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Kristoffer Nordli and Marius Rogstad

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**Be aware of the big bad wolf:
Intra-guild interactions influence
wolverine behavior at wolf kills**

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Forord

Arbeidet med dette studiet har vært motivert av dyp interesse og nysgjerrighet for store rovdyr, og anvendt økologi i bred forstand. Dette har vært den viktigste forutsetningen for oss, da det engang i løpet av vinteren 2014 sklei helt ut med feltarbeid og har siden den gang aldri blitt helt det samme. På bakgrunn av den mangelfulle evnen til å si nei, er dette studiet et resultat av flere tusen timer arbeid; i felt, gjennomgang av viltkamera bilder, dataorganisering, analyser og oppgaveskriving. Likevel hevder vi at dette har vært lystbetont, og det er med skrekk blandet fryd at dette markerer slutten av vårt bachelorløp, men også starten av vår mastergrad og nye eventyr på Evenstad. Hensikten vår med denne oppgaven er å frembringe økt og oppdatert kunnskap om det boreale-barskogsøkosystemet med hovedfokus på jerv, og ulv, samt ulvens hoved byttedyr elg - til forskning og forvaltning, men også til lokalsamfunn og berørte grunneiere.

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Sammendrag

De fleste rovdyr er åtseletere i tillegg til å drepe egne byttedyr, for slike fakultative predatorer/ åtseletere avhenger ikke bare valget av om å spise kadaver eller drepe selv kun av tilgjengeligheten til matressursen, men også avveiningen av risiko forbundet med å unytte seg av kadaver i forhold til interaksjoner som forstyrrelse– eller konkurranse predasjon. Men, ettersom interaksjoner og ressurstilgang endrer seg i tid og rom, må også åtseleteren tilpasse sitt matsøk og sine matvaner til disse forandringene. Vi presenterer her det første detaljerte studiet av jervens (*Gulo gulo*) utnyttelse av ulve (*Canis lupus*) -drepte hjortevilt i Europa, igjennom tre årstider; høst, vinter og sommer. Vi satt opp 33 viltkameraer på ulvedrepte hjortevilt i Hedmark fylke, Norge, for å undersøke frekvensen av besøk og tid på kadaver av både jerv og ulv. Jerven utnyttet kadavrene i høy grad om vinteren, i motsetning til lav utnyttelse om sommeren, når tilgjengelig biomasse fra nyfødte ulvedrepte elgkalver (*Alces alces*) var liten. Den gjennomsnittlige første besøkstiden for jerv var 5,7 dager senere på kadaver med et tidligere gjenbesøk av ulv, sammenlignet med de kadavrene som ikke ble gjenbesøket av ulv før jervens første besøk. Antall jervebesøk hadde en positiv sammenheng med antall gjenbesøk av ulv, men en negativ sammenheng med ulvens tid på kadaver. Vi foreslår at jerven bruker tilstedeværelse av ulv som en indikator for matressurs, men samtidig unngår høy tilstedeværelse av ulv av hensyn til risiko for konkurranse predasjon. Økt kunnskap om den økologiske rollen til jerven i den boreale barskogen er viktig for bevaring og forvaltning av rovdyr samfunnet, da dette også innebærer forvaltning av økonomiske viktige byttedyr som elg. De kompenserende eller additive effektene av sameksistensen mellom ulv og jerv, som predasjon og konsekvensene av høy utnyttelsesgrad bør undersøkes nærmere for å i møtekomme samfunnets, og fellesskapets interesser.

Nøkkelord: *Alces alces*, Biomasse konsumering, boreal barskog, kamerafeller, *Canis lupus*, fakultative åtseleter, furasjerings strategi, *Gulo gulo*, konkurranse predasjon, sesongvarierende matvaner

