller antallet elg per ulv. Elgbestanden i Skandinavia er regulert gjennom målrettet forvaltning, og ulven er heller en limiterende enn en regulerende faktor for elgbestanden. Ulvepredasjon er hovedsakelig additiv til annen dødelighet hos elg. Hvis ulvebestanden skal begrenses for å redusere predasjon på elg, kan uttak av ulvepar og små flokker gi en større effekt på drapsraten enn en reduksjon av antall ulver i store flokker.

List of publications

Paper 1: Zimmermann, B., Wabakken, P., Sand, H., Pedersen, H.C. & Liberg, O. (2007) Wolf movement patterns: a key to estimation of kill rates? *Journal of Wildlife Management*, **71**, 1177-1182.

Paper 2: Sand, H., Wabakken, P., **Zimmermann, B**., Johansson, Ö., Pedersen, H.C. & Liberg, O. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia,* **156**, 53-64.

Paper 3: Zimmermann, B., Taylor, L., Wabakken, P., Sand, H. & Liberg, O. Behavioral response of wolves to roads: Scale-dependent ambivalence. Submitted.

Paper 4: Zimmermann, B., Sand, H., Wabakken, P., Liberg, O. & Andreassen, H.P. Predator-dependent functional response in wolves: from food limitation to surplus killing. Submitted.

1. Introduction

1.1 Theoretical aspects of predatory behaviour

1.1.1 Predation – a species interaction

Predation is the process whereby consumers of one species consume all or part of individuals of another species (Krebs 2009). Herbivorous animals eating plants, parasites living on their hosts, omnivorous animals feeding on carrion, birds picking seeds, and carnivorous animals killing and feeding on prey species can all be called predators in the broadest sense. However, in the following I will define predation as the process whereby animals *kill* their prey to consume it and just include the latter example of predators, i.e. the carnivorous animals (Abrams 2000). This form of species interaction has important consequences as: 1) It triggers specific behaviours and can act as a selective force of specific traits of predators and prey to accomplish or avoid predation (Abrams 2000); 2) It can affect the distribution and abundance of populations and is therefore an important driver of population dynamics of both predator and prey (Lotka 1925; Volterra 1926); and 3) It can affect ecosystem dynamics and biodiversity through cascading effects, intra-guild predation, and through releasing or enforcing interspecific competition (Holt & Polis 1997; Chase *et al.* 2002).

To avoid being killed by a predator, and to improve the ability to search and kill prey, prey and predator species respectively have developed specific traits and continuously do so (Abrams 2000). Many of these traits are physical characteristics of the body, e.g. size, shape, muscles, teeth, coloration, or physiological adaptations. But the behaviour of predators and prey species has also been shaped by the selective force of predation.

As a prey animal can lose its life in an attack, while a predator just misses one meal if not successful, predation exerts a stronger selective force on the behavioural traits of prey species than on predatory species (Dawkins & Krebs 1979). Prey species have developed a broad array of anti-predator behaviours (Lima & Dill 1990), for example hiding, grouping, vigilance, defence, escape, and avoidance of habitats or periods of high predation risks. The energy allocated to these behavioural responses comes at the cost of body growth, survival and reproduction. The stress connected to the perceived risk of predation can alone be enough to constrain reproduction and survival in prey (Boonstra *et al.* 1998; Sheriff, Krebs

& Boonstra 2009). Direct mortality and the non-consumptive costs of predation mean predation is a limiting factor for prey populations, as has been demonstrated by many predator-manipulation experiments (Salo *et al.* 2010).

1.1.2 Functional and numerical response

Not only does the prey respond to the predator; the predator can also functionally respond to changes in prey densities. Predators can change the per capita kill rate, i.e. the number of prey animals killed per predator per unit time, by reducing the time allocated to find and handle prey as prey availability changes. The functional response of predators to prey was an essential element in the development of the Lotka-Volterra-model of predator-prey interactions (Lotka 1925; Volterra 1926). It has since undergone some modifications in theoretical ecology. In most predator-prey systems a linear relation between per capita kill rate and prey density (type I functional response) seems unreasonable because prey handling will always take some time, even at excessively high prey densities. An asymptotic response (type II response) showing predator satiation at high prey densities is more realistic (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 abundant refuges, at low prey density (Holling 1959a). In more recent models, per capita kill rates are related to prey-to-predator ratios, i.e. the per capita prey availability (Arditi & Ginzburg 1989; Berryman 1992). Predator-dependent models assume a negative correlation between per capita kill rates and predator density due to interference competition between predators or the prey being more alert at higher predator densities (Hassell & Varley 1969; Beddington 1975; DeAngelis, Goldstein & O'Neill 1975; Crowley & Martin 1989; Skalski & Gilliam 2001).

The numerical response of a predator is the change in predator abundance as prey availability changes (Holling 1959a). Daily access to food directly affects body growth, survival and reproduction of the predator. As for functional response models, the relationship between predator and prey abundance can be linear (type I), asymptotic (type II), or sigmoid (type III). The product of the numerical and the functional response is the total response of the predator population to its prey, i.e. the relationship between the total number of prey animals killed per time unit and prey density or abundance (Boyce 2000). This total response, divided by the population size of the prey, describes the density-dependent nature of the predation rate, i.e. the relationship between the proportion of the prey population that

is killed by predators per time unit and prey population size. If the predation rate is positively density-dependent, i.e. predation rate will increase with prey density, predation will be a regulating factor because prey numbers will be regulated by predation within a given range. In contrast, if predation rate is inversely density-dependent, predation rates are said to be depensatory, i.e. the predators will extirpate the prey population at low prey density, but will have only a minor limiting effect at high prey densities.

1.1.3 Predation in a multi-prey, multi-predator, heterogeneous, and anthropogenic landscape

Predation is a complex process, and we cannot study predation without taking into account other processes that may interact with it (DeWitt & Langerhans 2003). A food web usually consists of multiple prey and predator species at different trophic levels, some of them generalists, others specialists. Even within the same species, there can be individual or age- and sex-specific variation in predatory and anti-predator behaviour (DiRienzo, Pruitt & Hedrick 2013), and therefore, simple one-predator-one-prey models are often too simplistic (Sih, Englund & Wooster 1998). Intraguild prey and predators interact in complex, intra- and interspecific processes that may change with resource productivity (Amarasekare 2007) and along other environmental gradients.

Contrary to experimental settings, natural environments are heterogeneous. Prey vulnerability and the risk of predation may both vary, depending on the type of habitat (Gervasi et al. 2013), the degree of habitat fragmentation, and the form and size of habitat patches. In a review on predation and habitat heterogeneity (Gorini et al. 2012), the authors emphasize the need to analyze the different stages of predation (search, encounter, kill, and consume prey), and to work at multiple spatial scales, to understand the effect of habitat on predator-prey dynamics. The most pronounced habitat changes during the past centuries are man-made. Habitat loss, fragmentation by roads and power lines, habitat deterioration and enrichment can all affect predator-prey dynamics (Ryall & Fahrig 2006) and have triggered a broad set of conservation-oriented studies. The classical edge-effect studies, for example, look at kill- or predation rates along a spatial gradient across edge habitats. The results of these studies are, however, inconsistent (Lahti 2001; Vetter, Rücker & Storch 2013).

Not only do humans change habitat, we also impact predator-prey dynamics directly by 1) manipulating both predator and prey population numbers, legally or illegally (Jackson et al.

2001; Pauly *et al.* 2002; Packer *et al.* 2009; Liberg *et al.* 2012); 2) changing geographic distributions with local extirpation and introduction of predator and prey species (Berger *et al.* 2001; Kats & Ferrer 2003); and 3) performing selective harvesting of individuals with specific traits (Milner, Nilsen & Andreassen 2007; Allendorf *et al.* 2008; Darimont *et al.* 2009; Ciuti *et al.* 2012). Therefore, humans may play a key role in shaping the patterns of predator-prey interactions in many ecosystems.

1.2 The wolf (*Canis lupus*): a group-living apex predator

Within its geographical distribution, covering large parts of the Northern hemisphere, wolves inhabit a wide variety of habitats with a range of prey species available. Being a generalist apex predator, wolves prey mainly on large and intermediate-sized ungulates available in a given area (Okarma 1995; Peterson & Ciucci 2003). Wolves are socially organized in packs which usually consist of the adult breeding pair and their offspring, i.e. a family group (Mech & Boitani 2003). The pack roams in approximately the same territory from year to year, and scent-marks of the monogamous breeding pair serve to indicate territory borders. Pups commonly disperse at the age of 1-3 years. Early ideas on group formation and sociality in carnivores suggested that cooperative hunting was a means to increase food acquisition, and predicted per capita kill rates to increase with predator group size (Murie 1944; Nudds 1978). However, there is now much evidence that per capita kill rates in wolves decrease with increasing pack size (Thurber & Peterson 1993; Dale, Adams & Bowyer 1994; Hayes & Harestad 2000a), and that the proportion of successful attacks on moose (*Alces alces*) does not correlate with pack size for wolves in Scandinavia (Sand *et al.* 2006b). Formation of large family groups is therefore more likely the result of kin-selection, with the adult pair sharing surplus food with their hunting-inept offspring (Schmidt & Mech 1997; MacNulty *et al.* 2012).

1.2.1 Wolf kill rates and consumption rates

The assessment of kill rates and predatory behaviour of such a wide-ranging carnivore is challenging. When we started our predation studies in 2001, we were the first to apply a method based on instantaneous field checks of spatially clustered GPS positions from collared wolves after weekly remote downloads (Sand *et al.* 2005). Anderson and Lindzey (2003) also checked clustered GPS-positions of mountain lions (*Puma concolor*) for kill

remains, but they did so retrospectively after retrieval of the GPS-collar, i.e. with a time lag of up to one year, which makes it difficult to determine the cause of death and collect other types of information linked to the actual predation event. Conventional methods to discover remains of killed prey in the pre-GPS era (Merrill *et al.* 2010; Nilsen *et al.* 2012) were to monitor unmarked or VHF-collared wolves either by tracking them on snow or from the air (Burkholder 1959; Haglund 1966; Peterson 1977; Fuller 1989). These methods are time consuming and expensive. They are also constrained by snow or weather conditions. Aerial tracking is limited to daylight hours, while wolves are more active during dawn, dusk and night hours (Theuerkauf *et al.* 2003). The application of GPS-technology therefore opened up new opportunities for more detailed and accurate estimates of kill rates and has since become a standard method in large carnivore research (Merrill *et al.* 2010).

Globally, spatial and temporal variations in prey availability and vulnerability have generated a large array of region- and time-specific kill rate estimates. Prey consumption or availability expressed as biomass facilitates comparisons between different wolf-prey systems and provides for a more physiological approach to predation studies. The consumable parts of ungulate prey make up 65-75 % of the living weight of individuals, depending on the species and age class (Cederlund & Sand 1991; Jędrzejewski *et al.* 2002; Wilmers *et al.* 2003). Kill rates expressed as the amount of consumable biomass killed per time unit describes the biomass available to the predator, with the consumption rate being the effective amount that has been consumed by wolves per unit time. Wolf body growth, survival and reproduction all depend on how the consumption rate relates to the field metabolic rate, i.e. the biomass needed for daily maintenance of biological functions. For wolves, the field metabolic rate has been estimated to 3.25 kg fresh weight per day for wolves of 35 kg (Peterson & Ciucci 2003).