Abstract

Many carnivores are scavenging in addition to killing their own prey. For facultative scavengers, the choice between scavenging or predating not only depends on resource availability of prey versus scavenging opportunities, but also on risks associated with the utilization of carcasses, specifically interference competition and intra-guild predation. As resource availability and intra-guild interactions change in space and time, scavengers need to adapt their foraging behavior to these changes. Here we present the first detailed study from Europe on the utilization of wolf (*Canis lupus*)-killed ungulate carcasses by wolverine (*Gulo gulo*) during three seasons; fall, summer and winter. We set up 33 remote cameras at wolf kills in Hedmark County, Norway, to examine frequency of visits and time used at carcasses for both wolves and wolverines. Wolverines utilized wolf-killed ungulates to a high degree during winter, as opposed to low utilization during summer, when available biomass of killed neonate moose (*Alces alces*) was small. Wolverines arrived on average 5.7 days later on carcasses that were revisited by wolves, than those that were not revisited before the first wolverine visit. The number of wolverine visits was positively related to the number of wolf visits per carcass, but negatively related to the time wolves spent at a given carcass. We suggest that wolverines use wolf presence as an indicator of food availability, but avoid carcasses with extended wolf presence to reduce the risk of intra-guild predation. Increased knowledge on the ecological role of wolverines in the boreal forest is important for the conservation and management of the large carnivore guild, and economically important prey species, moose. Compensatory or additive effect by wolverines in relation to wolves, like predation and consequences of high utilization should be assessed to accommodate interests and needs of the society.

Keywords: *Alces alces*, biomass consumption, boreal forest, camera traps, *Canis lupus*, facultative scavenger, foraging strategy, *Gulo gulo*, intra-guild predation, seasonal diet shift.

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1 Introduction

Procurement of food resources within an ecosystem is an important component affecting animal survival (DeVault, Rhodes & Shivik 2003). Resource availability can change over the year (Loureiro *et al.* 2009). This is reflected in an animal's space use and diet shifts. Effects of food shortages have been described extensively for large carnivores (Schmidt 2008; Nelson *et al.* 2012). Carnivores must adapt to these temporal and spatial changes in resource availability by switching to alternative prey species, utilizing other foraging strategies (e.g. scavenging), or following migratory prey (Schmidt 2008; Henden *et al.* 2014; Pereira, Owen-Smith & Moleon 2014; Owen-Smith 2015; Walton 2015). However, spatio-temporal changes in resource availability can also provide food surpluses to carnivores (Owen-Smith 2008; Gormezano & Rockwell 2013; Romain, Obbard & Atkinson 2013), such as during ungulate calving season in spring when young animals are weak and vulnerable (Linnell, Aanes & Andersen 1995)

Scavenging is an alternative foraging strategy that animals may utilize in order to accommodate their resource needs. Almost all predators are scavenging at some level or extent (Wikenros *et al.* 2013). Obligate scavengers rely exclusively on food resources killed by other predators or dead of other reasons, e.g. most vultures (*Genus spp.*) (Sebastian-Gonzalez *et al.* 2013). Facultative scavengers use both predation and scavenging as a deliberately opportunistic strategy to adapt to changes in resource availability, and to existing competition within a scavenger community (Selva & Fortuna 2007). However, scavenging comes with a price as well. There are risks associated with exploiting food from other predators. Scavengers might be exposed to increased predation risk as a consequence of using carcasses for food, or interference competition on a common resource (Selva *et al.* 2005; Selva & Fortuna 2007). Scavengers have developed several strategies to meet these risks. Scavengers can change their activity patterns, e.g. utilize carcasses at different times of the day than the apex predator, or they can operate in groups, sharing the resource with other scavengers and thereby lowering individual risk of being predated through increased numbers (Palomares & Caro 1999; Hunter, Durant & Caro 2007). Another strategy is delayed arrival time at the food resource after the predators have left their carcass (Palomares & Caro 1999). This may lower the risk of encounter and intra-guild predation but also means that there will be fewer remains left of the resource as predators often consume a large extent of the resources themselves before leaving the area (Wikenros *et al.* 2013).

The wolverine (*Gulo gulo*) is known as a facultative scavenger with a foraging strategy that opportunistically switches between a variety of food sources depending on resource availability (Landa *et al.* 1997). However, utilization of ungulate carcasses has been regarded as the main foraging strategy in Scandinavia (Myhre & Myrberget 1975; Landa *et al.* 1997). Hunting success in wolverines is less documented (Haglund 1966; van Dijk *et al.* 2008a), and the relationship between scavenging and predation is proposed to underly the principles of optimal foraging, i.e. is driven by what is most energy efficient at a given time (Haglund 1966; van Dijk *et al.* 2008a). Wolverines are capable of killing large prey, including elk calves (*Cervus canadensis*) (Inman *et al.* 2012), calves and juvenile reindeer (*Rangifer tarandus*), domestic sheep (*Ovis aries*), and moose (*Alces alces*) (Haglund 1966; Mattisson *et al.* 2011), as well as small game including rodents (Haglund 1966; van Dijk *et al.* 2008a). The amount of biomass obtained from smaller prey, such as birds and rodents can be significant (Inman *et al.* 2012). During calving season for woodland caribou the wolverine is documented as the main predator of neonates (Gustine *et al.* 2006).