1.2.2 Functional response of wolves to changes in prey and predator densities

Most empirical studies of the functional response of large mammalian carnivores are from wolves, but see Fryxell *et al.* (2007) and Nilsen *et al.* (2009a). These wolf studies are not easily comparable because they were done in different predator-prey systems and at different spatial and temporal scales: 1) Time series of a study area limited to 1-3 wolf packs (Jost *et al.* 2005; Hebblewhite 2013); 2) Comparison of packs within a wolf population, partly with repeated measurements of the same pack in different seasons/years (Dale, Adams & Bowyer

1994; Hayes & Harestad 2000b; Jost *et al.* 2005; Becker *et al.* 2008, and this study); 3) A mixed scale of kill rates estimated at the pack level and prey density estimates at the study area level (Vucetich, Peterson & Schaefer 2002; Jost *et al.* 2005); and 4) meta-analyses across different studies (Messier 1994; Eberhardt 1997; Marshal & Boutin 1999; Messier & Joly 2000; Sand *et al.* 2012a). The earliest studies suggested that wolf predation was most similar to satiated prey-dependent models, i.e. Lotka-Volterra type II (Dale, Adams & Bowyer 1994; Messier 1994; Messier & Joly 2000). Eberhardt (1997) re-analyzed the meta-dataset of Messier (1994) after extending it with more studies and concluded that the kill rate was rather constant across different prey densities. Hayes and Harestad (2000b) could not detect any functional response of wolf kill rates to moose densities in the Yukon, Canada, even after repeating the analysis for different pack sizes separately. However, their data, if added to the meta-dataset of Messier (1994), changes the functional response curve significantly due to relatively high kill rates at low moose densities. For the wolf-moose system on Isle Royale, Jost *et al.* (2005) found support for a ratio-dependent response of wolf kill rates to yearly changes of moose abundance on the island. In addition, they found strong predator dependence, if both moose density and kill rates were estimated at the pack scale. Asymptotic ratio-dependent models performed best for wolf preying on elk (*Cervus elaphus*) in Yellowstone (Becker *et al.* 2008) and Banff National Parks (Hebblewhite 2013).

1.3 Why study wolf predatory behaviour in Scandinavia?

1.3.1 The gap between theory and empirical knowledge

With 1553 articles found by the Web of Science search engine for the term "*Canis lupus*", the wolf is the most studied large mammalian carnivore (Table 1). There are 1.3 times as many articles on wolves as on the brown bear which ranks second, and 1.7 as many as for the smaller relative of the wolf, the coyote (ranked 3). Still, many questions remain unanswered. As exemplified above, empirical studies focussing on the functional response in wolves have only been conducted in 5 study areas, all in North-America: Alaska, Yukon, Isle Royale, Yellowstone National Park, and Banff National Park (Dale, Adams & Bowyer 1994; Hayes & Harestad 2000b; Vucetich, Peterson & Schaefer 2002; Becker *et al.* 2008; Hebblewhite 2013). These study areas represent different types of predator-prey systems, differing in relation to prey and predator guild, climate, and degree of human interference with prey and predator populations.

Table 1: Articles found by Web of Science for selected mid- to large-sized mammalian, terrestrial carnivore species when searching by the scientific name, e.g. "Ursus arctos". Search date: November 5, 2013.

Common name	Latin name	Articles
Wolf	*Canis lupus*[a]	1553
Brown bear	*Ursus arctos*	1169
Coyote	*Canis latrans*	896
American black bear	*Ursus americanus*	757
Polar bear	*Ursus maritimus*	734
Lion	*Panthera leo*	694
Mountain lion	*Puma concolor*	535
Tiger	*Panthera tigris*	516
Spotted hyena	*Crocuta crocuta*	478
Cheetah	*Acinonyx jubatus*	462
Giant panda	*Ailuropoda melanoleuca*	403
Leopard	*Panthera pardus*	367
African wild dog	*Lycaon pictus*	334
Jaguar	*Panthera onca*	290
Eurasian lynx	*Lynx lynx*[b]	248
Wolverine	*Gulo gulo*	187
Asian black bear	*Ursus thibetanus*	176
Canadian lynx	*Lynx canadensis*	122
Sun bear	*Helarctos malayanus*	60
Striped hyena	*Hyaena hyaena*	59
Dhole	*Cuon alpinus*	56
Spectacled bear	*Tremarctos ornatus*	52
Snow leopard	*Uncia uncia*	47
Brown hyena	*Hyaena brunnea*	42
Sloth bear	*Melursus ursinus*	36

[a] For Canis lupus, the search term was extended with NOT («Canis lupus familiaris" OR "Canis lupus dingo") to exclude articles on house dogs and dingoes.

[b] For Lynx lynx, I used the term "Eurasian lynx" instead because the scientific name also included articles on other lynx species if their common name was followed by their scientific name, e.g. "…Canadian lynx (Lynx canadensis)…".

The majority of the scientific papers on wolves are from North-America. Contrary to North-American wolves, Eurasian wolves have been subject to heavy persecution by humans for thousands of years. They are now returning to the human-dominated landscapes of many European countries (Linnell *et al.* 2005). However, due to their history, Eurasian wolves are likely to be behaviourally different from North-American wolves. The behaviour of the prey may also be different, depending on population structure, current and historic management regime, and the prey's experience and history of co-existence with wolves (Sand *et al.* 2006a). In addition, human impact on wolves and their prey can be expected to differ depending on the rate of human harvest, poaching, and habitat exploitation (Sand *et al.*

2012a). Because of this we cannot expect all knowledge of wolf predation gained in North America, even in similar boreal forest habitats, to be relevant and applicable to the ecosystem of Scandinavia. Rather, we need to obtain new knowledge from empirical studies performed within the ecosystem of Scandinavia.

1.3.2 Conflicts related to wolf recolonization

When the wolves returned to south-central Scandinavia in the 1970s after a period of functional extinction (Wabakken *et al.* 2001), they met a much altered landscape. Forestry techniques had changed from selective harvesting to clear-cut logging with an extensive network of forest roads. This new form of forest exploitation together with new laws on moose management, including the age- and sex-selective harvest of ungulates, had allowed a rapid increase in the moose population size from the 1950s onwards (Lavsund, Nygrén & Solberg 2003). Harvesting of moose had become an important source of income and was also considered to be of high recreational value for the local societies (Storaas *et al.* 2001; Boman *et al.* 2011). Therefore, the recolonization of wolves raised the question of competition between hunters and wolves for the same prey species (Nilsen *et al.* 2009b).

Another change in land use was the extensive use of forests and mountain areas for grazing by unattended sheep in Norway (Zimmermann, Wabakken & Dötterer 2001). Measures to protect livestock had disappeared during the period with low or absent populations of large carnivore species (Kaczensky 1996). The recolonizing wolves predated on the easily accessible livestock, leading to a second complex of conflicts. A third area of conflict relates to the habit of wolves to kill dogs, especially dogs used for hunting. These dogs may be perceived by the wolves as intruders in the wolf territory or simply as prey (Kojola *et al.* 2004; Karlsson & Sjöström 2007). Lastly, there are conflicts relating to peoples' negative attitudes towards and fear of the wolf, shaped by century-old histories and myths (Zimmermann, Wabakken & Dötterer 2001; Ericsson & Heberlein 2003; Skogen, Mauz & Krange 2008).

The wolf is red-listed in Scandinavia and by 2010 was assigned to the category Critically endangered (CR) in the Norwegian and Endangered (EN) in the Swedish national red lists (Gärdenfors 2010; Kålås *et al.* 2010). Both countries have committed themselves to conserve wild wolves with country-specific population goals (Miljøverndepartementet 2004; Naturvårdsverket 2012). Along with the return of this conflict-prone species, sound

empirical data on several aspects of wolf ecology are urgently needed and important for conservation and management. In particular, data on wolf spatial ecology and predatory behaviour were and still are an area of primary interest to the management authorities in order to adjust moose hunting quotas, to implement measures to protect livestock and dogs, and to increase the overall public knowledge on and acceptance of wolves in Scandinavia.

2. Objectives

The main objective of this thesis was to study wolf predatory behaviour by monitoring individual wolves with GPS-collars. Being the first application of GPS-positioning data world-wide to estimate wolf kill rates, there were many methodological uncertainties. For example, how to program the collars and how to search clusters of GPS-positions in the field in order to find remains of different prey species, particularly ungulate prey (Sand *et al.* 2005). Wolves do not move continuously, but stop at various sites for resting, handling of prey, denning, or other social interactions. This pattern of integrated travel and stop-over sites looks like a necklace of single positions (small pearls) and clustered positions (large pearls) if GPS-data from collared wolves are plotted at a fine temporal scale of several positions per day (Figure 1). Handling of prey that is larger than the predators own body size, would cause the wolves to return to the same kill site repeatedly and at specific times of day. In this thesis, paper 1 asks: ***Do wolves exhibit a predictive movement behaviour that makes it easy to separate clusters of GPS-positions containing large-bodied kills from clusters stemming from resting or other types of behaviour?*** If so, field efforts to find prey remains could be reduced by targeting potential kill sites identified by detailed analysis of wolf movement.

During winter, wolf tracks on snow helped us to interpret wolf behaviour at single and clustered GPS-positions that we visited in the field (Figure 1). The next challenge was to extend kill rate studies to the summer period, when cohesion between the breeding pair was expected to be lower due to reproductive behaviour and the use of dens (Peterson, Woolington & Bailey 1984), and the presence of more smaller-bodied prey, such as neonate ungulates. Paper 2 asks the question: ***How does wolf predatory behaviour during summer differ from winter, with regard to kill rates and prey selection?*** In this study we also related prey acquisition to pack size, to the body growth of prey, and to the increased need of food for the growing pups.

We found a highly variable movement pattern of wolves in relation to kill sites and prey handling (paper 1), and one of the hypotheses to explain this high variation focused on human impact. The distance of the kill from sources of human activity, such as roads, which might result in direct disturbance and interruption of the handling of prey, could potentially impact on the time wolves spent handling kills. On the other hand, certain road types can be

useful for wolves to increase travel speed and decrease the time taken to find vulnerable prey. Paper 3 asks the question: *How do roads influence wolf movement behaviour during summer with regard to selection of travelling routes, bed sites and kill sites?* We examined this aspect at different spatial scales from single time-related steps of individual wolves to inter-pack comparisons.

While data on kill rates are useful to study food acquisition of the predator species, they do not give us much information on the impact that the predator has on its prey, if not linked to prey abundance. We estimated winter prey and predator densities for almost all wolf territories where data on winter kill rates existed. Paper 4 asks*: Is there a functional response during winter, i.e. do wolf kill rates vary with prey and/or predator abundance among packs?* We looked at this relationship for all available cervid species combined in terms of the total consumable biomass, and also specifically for moose because this was the predominant prey species in most wolf territories.
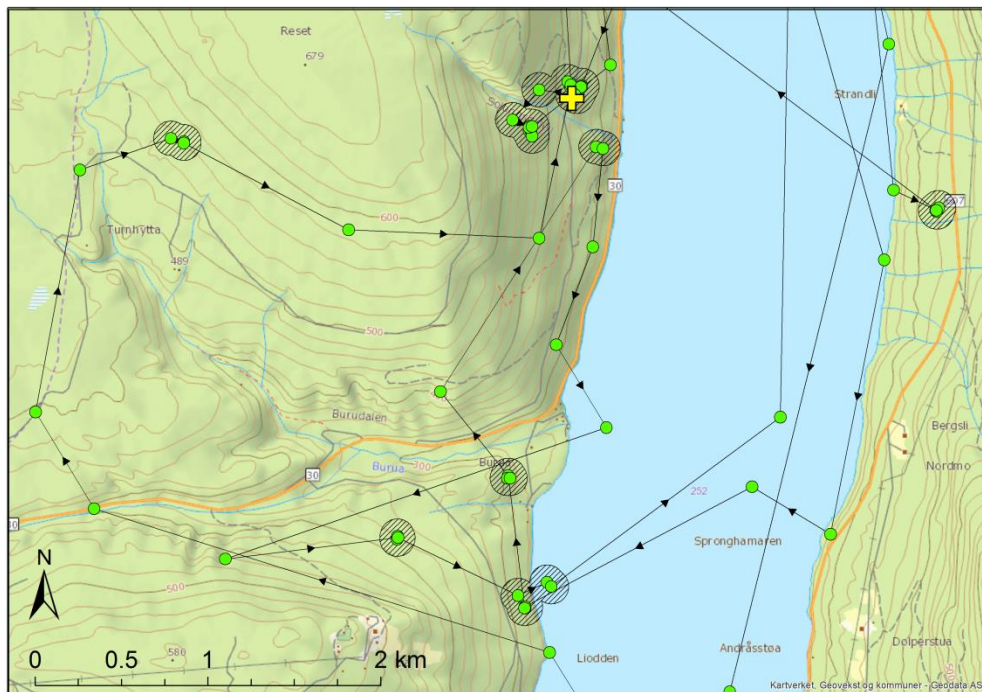
Figure 1: Hourly GPS-data (green points) of the first wolf collared with GPS by the Scandinavian Wolf Research Project and the first kill rate study on GPS-collared wolves worldwide (Gråfjell male, data from 3-7 March 2001, Lake Storsjøen in Stor-Elvdal and Rendalen municipalities, Norway). The hatched buffer area around clusters of positions within 200m or less of each other has been searched in the field for tracks of wolves and prey remains. The yellow cross indicates the place where prey remains of a wolf-killed moose calf were found (kill cluster). The other clusters of positions were defined as bed site clusters due to the absence of prey remains and, depending on snow conditions, the presence of bed sites on snow.

3. Methods

3.1 The wolf population in Scandinavia

The wolf became functionally extinct in all of Scandinavia (Figure 2) in the 1960s after a long period of severe persecution (Wabakken *et al.* 2001). Two immigrant Finnish-Russian wolves settled across the national border between Sweden and Norway in south-central Scandinavia and founded a new population after breeding in the early 1980s (Figure 2). When a third immigrant arrived seven years later (Wabakken *et al.* 2001; Vilà *et al.* 2003), the wolf population started to increase, and during winter 2012-13 Scandinavia was home to about 380 wolves, based on a total of 5 founder individuals (Wabakken *et al.* 2013). This population is still confined to south-central Scandinavia and is limited to the north by the southernmost semi-domestic reindeer (*Rangifer tarandus*) herding area, and to the west by the outer border of the Norwegian wolf protection zone, a narrow zone established to secure Norwegian wolf reproduction along the border with Sweden (Figure 2).

The study area of this thesis is the geographical breeding range of wolves in south-central Scandinavia, including both Swedish and Norwegian territories (60° N, 12° E, Figures 2, 3). During the period of this study, the wolf population increased from 13 (1999-2000) to 64 (2012-13) pairs and family groups (Wabakken *et al.* 1999; Wabakken *et al.* 2013). The ecotone was boreal forest and home to other large and medium-sized carnivores (brown bear, lynx, wolverine). The dominant prey species was the moose, with average winter densities of 1.3 moose per km^2 inside wolf territories (range 0.7 – 3.3, paper 4). In southern wolf territories, roe deer (*Capreolus capreolus*) reached densities of up to 3.4 individuals per km^2, but they were absent or at very low densities in central and northern territories. Red deer (*Cervus elaphus*) and wild and semi-domestic reindeer occurred only at very low densities and only in a few of the studied wolf territories (paper 4). Other potential prey species were beavers (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), and black grouse (*Lyrurus tetrix*).
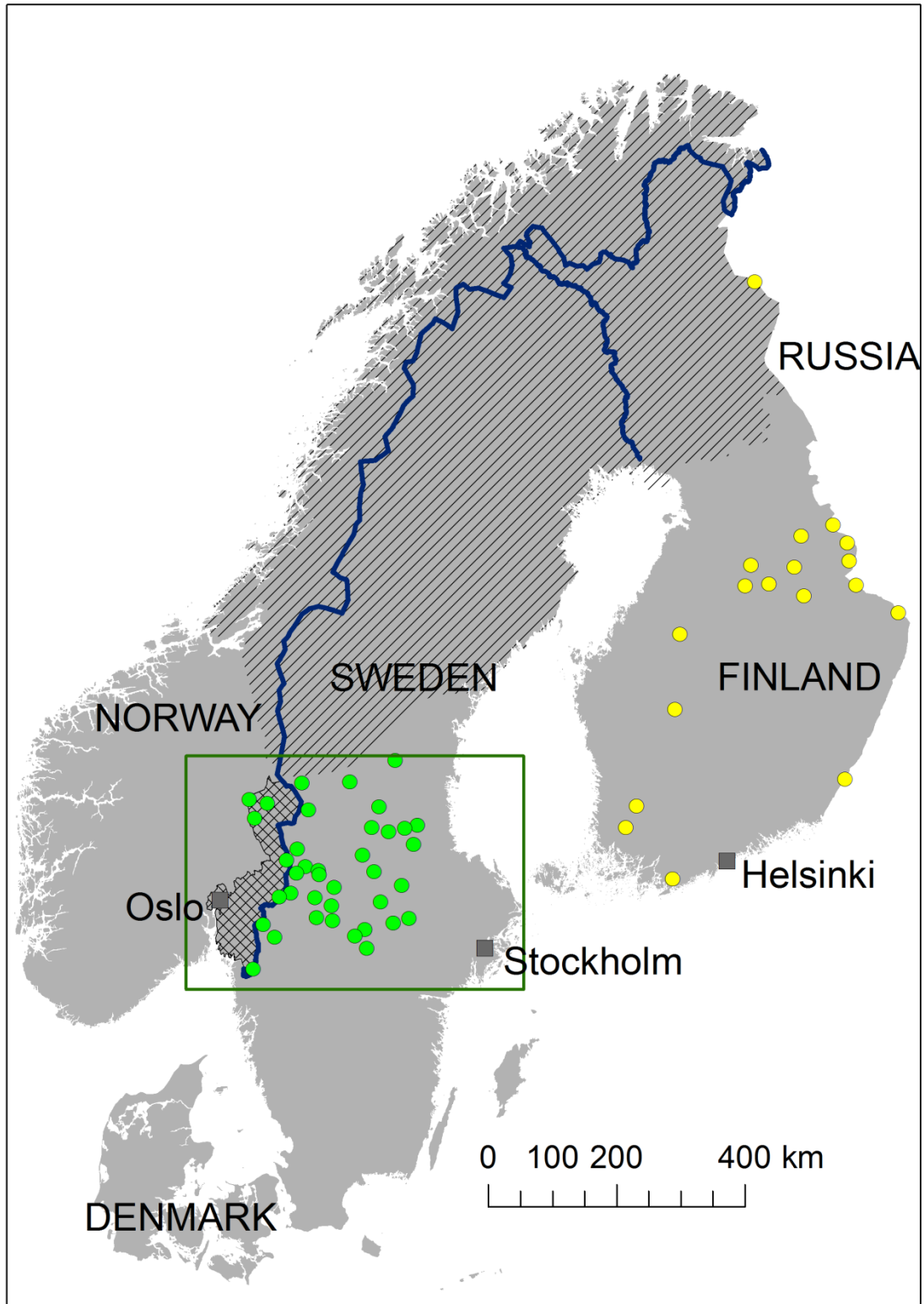
Figure 2: The distribution of wolf family groups in Fennoscandia (Finland and the Scandinavian Peninsula of Norway and Sweden) during winter 2012-13, with green dots for family groups in the cross-bordering Scandinavian population, and yellow dots for family groups in Finland (Wabakken et al. 2013). The hatched area is the herding range for semi-domestic reindeer, and the cross-hatched area is the Norwegian wolf protection zone. The green rectangle delineates the study area of Figure 3.