Wolverines are solitary except when females raise their young, and adults exhibit strong intra-sexual territoriality, with male territories being larger than the female's. And male territories can overlap with that of several females (Persson *et al.* 2006; Persson, Wedholm & Segerström 2010). Wolverines may use caching (ie. storing food for later use) as a strategy to acquire and save food during periods of limited resource availability. This is believed to be most important for adult females, as the rate of reproduction is limited to resource availability during wintertime (Persson 2005; Persson 2007; Koskela *et al.* 2013). However, food caching, also appears important during the summer possibly having an equally important role compared to winter foraging and utilization (Inman *et al.* 2012). Distinctive regional and seasonal availability of food resources, obtained from either scavenging or predation, is therefore important to consider in context of the wolverine's flexible behavior in use of food resources (Inman *et al.* 2012).

Compared to other apex predators in the Scandinavian large carnivore guild, such as the wolf (*Canis lupus*), the brown bear (*Ursus arctos*), and the Eurasian lynx (*Lynx lynx*), wolverines are the smallest species. However, they are still able to kill prey considerably larger than themselves (Zager & Beecham 2006; Mattisson *et al.* 2011; Zimmermann *et al.* 2015). Interspecific interactions between wolverines and the other predators in the large carnivore

guild indicate that wolverines successfully utilize carcasses killed by others, thus benefiting from scavenging opportunities provided by co-existence with others predators (Mattisson *et al.* 2011). This phenomenon has been described for lynx (Haglund 1966; Mattisson *et al.* 2011) and wolf (van Dijk *et al.* 2008b; Koskela *et al.* 2013; Wikenros *et al.* 2013). To what extent scavengers can influence the behavior and kill rates of the original predator, is however much debated (Kaczensky, Hayes & Promberger 2005; Mattisson *et al.* 2011; Krofel, Kos & Jerina 2012).

Intra-guild competition is a common phenomenon related to species with overlapping niches, possibly leading to interference competition and intra-guild predation (Polis, Myers & Holt 1989; Palomares & Caro 1999; Linnell & Strand 2000). Effects of intra-guild competition in large carnivores is greater with increasing spatial and dietary overlap, and may have an asymmetrical outcome on the population dynamics of the species involved (May *et al.* 2008). Interspecific killing by wolves of typically smaller medium-sized carnivores like coyotes (*Canis latrans*), wolverines, martens (*Martes martes*) and the red fox (*Vulpes vulpes*) is well confirmed (Palomares & Caro 1999; White *et al.* 2002; Berger & Gese 2007). Intraguild predation by interference dynamics has been reported for a variety of species, from leopards (*Panthera pardus*) that prey on lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and spotted hyenas (*Crocuta crocuta*) to tigers (*Phanthera tigris*) which prey on bear, lynx and wolves (Polis, Myers & Holt 1989).

All four large carnivores in the Scandinavian carnivore guild were considered functionally extinct in Norway and Sweden during the 20th century, mainly due to a policy of heavy persecution (Swenson *et al.* 1995; Wabakken *et al.* 2001; Flagstad *et al.* 2004; Khalil, Pasanen-Mortensen & Elmhagen 2014). Among wolverines, a few small populations reportedly survived in the remote mountain areas in northern Norway (Flagstad *et al.* 2004). After being protected by law in 1966 in Sweden and in the 1970s and 1980s in Norway, the Norwegian part of the population increased in numbers, and during the late 1990s expanded to the eastern boreal forest areas after the recolonization by wolf a few years earlier (Wabakken *et al.* 2001; Flagstad *et al.* 2004; van Dijk *et al.* 2008a). In a spatially heterogeneous landscape, wolverines have been considered as a high altitude dwelling species that seems to prefer mountains as a spatial refuge, while the other three large carnivore species in Scandinavia seem to benefit more from lower altitude boreal forests with relatively similar habitat preferences (May *et al.* 2008). Nevertheless, wolverine numbers have

continued to increase throughout the last decade in forested areas (Flagstad *et al.* 2004; van Dijk *et al.* 2008a; Persson, Ericsson & Segerström 2009). The wolverine seems to re-establish in the forested lowlands including the southernmost counties of Norway, where it had its distribution before the period of heavy persecution (Landa, Linden & Kojola 2000). Additionally it is thought that the previous eradication of wolves also caused a decrease in wolverine numbers, due to less available wolf-killed ungulates to scavenge from in areas where they previously coexisted (Landa & Skogland 1995).