Human densities were generally low, in most territories < 1 inhabitant per km^2 (Wabakken *et al.* 2001; Mattisson *et al.* 2013). This was also reflected by the relatively low density of main roads (mean ± SE for n= 15 territories: 0.19 ±0.02 km/km^2, paper 3). The principal forestry technique was clear-cutting, with an extensive network of gravel roads (density 0.88 ± 0.05 km/km^2, paper 3).
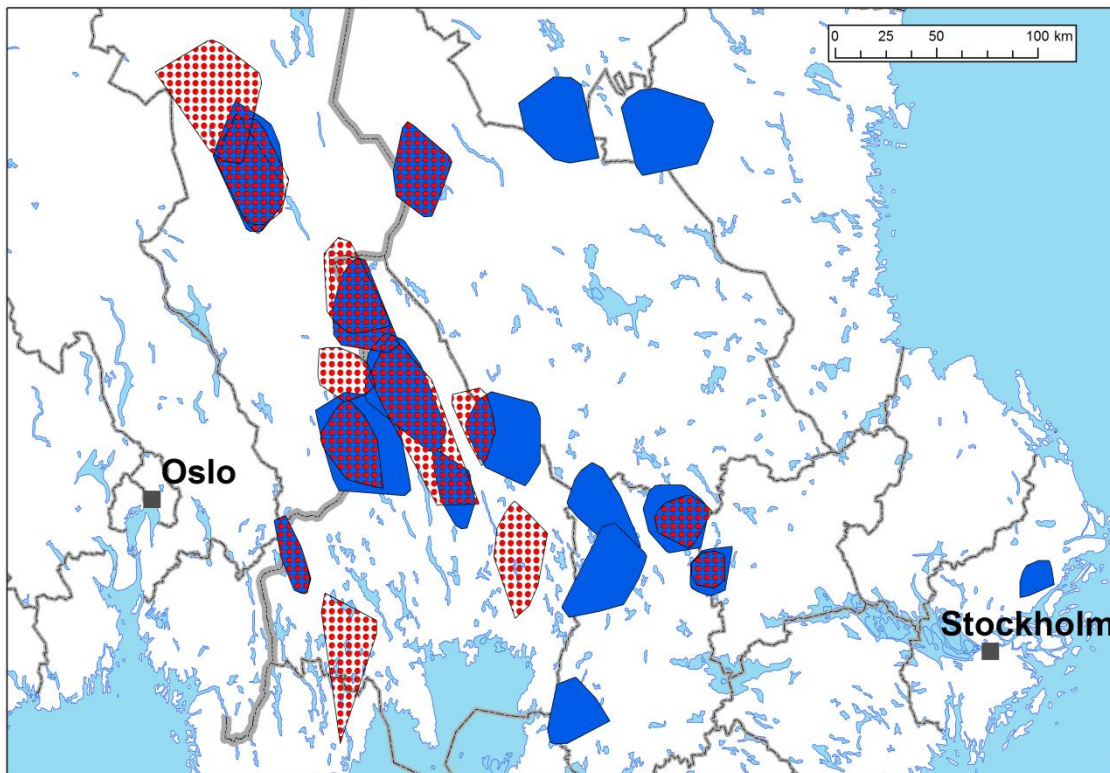
Figure 3: Study area with wolf territories used for assessment of kill rates during winter (blue polygons) and summer (red-dotted polygons). The thick grey line indicates the border between Norway to the west and Sweden to the east. Thinner lines are county borders.

3.2 GPS-tracking of wolves

The Scandinavian Wolf Research Project (SKANDULV; http://skandulv.nina.no/) has immobilized wolves from helicopters and fitted them with GPS-collars, following procedures described elsewhere (Sand *et al.* 2006b; Arnemo, Evans & Fahlman 2011). We deployed Simplex and Tellus collars from Televilt AB Sweden (now Followit Sweden), and GPS-plus from Vectronic Germany. The collars were usually programmed to acquire one position every 4 hours, i.e. 6 positions per day. All collars had the option for remote downloads, so that data was sent either at given time intervals as VHF-coded signals to a

mobile receiver in the field, or continuously as SMS text messages. Downloaded data could also be checked against the data stored in the collar when it was retrieved from the wolf, either during re-collaring or if found dead.

3.3 Kill rate studies

For kill rate studies, we programmed the GPS-collars to take hourly or half-hourly positions during periods of 2-19 weeks. Data were retrieved continuously with the remote download option, displayed on digital maps (Figure 1) and transferred to hand-held GPS units. We used a geographic information system (GIS) buffering method to separate clusters of positions from single positions (Figure 1, paper 1). All clusters, and a large proportion of single positions, together with some additional stretches of snow-tracking between single positions in winter, were visited in the field, on average 8 days after positioning, to look for carcass remains and other behavioural signs (Sand *et al.* 2005). We determined species, sex and age of carcasses, as well as cause of death, and calculated kill rates. For summer studies, when snow could not assist us to find the tracks of wolves, we used field-trained dogs to locate carcasses (paper 2).

3.4 Movement in relation to roads

We used the wolf GPS-positions from the summer predation studies, mostly with half-hourly positioning schedules, and measured the distance between positions and the closest gravel road and main road (paper 3). Positions < 30 m from the closest road were defined as being 'on the road'. We compared the travel speed of wolves moving off roads, on roads, or going to/coming from roads. We used step selection functions to estimate the selection for roads for different times of day, behavioural states (travelling, handling prey, resting), and road types. Within home ranges, we used resource utilisation functions to investigate the selection of areas with different road densities. We also compared gravel road use between wolf packs in relation to overall gravel road density in the home range, i.e. the functional response of road use to road availability.

3.5 Prey density estimation

We estimated winter moose densities in all the wolf territories where we had conducted winter kill rate studies, using the pellet count method (Neff 1968; Rönnegård *et al*. 2008). Following snow melt in spring, we counted the number of moose pellet piles on sample plots of 100m^2, arranged along the outer lines of a 1 km^2 square (40 sample plots per square, paper 4). We visited 42 to 130 squares per wolf territory depending on territory size. The average number of piles per square was used to estimate moose densities by taking into account a constant defecation rate of 14 piles per day (Rönnegård *et al*. 2008) and the number of days from leaf fall to sampling date. After interpolation of the moose data for each territory using Thiessen polygons (Thiessen 1911), we ended up with moose density maps (paper 4).

3.6 Modelling the functional response

The functional response describes the change in kill rate in response to changes in prey availability. We first looked at the individual, sex- and age-specific contribution of different pack members to the pack kill rate (paper 4). We then applied a set of 18 different functional response models for per capita kill rate expressed as moose/wolf/day and kg cervid biomass/wolf/day. Thirdly, we studied to what degree wolf kill rates exceeded or dropped below the daily energetic needs (field metabolic rate) of the pack, and how this depended on prey availability and pack size (paper 4).

4. Results

4.1 Highly variable handling of kills by wolves makes prediction of kill sites difficult

Field checking of clusters of positions is a very time consuming and expensive activity. We wanted to test whether we could reduce field effort by analysing the wolves' movement patterns and identifying clusters that were most likely to contain kills (paper 1). This would help us to eliminate the need for field work entirely or to reduce the effort to just visiting clusters with a high likelihood of containing a kill. However, because of the high variation in how often the wolves returned to a kill, how much time they spent at each kill, and at what time of the day they were at kills, we concluded that all clusters of positions had to be checked in the field and additionally a significant proportion of single positions.

4.2 Seasonal variation of diet and kill rates

Moose was the predominant prey species of wolves in Scandinavia, both in winter and in summer (Table 2). The higher proportion of roe deer individuals found in winter kills compared to summer kills can be explained by the fact that two winter studies were conducted in wolf territories with high roe deer densities (paper 4). The diversity of prey species killed, i.e. the number of different species, did not differ between winter and summer (Table 2). Kill rates expressed as the number of prey animals killed per pack in summer were about double those in winter (Table 2). This was mainly a consequence of the wolves' strong selection for neonate moose in summer (paper 2). The kill rate decreased with time during summer, probably due to the increased biomass of the growing calves, and this pattern occurred despite the increasing weight and nutritional needs of the growing wolf pups (paper 2). Moose calves were also the predominant prey type in winter (Table 2) (Sand *et al.* 2012a). Kill rate expressed as edible biomass per pack per day did not differ between winter and summer ($t = 1.10$, $df = 20$, $p = 0.28$, Table 2). Annual predation of wolves on moose summed up to an average of 120 moose per pack (summed lower and upper 95% confidence limits: 100 – 144 moose per pack, Table 2).

Table 2: Compiled seasonal predation data for wolves in Scandinavia from 38 studies, with each study carried out in one wolf territory in one season. The summer values are published in paper 2. The winter data is the dataset used in paper 4, but extended with information on prey species other than moose and roe deer. For winter weights of moose and roe deer see paper 4, for other species I adapted the values presented in paper 2 and added wolf (35 kg), red fox (5.5 kg), black grouse (1 kg), capercaillie (3 kg) and red squirrel (0.3 kg). For estimation of the seasonal predation of moose, I excluded data from the two territories where roe deer dominated over moose.

		Winter	Summer
N studies		23	15
N study days		1287	322
Prey animals	Moose	69.2 %	74.4 %
	Roe deer	23.8 %	4.5 %
	Beaver	2.0 %	2.5 %
	Red squirrel	0.2 %	0.0 %
	Hare	1.0 %	3.0 %
	Badger	0.0 %	5.0 %
	Red fox	0.7 %	0.0 %
	Wolf	0.5 %	0.0 %
	Grouse sp	2.2 %	8.2 %
	Birds	0.2 %	1.9 %
	Livestock	0.0 %	0.5 %
Edible prey biomass	Moose	95.1 %	95.6 %
	Roe deer	4.2 %	1.6 %
	Other species	0.7 %	2.8 %
Age of killed moose	Adult > 2 yrs	15.4 %	0.0 %
	Yearling 1-2 yrs	11.8 %	10.1 %
	Calf <1 yr	72.8 %	89.9 %
Kill rate per pack per day	N prey animals (mean ± SE)	0.31 ± 0.04	0.60 ± 0.05
	Range (min-max)	0.10 - 0.95	0.43 - 0.83
	Edible biomass (kg, mean ± SE)	28.2 ± 2.3	24.0 ± 3.0
	Range (min-max)	10.2 - 52.0	10.4 - 38.4
Seasonal predation (moose per pack)	N days	243 (Oct-May)	122 (Jun-Sep)
	Mean N of moose	54	66
	95%-confidence limits	44 - 63	56 - 81

4.3 Roads influence wolf movements and selection of kill sites during summer

The response of wolves to roads depended on the spatial scale, road type, time of day, and behavioural or social state (paper 3). Wolves selected roads for travel, and did more so during night than daytime. The importance of roads for wolf travel was obvious from the speed analysis: Wolves travelled twice as fast on roads as off roads. During handling of prey and while bedding, wolves mostly selected for intermediate distances to roads. Within territories, wolves selected for areas with low gravel road densities, and this selection pattern was stronger for breeding than non-breeding adults. The functional response of wolves' use of roads in relation to road density at the across-pack scale was less than proportional to road availability. Wolves in Scandinavia have adapted to use roads for ease of travel and probably also scent-marking, but at the same time they seem to have developed a cryptic behaviour to avoid human encounters.