After decades of breeder absence, wolves have recolonized southern parts of Scandinavia through natural immigration from the Finnish-Russian population in the late 1970s, with the first successful reproduction in a cross border territory between Sweden and Norway in 1983 (Wabakken *et al.* 2001). In 2015, the Scandinavian wolf population counted approx. 460 individuals (Wabakken *et al.* 2015). Within this ecosystem, moose are the main prey of wolves throughout the year, especially moose calves, and juveniles in particular. However, as the moose calves grow older, the biomass (kg) of moose calves increases throughout the year (Cederlund, Sand & Pehrson 1991; Sand *et al.* 2008). Thus, while still selecting moose calves as their main prey, wolves switch from moose neonates in the summer period, to almost adult sized calves in the winter. As a consequence, wolf-kill rates change between seasons, since a higher kill rate is needed when prey biomass is less per kill (Sand *et al.* 2008; Zimmermann *et al.* 2015).

There has been limited research regarding this boreal forest recolonization by wolverines, sympatric with wolves. However, wolverines in boreal forests have been found to utilize different food resources compared to wolverines in more alpine areas. Diet studies, using scat analysis, have shown differences in the wolverine diet, where reindeer, hare, birds and rodents were most common in the alpine areas without wolf presence, to mainly consisting of moose in the boreal forest, where sympatric with wolves (van Dijk *et al.* 2008b). Moreover, wolverines were found to use lower elevations during the winter season in order to scavenge on wolf kills, but are, in general more active at higher elevation possibly to avoid predation risk by wolves (van Dijk *et al.* 2008a). Wolverines are also reported to avoid using wolf tracks to locate carcasses killed by wolves, and wait up to two weeks before they utilize a wolf-killed ungulates (van Dijk *et al.* 2008a).

Here we present the first detailed European study on wolverine utilization of and behavior at wolf-killed ungulate carcasses in relation to intra-guild interactions. Our main objective is to highlight the spatio-temporal facultative scavenging strategy of the wolverines in relation to intra-guild interactions with wolves at carcasses of wolf-killed ungulates by using remote cameras during three seasons: early summer, fall and winter. Implications regarding how the wolverine relates to interactions with wolves, and the rate of utilization within and between seasons is important for managing and conserving large carnivores within the boreal ecosystem. Additionally, to understand how wolves respond to carcass utilization by wolverines may be important for human harvested moose populations, as a possible effect could be increased wolf-kill rates on moose.

We hypothesize that 1) facultative scavenging by wolverines depends on the seasonally changing available biomass per wolf-killed ungulate. We further predict that 2) wolverine utilization of wolf-killed ungulates depends on the elevation of the kill site. Higher elevations are considered safer compared to lower elevations due to avoidance of wolf presence. Moreover, as wolverines are likely to be influenced by the presence of wolves, we predict that 3) the most important factor for the wolverine utilization rate at wolf kills, estimated as the number of visits and the time at wolf kills, is related to the number of revisits by wolves on carcasses and available biomass. However, as wolves are both pack animals and intra-guild apex predators, we predict that 4) wolverines and wolves will not be at the carcass simultaneously. Additionally, because the available biomass at the carcass is suspected to be important for both wolves and wolverines we also predict that 5) both species use of carcasses will be affected by the amount of biomass remaining. Further we also investigate the timing of the first visit by wolverine in relation to estimated time of death of the ungulate and predict that 6) wolverine do not visit carcasses before two weeks after death to avoid intra-guild interactions (van Dijk *et al.* 2008a).