4.4 Wolves display a predator-dependent functional response

Satiated functional response models that included a strong predator component best described inter-pack variation in per capita kill rates during winter (paper 4). From the observation that GPS-collared wolf pups did not kill cervid prey when travelling without their parents, we concluded that the adult wolf pair provided all cervid kills used by the pack. They increased kill rates with increasing cervid abundance, but the form of this relationship depended strongly on the litter size. While non-breeding pairs of wolves killed > 3 times as many ungulates as needed to cover their field metabolic rate even if cervid abundance was relatively low, pairs with large litters did not provide enough food to cover the pack's total field metabolic rate at low to intermediate cervid abundance. This negative relationship between the ratio of acquired to required biomass and pack size was similar in summer and winter (Figure 4).
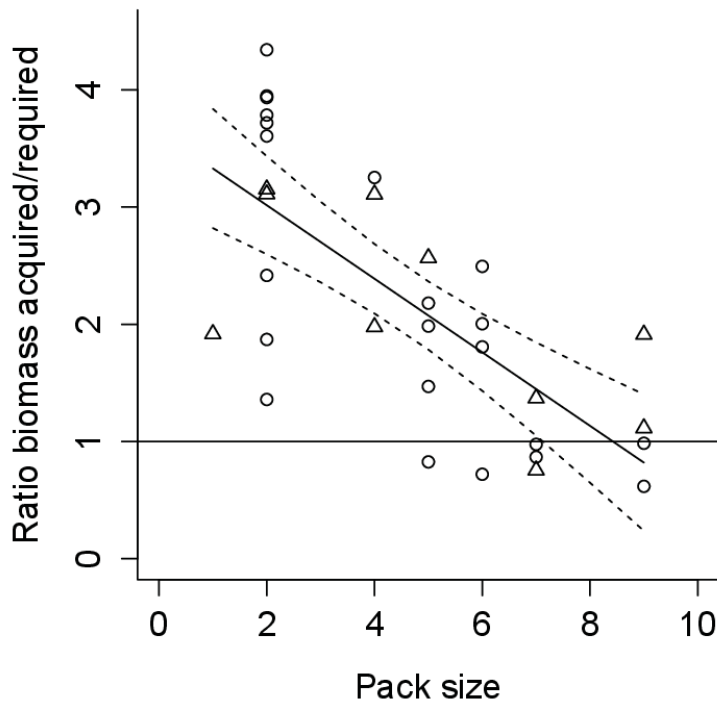
Figure 4: The ratio of acquired to required biomass in relation to pack size for wolves in Scandinavia, from predation studies conducted in winter (circles, paper 4, cervid biomass), and in summer (triangles, paper 2, required biomass was re-calculated for this figure in the same way as presented in paper 4), with fitted regression line (y = 3.64 - 0.31*x, R^2 = 0.51) and 95% confidence limits. Because season (summer or winter) was not significant in interaction with (p = 0.12) or additive to (p = 0.91) pack size, it was not considered in the linear regression model. A part of the unexplained variation of the winter data can be attributed to variation in prey availability (functional response, paper 4).

5. Discussion

5.1 What causes the high intra-pack variation in handling time at moose kills?

We observed that the movement behaviour of Scandinavian wolves in relation to kill sites was highly variable in winter and were not able to predict kill sites from the movement pattern alone (paper 1). The time between kills also showed large variation during summer (paper 2). To get reliable kill rate estimates, we needed to 1) program the GPS-collars for an intensive positioning schedule of 30 to 60 minutes between positioning attempts, thereby limiting battery life of the GPS-collar; and 2) visit all clusters of positions in the field, and in summer preferably also all single positions shortly after the wolves had left those locations. Several factors may have caused this high variation in kill handling and movement patterns, including prey size (paper 2), season (paper 2) (Metz *et al.* 2011; Lake *et al.* 2013), and spatial and temporal variation in climatic conditions such as snow depth and structure (Post *et al.* 1999; Jędrzejewski *et al.* 2002). In particular, I want to discuss four additional hypotheses that relate this variation to several aspects of wolf ecology and which all are included in the papers of this thesis.

1) Social behaviour and intra-pack interference: Jeschke (2007) describes large carnivores as "full and lazy", i.e. if per capita prey availability is sufficient, they are not time-constrained by food acquisition, but have time left for other activities. Social interactions are common in wolves and canids in general. After the denning period, pups follow their parents to kills where they are left at so-called rendez-vous sites (Jędrzejewski *et al.* 2001; Mech & Boitani 2003). During winter, we have seen pups split up from existing sibling groups, form new sibling groups, travel on their own (SKANDULV unpubl. data), and follow the breeding pair for short periods (paper 4). As it is essentially the breeding pair that acquires the food for the entire pack, even during winter (paper 4), the temporal variation in group size and other social interactions may be the cause of some of the observed variation in kill handling time. By contrast, solitary carnivores such as many felid species show a much more consistent pattern of prey handling, with regular returns to a kill site in consecutive nights until the kill is totally exploited (Breitenmoser & Haller 1993; Pedersen *et al.* 1999; Anderson & Lindzey 2003).

2) Scavengers: Remains of large prey items are an important food source for scavenging species (Hayes *et al.* 2000; Kaczensky, Hayes & Promberger 2005; Wikenros *et al.* 2013). Attendance at kill sites can reduce the loss to scavengers. Wolf pups that we describe as scavengers themselves (paper 4) often remain at a kill site (SKANDULV unpubl. data). The spatio-temporal intra-pack dynamics and group size variation may therefore be an important determinant of food loss to scavengers and therefore also to the variation in kill handling time.

3) Local cervid densities: Winter cervid densities vary strongly within the wolf territories as a consequence of habitat heterogeneity (Gervasi *et al.* 2013) and seasonal patterns of moose migration (Gundersen 2003; Lavsund, Nygrén & Solberg 2003). Wolves select for areas of high prey densities while hunting (Kunkel & Pletscher 2000; McPhee, Webb & Merrill 2012), and in areas of locally high cervid densities we expect the time wolves need to search for prey to be lower than in areas of low densities. At least at the inter-pack level, our data support this functional response of wolves to different prey densities (paper 4).

4) Human disturbance: Based on occasional observations during the winter predation studies (paper 1), we predict that wolves may abandon a kill if it is situated in close proximity to a road or human settlements, while they spend more time at kill sites in more remote areas. The heavy persecution of wolves for centuries may have favoured the observed cryptic behaviour of wolves by avoiding sites and time periods linked to increased human activity (paper 3). Cervids however, often aggregate close to human infrastructure because they select, similarly to humans, for productive habitats in climatically favourable valley bottoms, and make use of agricultural lands, clear-cuts and road sides (Laurian *et al.* 2008; Hebblewhite, Munro & Merrill 2009; Gervasi *et al.* 2013). The observed preference of wolves for intermediate distances to roads when handling prey during summer (paper 3) is likely best viewed as a trade-off between selecting prey-rich habitats and avoiding human presence. The degree of prey utilization has been shown to be a function of distance to human infrastructure for wolves in Yellowstone National Park (Wilmers *et al.* 2003) and our results suggest that the same type of pattern occurs in Scandinavia.

5.2 How wolf kill rates relate to season, prey density and pack size

The wolves in our study killed twice as many moose per wolf during summer as compared to winter as a result of the strong selection for the smaller-bodied new-born calves in summer (Table 2, paper 2). However, available killed biomass per wolf did not differ between seasons (Table 2). In general, neonate ungulates seem to be an important source of summer food for wolves (Ballard, Whitman & Gardner 1987; Mech *et al.* 1998; Jędrzejewski *et al.* 2002; Metz *et al.* 2012), and also for brown bears (Swenson *et al.* 2007; Gervasi *et al.* 2012). Neonates must be highly vulnerable to these large carnivores to outweigh the low biomass gain per attack. Cross-continental behavioural analysis of moose cows with new-born calves strongly indicates that moose cows in Scandinavia are more naïve and less aggressive than their North-American counterparts (Sand *et al.* 2006a).

The assessment of summer kill rates was a methodological challenge before the onset of GPS-technology. In order to obtain annual kill rates, many studies have either extrapolated winter kill rates (Keith 1983; Messier 1994; Vucetich, Smith & Stahler 2005), used scat analyses (Fuller 1989) or assumed daily consumption (Pimlott 1967) as an indirect estimation of kill rates during summer months. By extrapolating winter kill rates we would have strongly underestimated annual estimates of moose killed by wolves in Scandinavia.

Although the phenomenon of the negative relationship between per capita kill rate and pack size is well-known for wolves (Schmidt & Mech 1997; Hayes *et al.* 2000; Metz *et al.* 2011; Sand *et al.* 2012a), we found the predator dependence to be stronger in Scandinavia than in other studies from North America, both during summer and winter (Figure 4, papers 2 and 4). Small packs consisting of only the two adults or just a few pups had kill rates that resulted in the acquisition of biomass that by far exceeded their energetic requirements. The prey acquisition by the adult pair was even high enough to provide food for packs of intermediate to large size (paper 4). These wolves cannot be characterized as 'full and lazy' (Jeschke 2007), but rather 'full and busy' by providing high kill rates and maintaining large territories despite small pack sizes (Mattisson *et al.* 2013). Since wolves probably do not cache food during winter (Peterson & Ciucci 2003) as described for other carnivores (Haglund 1966; Oksanen, Oksanen & Fretwell 1985; Laundré & Hernández 2003), surplus-killing as a means to store food for times of higher requirements or lower food availability does not seem reasonable for our study.

More likely, surplus-killing in wolves is a result of an optimal foraging strategy (MacArthur & Pianka 1966): If costs to access a new food patch (here, a cervid kill) are low (i.e. high prey abundance and vulnerability), it makes sense to leave the old food patch after having devoured the parts with the highest energy content (Vucetich, Vucetich & Peterson 2012). Wolves have been shown to devour the highly nutritious organs of killed elk first (Stahler, Smith & Guernsey 2006). Left-overs are valuable food for hunting-inept pups (MacNulty *et al.* 2012), causing a positive relationship between prey consumption (the proportion of the kill consumed by wolves) and pack size (Paquet 1992; Wilmers *et al.* 2003). The optimal foraging pattern can also be influenced by the cost or risk of being detected by humans if staying at a carcass over a long time period. Wilmers *et al.* (2003) observed that consumption rates depended on the distance to roads: Kills close to roads were on average consumed less than those further from roads. We have so far not studied this relationship in Scandinavia, but the avoidance of areas close to roads when wolves handled prey (paper 3) is an indication that human disturbance affects prey consumption and kill rates.

In contrast to small and intermediate packs, large packs in our study seemed to be food limited both during summer and winter (Figure 4), and the adult pair of these packs could be characterized as 'hungry and busy' rather than 'full and lazy' (Jeschke 2007). Caution however has to be given to the crude estimates of the field metabolic rate, prey body size and the proportion of edible biomass, which may have been inaccurate. In addition, all kill rate studies of large packs (> 6 wolves) were conducted in wolf territories with cervid abundances below the study average, while the functional response models of paper 4 showed us that kill rates of large packs with an abundance of > 194 tons cervid biomass would have exceeded the energetic requirements of the pack. The observed negative relationship between litter size and body weight of wolf pups caught during winter (paper 4) provided supporting evidence of food limitation in large packs.

Hypothetically, the observed surplus killing by small wolf packs and potential food limitation of large packs may be the result of a stabilizing selective force in European wolves that causes the adult wolf pair to kill prey to sustain a pack of about 6 wolves, independent of the current pack size. Average pack size in Scandinavia is 6.3 ± 1.6 (SD) wolves (Wabakken *et al.* 2001) and has not exceeded 10 wolves so far (Mattisson *et al.* 2013). Similar or even lower pack sizes and simple pack structures consisting usually of the adult pair and their offspring of the year have been reported for other European populations (Okarma *et al.* 1998; Jędrzejewski *et al.* 2002; Apollonio *et al.* 2004). The social

organization of wolves in Europe contrasts with the description of larger and more complex wolf packs with additional adults, mostly offspring from previous years, in many North American studies (Thurber & Peterson 1993; Hayes *et al.* 2000; Mech & Boitani 2003; Smith *et al.* 2004).