2 Methods

2.1 Study area

The study area covered the territory of the Julussa wolf pack and was located in Hedmark county in southeastern Norway (Fig. 1, 61°N, 08°E). The wolf territory size was 904 km² during the years 2014 and 2015 (100% Minimum Convex Polygon MCP)(ArcGIS 2014). It is characterized by mountain ridges and the two main valleys of Glomma and Rena rivers. Elevations ranged from 215 – 1009 m above sea level, and the tree line is at 800 – 900 m above sea level. Boreal coniferous forest is dominating the area with spruce (*Picea abies*) and pine (*Pinus sylvestris*), interspersed with deciduous trees of birch (*Betula pubescens*), willow (*Salix caprea*), aspen (*Populus tremula*) and rowan (*Sorbus aucuparia*). The area has a continental inland climate with dry and cold winters. Snow cover from mid October to end of April (eKlima 2015).

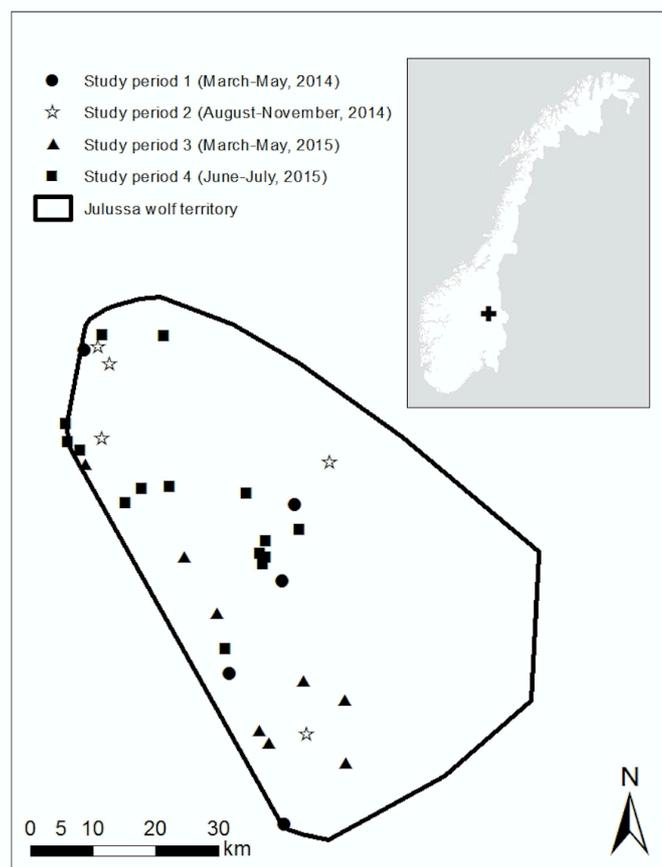


Figure 1. Distribution of monitored carcasses in the Julussa wolf territory for all periods. The symbols represent the carcass location within the wolf territory (100% MCP of all wolf positions in 2014 and 2015).

Moose is the largest and the most abundant ungulate inside the study area and represents the main prey species for wolves throughout the whole year (Sand *et al.* 2005; Gundersen *et al.* 2008; Sand *et al.* 2008). The average moose density was estimated to relatively high at 1.2 moose/km² during the winter 2002-03 (Zimmermann *et al.* 2007). The majority of the moose in the study area is seasonally migrating from the valley bottoms at 250 - 400m above sea level in the winter to higher elevations at 600 - 850 m above sea level during summer (Gundersen, Andreassen & Storaas 2004; Storaas *et al.* 2005; Eriksen *et al.* 2011). The migration normally starts between November/December for the winter season and April/May for the summer season, and is correlated to snow depth and temperature (Gundersen 2003; Eriksen *et al.* 2011). Other ungulates and potential prey for wolves are red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), both at low densities of 0.01 per km² (Zimmermann *et al.* 2007). Large carnivores, lynx and brown bear, in addition to wolves and wolverines, reside within the study area.

2.2 Study animals

Wolves in the Julussa wolf territory were immobilized from helicopter with the permission granted by the FDU (Forsøksdyrutvalget - Norway) and the Norwegian Environmental Agency (Miljødirektoratet – Norway) according to the protocols described by (Arnemo, Ahlqvist & Segerström 2004). All captured wolves were equipped with GPS neck collars with GSM download link (GPS plus, Vectronics Aerospace, Germany). The collars were programmed to take six GPS positions per day (UTC+1 00:00 - 04:00 - 08:00 - 12:00 - 16:00 - 20:00) and to send the positioning data once per day in packages of 6 positions per SMS.