5.3 Wolf predation in Scandinavia: a different story?

A meta-analysis of North-American wolf-moose systems pinpointed a type II functional response when comparing kill rates and moose densities across studies (Messier 1994) (Figure 5). This data was extended in the lower end by the Yukon study (Hayes & Harestad 2000b) and most recently by a study from Alaska (Lake *et al.* 2013) with even lower moose densities (0.11 moose / km^2) (Figure 5). None of these studies fitted the original functional response curve of Messier (1994) (Figure 5), and Lake *et al.* (2013) suggested that wolves respond numerically rather than functionally at such low prey densities. Our data from Scandinavia extend the dataset of Messier at the intermediate and upper range of moose densities, but fit poorly to the proposed functional response model. Our average kill rate estimate for wolf family groups is higher than all estimates of the North-American studies (Figure 5) and would be even higher if the kill rate estimates of wolf pairs were to be included. The functional response curve of the prey density dependent model (paper 4) predicts a close to linear relationship between per capita kill rate and moose density for family groups in Scandinavia (Figure 5).

Several potential factors may contribute to the higher kill rates of wolves observed in Scandinavia as compared to other studies: 1) higher prey-to-predator ratios in Scandinavia (Sand *et al.* 2012a); 2) a higher proportion of moose calves in the diet as a result of a higher proportion of moose calves in the prey population (Sand *et al.* 2012a); 3) greater predator-naïvity among Scandinavian moose as a consequence of decades of low predation pressure and/or selective human hunting for aggressive individuals with wolf-specific anti-predator behaviour (Sand *et al.* 2006a); 4) a higher degree of interspecific competition from scavengers (Wikenros *et al.* 2013); and 5) a higher degree of human disturbance and/or a higher sensitivity of wolves to human disturbance resulting in the abandonment of kills at an earlier state of consumption in Scandinavia.
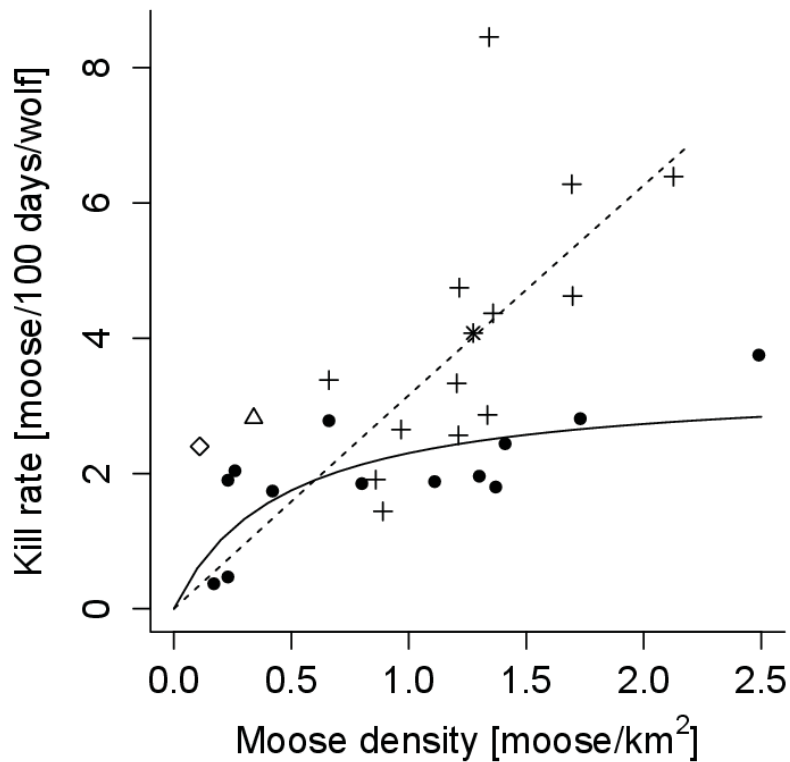
Figure 5: The functional response model proposed by Messier (solid line) based on North-American meta-data (Messier 1994) (filled circles), extended with a study from the Yukon (triangle, average of the four estimates for medium and large packs given by (Hayes & Harestad 2000b)), a study from Alaska (diamond, Lake et al. (2013)), and the Scandinavian data for family groups of more than 2 wolves (crosses, the star indicates the average value, and the dotted line is the prediction of the functional response model DDS of paper 4). All data are from winter studies.

5.4 Implications for wildlife management

For moose management, a central question is how wolves affect moose populations, and if and how moose hunting quotas should be adjusted to the predation pressure of wolves in wolf territories. Based on the kill rate studies from summer and winter, we estimated the annual average kill rate by a wolf pack to be 120 moose (Table 2). How this mortality affects moose population dynamics depends primarily on the size of the moose population, the selection of specific age- and sex-classes by wolves, and the degree to which wolf predation is additive or compensatory mortality.
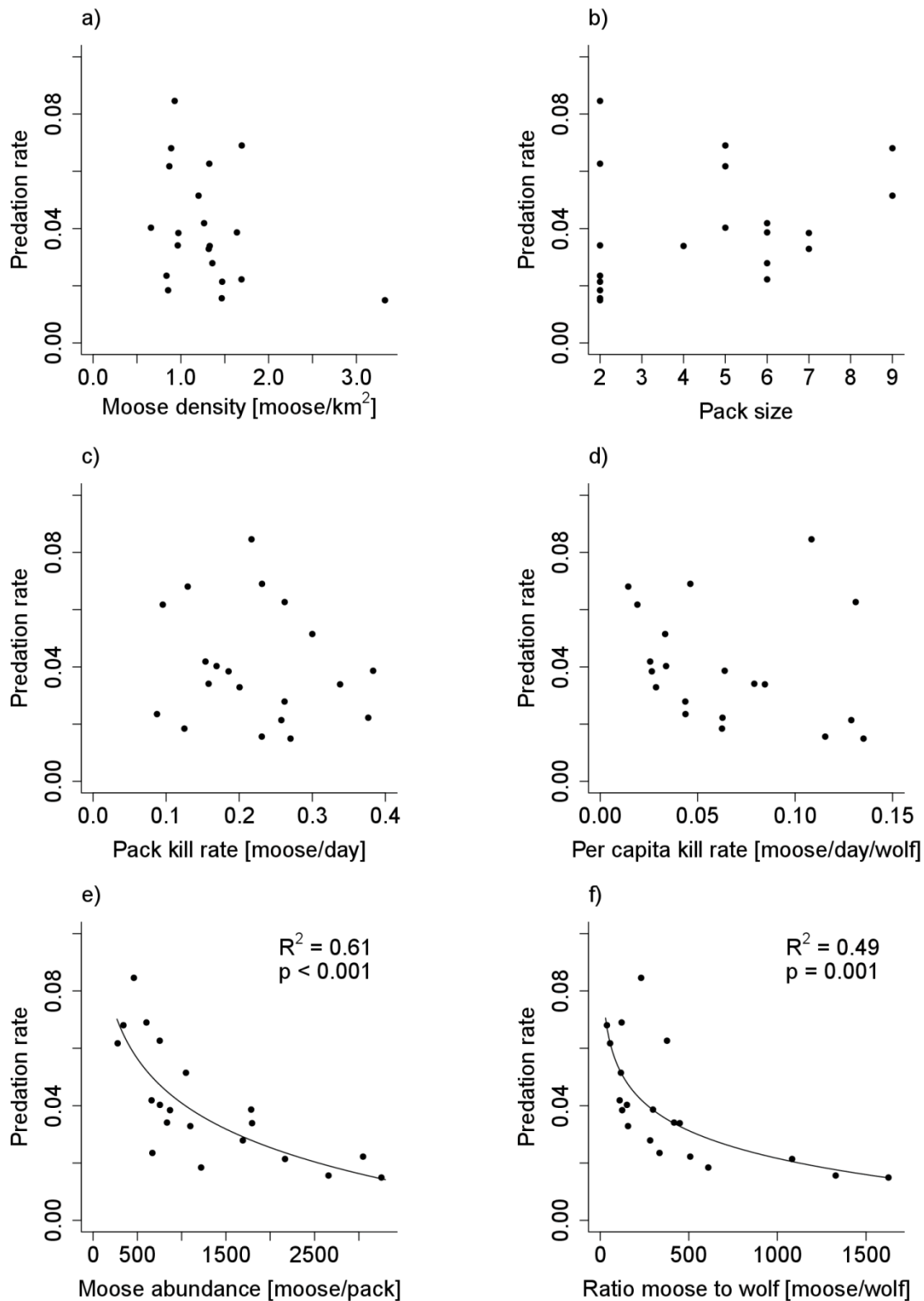
Figure 6: Winter predation rates for moose in Scandinavian wolf territories, in association with moose density (a), wolf pack size (b), pack kill rate (c), per capita kill rate (d), moose abundance (e), and ratio of moose to wolf, i.e. moose abundance divided by pack size (f), in Scandinavia. For each combination, I applied linear, quadratic, logarithmic, exponential, and power functions, similar to the method used by Vucetich et al. (2011). None of these functions were significantly different from the null model (P > 0.05) in figures a) to d). For figures e) and f), all functions were significant, and I fit the logarithmic function due to lowest AICc and highest R^2-value. Estimation of R^2 for non-linear models is described in paper 4.

During winter (180 days from November to April), the wolves in our study killed on average 4.0 % (2 SE = 0.9 %, range 1.5 – 8.5 %) of the moose present within their territory. Winter predation rates were not correlated with moose density, pack size, or either pack or per capita kill rates, i.e. predation rates were not higher in areas of low moose density, for large wolf packs, for packs with high kill rates, or for packs with high per capita kill rates (Figures 6a-d). The only important factor was the abundance of moose in the wolf territory (Figure 6e). The model predicts that predation rates may be as high as 7% in the areas of lowest abundance of moose but fall below 2% in territories with a high abundance of moose. Vucetich et al. (2011) investigated the relationship between predation rate, kill rate and the ratio of predator-to-prey (the inverse of moose-to-wolf used in Figure 6f) for three different study areas (Isle Royale, Yellowstone NP, and Banff NP). As in our study, they concluded that per capita kill rate was not a useful predictor of predation rate, irrespective of study area. The ratio of wolves-to-prey, however, was a significant predictor of predation rates in all three studies, and it correlated strongly with prey population growth for two of the studies. Our study showed that moose abundance in the territory was an even better predictor of predation rate than the ratio of moose per wolf (Figure 6f).

To predict predation rates for a proper moose management within the distribution of resident Scandinavian wolves, the assessment of moose abundance within the wolf territories is therefore essential. To do so, managers need to obtain data on both moose density and wolf territory size (moose abundance = moose density * wolf territory size).