In February and March 2014 the alpha female (M1409) and male (M1410) together with three nine months old pups (males M1406 and M1408 and female M1407) were collared. During the spring and early summer 2014, M1406 and M1408 dispersed from the natal territory, while the female pup stayed within the territory boundaries. During the subsequent winter the alpha pair was re-collared. The amount of GPS-data used in our study varied depending on functioning collars and individuals still present within the territory. We mainly studied the alpha female (M1409), the alpha male (M1410), and the young female (M1407) from the litter born in 2013. But we included also data of the two male pups (M1406, M1408) during winter and spring 2014, before they dispersed. The number of study animals within study periods did not reflect the total pack size. The pack size was determined by snow tracking and DNA sampling of feces by the Scandinavian wolf monitoring program (Wabakken *et al.*

2013; Wabakken *et al.* 2014; Wabakken *et al.* 2015), and all DNA samples were analyzed with microsatellites markers by Rovdata, Trondheim. Pack size was estimated at n=8 in winter 2013/2014, n=7 in winter 2014/2015, and n=10 in winter 2015/2016. A new litter was born each year, confirmed by DNA, and visual counts of approx. 3 weeks old pups in the denning area (Wabakken *et al.* 2015).

Regarding numbers and distribution of wolverines inside the study-area the situation is unclear, however three spatially separated breeding site for wolverines have been confirmed, where reproduction has occurred at least on two sites simultaneously (Norwegian Environmental Agency 2015). By using the Norwegian population estimates (Rovdata 2015) (65 litters/340 adult individuals), and the extrapolating this proportion to the Julussa wolf territory (conversion factor of 5,23 per breeding site), potentially they were 10-15 adult individuals within this wolf territory of study.

2.3 Wolf-killed ungulates

We defined four study periods of 40 to 67 days, two of them during late winter, one during summer and one during fall (Table 1). Our objective was to find wolf-killed ungulates of large ungulates and put up camera traps as fast as possible after time of death, by checking wolf positions. During all four intensive study periods we had contact with at least two wolves whose collars regularly sent positions. The GPS success rate, i.e. the ratio of acquired to programmed number of positions varied between study periods (Table 1). All acquired positions received by GSM were entered into ArcGIS the same or following day and buffered with 100m. Overlapping buffers, i.e. positions within 200 m of each other, were defined as 'clusters' (Sand *et al.* 2005; Zimmermann *et al.* 2007), while positions > 200m from the closest neighbor were termed 'single positions'. Based on wolf movement patterns, time use, and time of the day, we set up a list of prioritized clusters and single positions to be visited in the field.

Table 1. Study periods defined by start and end date for each period, GPS success, number of positions checked, number of carcasses found, and number of carcasses where cameras were mounted.

Field periods	Start date	End date	Field days	Acquired positions	Positions checked	GPS success	Carcasses	Cameras
1 Winter	27.03.14	19.04.14	23	676	509	93.9%	24	5
2 Fall	28.08.14	18.09.14	21	369	72	93.2%	5	5
3 Winter	20.03.15	20.04.15	31	439	97	76.2%	9	8
4 Summer	01.06.15	30.06.15	29	320	136	59.3%	17	15
Total			104 days	1804	814	80.6%	55	33

All prioritized positions and clusters were checked the same or following day depending on the current location of the wolves, in order to minimize our disturbance at carcasses. We did not visit positions closer than 1 km to the natal den during the denning period in summer 2015. We postponed check of positions if the most recent wolf position was within 1 km. Postponed positions were checked the following day. Time lag in scheduled delivery of positions occurred several times during period 1 (n=2 carcasses) and period 4 (n= 2 carcasses). Time between death date and camera placed at these carcasses was skewed by 3-4 days.

To estimate body weight and biomass of the carcasses, we categorized the kills into different age classes: Newborn calf (0-1 month old), calf (>2 months old), yearling (12-23 months old), and adult (>2 years old). Age class was determined by size, tooth wear or tooth development in the field. Sex was determined by genitalia, antlers, or rosary sockets. Consumption stage (%) was visually determined in field and reassured by comparing pictures of all carcasses afterwards. Available biomass at carcass was calculated with the assumption of linear growth for newborn calves of $y=1.123x + 13$, with y being the estimated weight (kg), 13 kg as supposed birth weight, and x being number of days from the 1 June (Sand *et al.* 2008). For yearling and adult moose, we used an average constant weight depending on the time of the year for both sexes (Zimmermann *et al.* 2015). Snow cover (%), snow depth (mm) and tracks or signs of other species present prior to camera placement were noted as well. Time of death was estimated in the field as a timespan from earliest to latest assumed date of death, based on blood coagulation, consumption, and decomposition. In addition, we estimated time of death in ArcGIS by identifying the first wolf position within 100 m of the carcass. If this date concurred with the timespan registered in field, we defined it as death date. Doing so, we confirmed death date for all carcasses. We also concluded that all carcasses were killed by

either the alpha female (M1409) or male (M1410), except of two neonates calves in study period 4 which were killed by the two-year-old female M1407.