Despite the observed high kill rates of wolves preying on moose and the functional response to moose abundance, we conclude that wolf predation in Scandinavia is limiting rather than regulating the moose population. Moose populations are highly managed, with the overwhelming mortality factor being human harvest (Solberg et al. 2000; Rönnegård et al. 2008). However, hunting may to a high degree be considered compensatory to predation simply because the management often adjusts hunting quotas to wolf presence (Jonzén et al. 2013). It is also relevant that wolves prefer the non-recruiting segment of the moose population (calves, old animals), and that the body condition of the wolf-killed moose is only marginally poorer than that of harvested moose (Sand et al. 2012b). Consequently wolf predation is largely additive rather than compensatory to other types of non-hunting mortality. Still, wolf predation on moose is an important source of conflict because hunters have to share some of the sustainable harvest with the wolf. Jonzen at al. (2013) used data from wolf and moose research from this system to build a population and harvesting model

for moose under different harvesting regimes without or in combination with predation by wolf and/or brown bear in Scandinavia (http://www.algforvaltning.se/moosemodel/). Their model suggests that moose densities may be maintained despite a high predation pressure from wolves and brown bears if the increase in predation is balanced by applying a more male-biased adult harvest in combination with moose calves making up a significant part of the quota.

Although Scandinavia could sustain a large wolf population (Karlsson *et al.* 2007), conflicts of interest limit the wolf population today and in the near future to a size far below the natural carrying capacity. Predator control in the form of licensed hunting and selective removal has been implemented in Norway and Sweden to limit wolf population growth and as a tool to dampen conflicts. Because hunters usually have to share regional wolf quotas over large areas, they are more likely to reduce the pack size in several wolf packs than reduce the number of packs by killing all pack members. However, if wolf hunting should be applied as a tool to reduce predation on moose, we would recommend the complete removal of selected pairs of wolves rather than the reduction of pack size in larger family groups. Pack size reduction in medium to large-sized packs will most likely not reduce the kill rates of wolf packs (paper 4). Furthermore, it could lead to packs dissolving, thereby destabilizing the predictive territorial structure, if a breeding wolf is shot instead of a pup (Brainerd *et al.* 2008). Any form of control should however be guided by a careful assessment of the genetic contribution of individual wolves to this highly inbred population (Liberg *et al.* 2005; Bensch *et al.* 2006).

References

Abrams, P.A. (2000) The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics,* **31,** 79-105.

Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A. & Ryman, N. (2008) Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution,* **23,** 327-337.

Amarasekare, P. (2007) Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. *Ecology,* **88,** 2720-2728.

Anderson, C.R. & Lindzey, F.G. (2003) Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management,* **67,** 307-316.

Apollonio, M., Mattioli, L., Scandura, M., Mauri, L., Gazzola, A. & Avanzinelli, E. (2004) Wolves in the Casentinesi Forests: Insights for wolf conservation in Italy from a protected area with a rich wild prey community. *Biological Conservation,* **120,** 249-260.

Arditi, R. & Ginzburg, L.R. (1989) Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology,* **139,** 311-326.

Arnemo, J.M., Evans, A. & Fahlman, Å. (2011) Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. *Hedmark University College, Evenstad, Norway.*

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

Becker, M.S., Garrott, R.A., White, P.J., Jaffe, R., Borkowski, J.J., Gower, C.N. & Bergman, E.J. (2008) Wolf kill rates: Predictably variable? *The ecology of large mammals in central Yellowstone: Sixteen years of integrated field studies* (eds R.A. Garrott, P.J. White & F.G.R. Watson), pp. 339-369. Elsevier.

Beddington, J.R. (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology,* **44,** 331-340.

Bensch, S., Andrén, H., Hansson, B., Pedersen, H.C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M. & Liberg, O. (2006) Selection for heterozygosity gives hope to a wild population of inbred wolves. *PLoS ONE,* **1,** e72.

Berger, J., Stacey, P.B., Bellis, L. & Johnson, M.P. (2001) A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications,* **11,** 947-960.

Berryman, A.A. (1992) The origins and evolution of predator-prey theory. *Ecology,* **73,** 1530-1535.

Boman, M., Mattsson, L., Ericsson, G. & Kriström, B. (2011) Moose hunting values in Sweden now and two decades ago: The Swedish hunters revisited. *Environmental and Resource Economics,* **50,** 515-530.

Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs,* **68,** 371-394.

Boyce, M.S. (2000) Modeling predator-prey dynamics. *Research techniques in animal ecology* (eds L. Boitani & T.K. Fuller), pp. 253-287. Columbia University Press, New York, USA.

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jimenez, M.D., Jozwiak, E.A., Liberg, O., Mack, C.M., Meier, T.J., Niemeyer, C.C., Pedersen, H.C., Sand, H., Schultz, R.N., Smith, D.W., Wabakken, P. & Wydeven, A.P. (2008) The effects of breeder loss on wolves. *The Journal of Wildlife Management,* **72,** 89-98.

Breitenmoser, U. & Haller, H. (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. *Journal of Wildlife Management,* **57,** 135-144.

Burkholder, B.L. (1959) Movements and behavior of a wolf pack in Alaska. *Journal of Wildlife Management,* **23,** 1-11.

Cederlund, G. & Sand, H. (1991) Population dynamics and yield of a moose population without predators. *Alces,* **27,** 31-40.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M. & Case, T.J. (2002) The interaction between predation and competition: a review and synthesis. *Ecology Letters,* **5,** 302-315.

Ciuti, S., Muhly, T.B., Paton, D.G., McDevitt, A.D., Musiani, M. & Boyce, M.S. (2012) Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B-Biological Sciences,* **279,** 4407-4416.

Crowley, P.H. & Martin, E.K. (1989) Functional responses and interference within and between year classes of a dragonfly population. *Journal of the North American Benthological Society,* **8,** 211-221.

Dale, B.W., Adams, L.G. & Bowyer, R.T. (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology,* **63,** 644-652.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C. (2009) Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences,* **106,** 952-954.

Dawkins, R. & Krebs, J.R. (1979) Arms races between and within species. *Proceedings of the Royal Society B-Biological Sciences,* **205,** 489-511.

DeAngelis, D.L., Goldstein, R.A. & O'Neill, R.V. (1975) A model for trophic interaction. *Ecology,* **56,** 881-892.

DeWitt, T.J. & Langerhans, R.B. (2003) Multiple prey traits, multiple predators: keys to understanding complex community dynamics. *Journal of Sea Research,* **49,** 143-155.

DiRienzo, N., Pruitt, J.N. & Hedrick, A.V. (2013) The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Animal Behaviour,* **86,** 317-322.

Eberhardt, L.L. (1997) Is wolf predation ratio-dependent? *Canadian Journal of Zoology,* **75,** 1940-1944.

Ericsson, G. & Heberlein, T.A. (2003) Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. *Biological Conservation,* **111,** 149-159.

Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. (2007) Group formation stabilizes predator-prey dynamics. *Nature,* **449,** 1041-1043.

Fuller, T.K. (1989) Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs,* **105,** 3-41.

Gervasi, V., Nilsen, E.B., Sand, H., Panzacchi, M., Rauset, G.R., Pedersen, H.C., Kindberg, J., Wabakken, P., Zimmermann, B. & Odden, J. (2012) Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. *Journal of Animal Ecology,* **81,** 443-454.

Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P. & Linnell, J.D.C. (2013) Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications,* **23,** 1722-1734.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. & Nilsen, E.B. (2012) Habitat heterogeneity and mammalian predator–prey interactions. *Mammal review,* **42,** 55-77.

Gundersen, H. (2003) Vehicle collisions and wolf predation: Challenges in the management of a migrating moose population in southeast Norway. Dissertation for the degree of Doctor Scientarium, University of Oslo.

Gärdenfors, U. (2010) *Rödlistade arter i Sverige 2010-The 2010 Red List of species in Sweden*. ArtDatabanken, SLU Uppsala.

Haglund, B. (1966) De store rovdjurens vintervanor I. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. *Viltrevy,* **4,** 81-310.

Hassell, M.P. & Varley, G.C. (1969) New inductive population model for insect parasites and its bearing on biological control. *Nature,* **223,** 1133-1137.

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

Hayes, R.D. & Harestad, A.S. (2000a) Demography of recovering wolf population in the Yukon. *Canadian Journal of Zoology,* **78,** 36- 48.

Hayes, R.D. & Harestad, A.S. (2000b) Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology,* **78,** 60-66.

Hebblewhite, M. (2013) Consequences of ratio-dependent predation by wolves for elk population dynamics. *Population Ecology,* **55,** 511-522.

Hebblewhite, M., Munro, R.H. & Merrill, E.H. (2009) Trophic consequences of postfire logging in a wolf-ungulate system. *Forest Ecology and Management,* **257,** 1053-1062.

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

Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist,* **91,** 385-398.

Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *The American Naturalist,* **149,** 745-764.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science,* **293,** 629-637.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. & Okarma, H. (2001) Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology,* **79,** 1993- 2004.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. & Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). *Ecology,* **83,** 1341- 1356.

Jeschke, J.M. (2007) When carnivores are "full and lazy". *Oecologia,* **152,** 357-364.

Jonzén, N., Sand, H., Wabakken, P., Swenson, J.E., Kindberg, J., Liberg, O. & Chapron, G. (2013) Sharing the bounty—Adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. *Ecological Modelling,* **265,** 140-148.

Jost, C., Devulder, G., Vucetich, J.A., Peterson, R.O. & Arditi, R. (2005) The wolves of Isle Royale display scale-invariant satiation and ratio-dependent predation on moose. *Journal of Animal Ecology,* **74,** 809-816.

Kaczensky, P. (1996) *Large carnivore - livestock conflicts in Europe*. Munich Wildlife Society, Ettal.

Kaczensky, P., Hayes, R.D. & Promberger, C. (2005) Effect of raven *Corvus corax* scavenging on the kill rates of wolf *Canis lupus* packs. *Wildlife Biology,* **11,** 101-108.

Karlsson, J., Broseth, H., Sand, H. & Andren, H. (2007) Predicting occurrence of wolf territories in Scandinavia. *Journal of Zoology,* **272,** 276-283.

Karlsson, J. & Sjöström, M. (2007) Human attitudes towards wolves, a matter of distance. *Biological Conservation,* **137,** 610-616.

Kats, L.B. & Ferrer, R.P. (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and Distributions,* **9,** 99-110.

Keith, L.B. (1983) Population dynamics of wolves. *Wolves in Canada and Alaska* (ed. L.N. Carbyn), pp. 66-77. Canadian Wildlife Service Report Series Number 45.

Kojola, I., Ronkainen, S., Hakala, A., Heikkinen, S. & Kokko, S. (2004) Interactions between wolves *Canis lupus* and dogs *C. familiaris* in Finland. *Wildlife Biology,* **10,** 101-105.

Krebs, C.J. (2009) *Ecology: the experimental analysis of distribution and abundance.* Pearson Benjamin Cummings.

Kunkel, K.E. & Pletscher, D.H. (2000) Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology,* **78,** 150-157.

Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010) The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Trondheim.*

Lahti, D.C. (2001) The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation,* **99,** 365-374.

Lake, B.C., Bertram, M.R., Guldager, N., Caikoski, J.R. & Stephenson, R.O. (2013) Wolf kill rates across winter in a low-density moose system in Alaska. *The Journal of Wildlife Management,* **77,** 1512-1522.

Laundré, J.W. & Hernández, L. (2003) Winter hunting habitat of pumas *Puma concolor* in northwestern Utah and southern Idaho, USA. *Wildlife Biology,* **9,** 123-129.

Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M. & Breton, L. (2008) Behavior of moose relative to a road network. *Journal of Wildlife Management,* **72,** 1550-1557.

Lavsund, S., Nygrén, T. & Solberg, E.J. (2003) Status of moose populations and challenges to moose management in Fennoscandia. *Alces,* **39,** 109-130.

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

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B-Biological Sciences,* **279,** 910-915.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology,* **68,** 619-640.

Linnell, J.D.C., Promberger, C., Boitani, L., Swenson, J.E., Breitenmoser, U. & Andersen, R. (2005) The linkage between conservation strategies for large carnivores and biodiversity: The view from the "half-full" forests of Europe. *Large carnivores and the conservation of biodiversity* (eds J.C. Ray, K.H. Redford, R.S. Steneck & J. Berger), pp. 381-398. Island Press, U.S.A.

Lotka, A.J. (1925) *Elements of physical biology.* Williams & Williams, Baltimore.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist,* **100,** 603-609.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2012) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology,* **23,** 75-82.

Marshal, J.P. & Boutin, S. (1999) Power analysis of wolf-moose functional responses. *Journal of Wildlife Management,* **63,** 396- 402.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D., Rauset, G.R. & Pedersen, H.C. (2013) Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia,* 1-13.

McPhee, H.M., Webb, N.F. & Merrill, E.H. (2012) Hierarchical predation: Wolf (*Canis lupus)* selection along hunt paths and at kill sites. *Canadian Journal of Zoology,* **90,** 555-563.

Mech, L.D., Adams, L.G., Meier, T.B., Burch, B.W. & Dale, W.B. (1998) *The wolves of Denali*. University of Minnesota Press, Minneapolis, London.

Mech, L.D. & Boitani, L. (2003) Wolf social ecology. *Wolves: behavior, ecology and conservation* (eds L.D. Mech & L. Boitani), pp. 1-34. The University of Chicago Press, Chicago.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J.L. (2010) Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **365,** 2279-2288.

Messier, F. (1994) Ungulate population models with predation: A case study with the North American moose. *Ecology,* **75,** 478- 488.

Messier, F. & Joly, D.O. (2000) Comment: Regulation of moose populations by wolf predation. *Canadian Journal of Zoology,* **78,** 506-510.

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology,* **81,** 553-563.

Metz, M.C., Vucetich, J.A., Smith, D.W., Stahler, D.R. & Peterson, R.O. (2011) Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PLoS ONE,* **6,** e17332.

Miljøverndepartementet (2004) *Rovvilt i norsk natur. Stortingsmelding nr 15 (2003-2004)* Det Kongelige Miljøverndepartementet, Oslo.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology,* **21,** 36-47.

Murie, A. (1944) *The wolves of Mount McKinley*. U.S. G.P.O., Washington.

Naturvårdsverket (2012) *Nationell förvaltningsplan för varg 2012-2017*. Naturvårdsverket, Stockholm, Sweden.

Neff, D.J. (1968) The pellet-group count technique for big game trend, census, and distribution: A review. *Journal of Wildlife Management,* **32,** 597-614.

Nilsen, E.B., Christianson, D., Gaillard, J.-M., Halley, D., Linnell, J.D.C., Odden, M., Panzacchi, M., Toïgo, C. & Zimmermann, B. (2012) Describing food habits and predation: field methods and statistical considerations. *Carnivore ecology and conservation: A handbook of techniques* (eds L. Boitani & R.A. Powell), pp. 256-272. Oxford University Press, Oxford.

Nilsen, E.B., Linnell, J.D.C., Odden, J. & Andersen, R. (2009a) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *Journal of Animal Ecology,* **78,** 741-751.

Nilsen, E.B., Skonhoft, A., Mysterud, A., Milner, J.M., Solberg, E.J., Andreassen, H.P. & Stenseth, N.C. (2009b) The role of ecological and economic factors in the management of a spatially structured moose *Alces alces* population. *Wildlife Biology,* **15,** 10-23.

Nudds, T.D. (1978) Convergence of group size strategies by mammalian social carnivores. *The American Naturalist,* **112,** 957-960.

Okarma, H. (1995) The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica,* **40,** 335-386.

Okarma, H., Jędrzejewski, W., Schmidt, K., Sniezko, S., Bunevich, A.N. & Jędrzejewska, B. (1998) Home ranges of wolves in Bialowieza Primeval Forest, Poland, compared with other Eurasian populations. *Journal of Mammalogy,* **79,** 842- 852.

Oksanen, T., Oksanen, L. & Fretwell, L.O. (1985) Surplus killing in the hunting strategy of small predators. *The Amercian Naturalist,* **126,** 328-346.

Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009) Sport hunting, predator control and conservation of large carnivores. *PLoS ONE,* **4,** e5941.

Paquet, P.C. (1992) Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy,* **73,** 337-343.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. & Zeller, D. (2002) Towards sustainability in world fisheries. *Nature,* **418,** 689-695.

Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andrén, H., Linden, M. & Segerström, P. (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildlife Biology,* **5,** 203-211.

Peterson, R.O. (1977) Wolf ecology and prey relationships on Isle Royale. *United States National Park Service Science Monograph Series,* **11,** 1-210.

Peterson, R.O. & Ciucci, P. (2003) The wolf as a carnivore. *Wolves: behavior, ecology and conservation* (eds L.D. Mech & L. Boitani), pp. 104-130. The University of Chicago Press, Chicago.

Peterson, R.O., Woolington, J.D. & Bailey, T.N. (1984) Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs,* **88,** 1-52.

Pimlott, D.H. (1967) Wolf predation and ungulate populations. *American Zoologist,* **7,** 267-278.

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

Ryall, K.L. & Fahrig, L. (2006) Response of predators to loss and fragmentation of prey habitat: A review of theory. *Ecology,* **87,** 1086-1093.

Rönnegård, L., Sand, H., Andrén, H., Månsson, J. & Pehrson, Å. (2008) Evaluation of four methods used to estimate population density of moose *Alces alces*. *Wildlife Biology,* **14,** 358-371.

Salo, P., Banks, P.B., Dickman, C.R. & Korpimäki, E. (2010) Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. *Ecological Monographs,* **80,** 531-546.

Sand, H., Vucetich, J.A., Zimmermann, B., Wabakken, P., Wikenros, C., Pedersen, H.C., Peterson, R.O. & Liberg, O. (2012a) Assessing the influence of prey–predator ratio, prey age structure and packs size on wolf kill rates. *Oikos,* **121,** 1454-1463.

Sand, H., Wikenros, C., Ahlqvist, P., Strømseth, T.H. & Wabakken, P. (2012b) Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality. *Canadian Journal of Zoology,* **90,** 403-412.

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006a) Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B-Biological Sciences,* **273,** 1421-1427.

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006b) Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour,* **72,** 781-789.

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

Schmidt, P.A. & Mech, L.D. (1997) Wolf pack size and food acquisition. *The American Naturalist,* **150,** 513-517.

Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009) The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology,* **78,** 1249-1258.

Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution,* **13,** 350-355.

Skalski, G.T. & Gilliam, J.F. (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology,* **82,** 3083-3092.

Skogen, K., Mauz, I. & Krange, O. (2008) Cry Wolf!: Narratives of wolf recovery in France and Norway. *Rural Sociology,* **73,** 105-133.

Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone national park, 1995-2000. *Journal of Wildlife Management,* **68,** 153- 166.

Solberg, E.J., Loison, A., Sæther, B.-E. & Strand, O. (2000) Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology,* **6,** 41- 52.

Stahler, D.R., Smith, D.W. & Guernsey, D.S. (2006) Foraging and feeding ecology of the gray wolf (*Canis lupus*): Lessons from Yellowstone National Park, Wyoming, USA. *The Journal of Nutrition,* **136,** 1923-1926.

Storaas, T., Gundersen, H., Henriksen, H. & Andreassen, H.P. (2001) The economic value of moose in Norway - a review. *Alces,* **37,** 97-107.

Swenson, J.E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Söderberg, A., Wallin, K. & Cederlund, G. (2007) Predation on moose calves by European brown bears. *Journal of Wildlife Management,* **71,** 1993-1997.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K., Okarma, H., Ruczynski, I., Sniezko, S. & Gula, R. (2003) Daily patterns and duration of wolf activity in the Bialowieza forest, Poland. *Journal of Mammology,* **84,** 243- 253.

Thiessen, A.H. (1911) Precipitation averages for large areas. *Monthly Weather Review,* **39,** 1082-1089.

Thurber, J.M. & Peterson, R.O. (1993) Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy,* **74,** 879-889.

Vetter, D., Rücker, G. & Storch, I. (2013) A meta-analysis of tropical forest edge effects on bird nest predation risk: Edge effects in avian nest predation. *Biological Conservation,* **159,** 382-395.

Vilà, C., Sundqvist, A.K., Flagstad, Ø., Seddon, J., Björnerfeldt, S., Kojola, I., Casulli, A., Sand, H., Wabakken, P. & Ellegren, H. (2003) Rescue of a severely bottlenecked wolf (Canis lupus) population by a single immigrant. *Proceedings of the Royal Society B-Biological Sciences,* **270,** 91-97.

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

Vucetich, J.A., Hebblewhite, M., Smith, D.W. & Peterson, R.O. (2011) Predicting prey population dynamics from kill rate, predation rate and predator–prey ratios in three wolf-ungulate systems. *Journal of Animal Ecology,* **80,** 1236-1245.

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

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos,* **111,** 259-270.

Vucetich, J.A., Vucetich, L.M. & Peterson, R.O. (2012) The causes and consequences of partial prey consumption by wolves preying on moose. *Behavioral Ecology and Sociobiology,* **66,** 295-303.

Wabakken, P., Aronson, Å., Sand, H., Steinset, O.K. & Kojola, I. (1999) Ulv i Skandinavia: statusrapport for vinteren 1998-99. *Rapport Høgskolen i Hedmark,* **19-99**.

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

Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T.H., Flagstad, Ø., Åkesson, M. & Zetterberg, A. (2013) *Ulv i Skandinavia og Finland: Sluttrapport for bestandsovervåking av ulv vinteren 2012 - 2013.* Høgskolen i Hedmark, Elverum.

Wikenros, C., Sand, H., Ahlqvist, P. & Liberg, O. (2013) Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. *PLoS ONE,* **8,** e77373.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M. (2003) Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology,* **72,** 909-916.

Zimmermann, B., Wabakken, P. & Dötterer, M. (2001) Human-carnivore interactions in Norway: How does the re-appearance of large carnivores affect people's attitudes and levels of fear? *Forest, Snow and Landscape Research,* **76,** 137-153.