2.4 Camera use and picture registration

At the confirmed wolf-killed ungulates we put up camera traps (n=33, Table. 1). All cameras were of the type Reconyx HC 600 supported with covert IR diodes (Reconyx, USA). Cameras were adjusted with correct date and time, and were programmed with advanced setup as following; 1) Time lapse scheduled to 5 minute intervals, 2) motion trigger with series of three pictures with one second interval and a quiet period for 1 minute between each burst, 3) sensor trigger at high sensitivity and 4) image quality at maximum. The cameras were placed with a standardized procedure of having the carcass in the center point of the cameras' detection angle, and detection range (40 degree of field view, 30 meter detection range) (Reconyx 2013). Prior placing, detection and illumination were tested at various distances. To successfully determine pictures by night and day we experienced that camera distance should not exceed more than 12 meters. Thus distance, height and tilt of camera differed due to the placement availability between carcasses, mean camera distance 5.1 meter (1-9 meter) and mean camera height 1.2 meter (0.6- 2.6 meter).

We checked as many positions as possible in the first study period, as this was our pilot period. We therefore detected far more carcasses than the number of available cameras (Table 1). However, cameras within this period were placed randomly regardless of carcass biomass or altitude. During study period 4 (summer 2015), we checked as many single positions as possible in addition to the clusters and used a dog on a leash (Sand *et al.* 2008). This extra effort was required because wolves prefer to kill newborn moose calves in this time period (Sand *et al.* 2008) and often there are only a few bone splinters and tufts of hair left at the kill site.

Review of all camera pictures (n=377.220; Table 2) was done using Reconyx Mapview Professional (Reconyx 2014). For each picture, we manually registered the number of animals per species for all mammals and golden eagle (*Aquila chrysaetos*). We also registered number and type of failure; illumination, snow, mists, camera displaced, carcass displaced, and disturbance by humans or dogs. Metadata such as date, time, year, temperature, moon phase, trigger type time-lapse (TP) and motion (MP) was, along with the manually registered data,

transferred into Microsoft excel (Microsoft Corporation 2014). For each picture, we defined if it was taken during dawn, day, dusk or night based on light conditions. We used day-specific times of sunrise, sunset and civil twilight (the centre of the sun $\leq 6^\circ$ below the horizon) (U.S. Naval Observatory Washington DC) to classify time of day into the four categories.

Table 2. Number of monitored carcasses per study period, with start and end date, number of camera days, and the number of time lapse pictures and motion pictures.

Season	Start date	End date	Operation days	Carcasses	Camera days	Time lapse p.	Motion p.
1 Winter	27.03.14	07.05.14	41	5	149	40.423	2.053
2 Fall	28.08.14	05.11.14	69	5	287	85.698	919
3 Winter	20.03.15	21.05.15	62	8	371	105.601	17.877
4 Summer	01.06.15	12.07.15	41	15	403	10.921	13.728
Total			213	33	1210	342.643	34.577

2.5 Visits at carcass

Cameras operated during 14 - 67 days. To standardize camera periods, we therefore included only the first 18 days of the cameras' operation time. This cut-off time was motivated by the presence of wolf and wolverine at the carcass within the total operation time: 82% and 81% of all visits of wolves and wolverines, respectively, occurred within the first 18 days. We merged data of study period 1 and 3, as they were both from the same season, but from different years (Table 1, Table 2, and Table 3).

We defined a visit to the carcass by either wolf or wolverine as a time sequence of presence pictures. Sequences interrupted by less than 30 minutes of absence pictures were considered as one visit. If it took more than half an hour to the next presence picture, we considered this a new visit. The time interval of 30 minutes was chosen due to the frequency distribution of the time intervals between visits. This distribution showed a sudden change at 30 minutes for both wolf and wolverine from high to low number of intervals. From the start and end time of each visit, we calculated the total time spent at the carcass. If multiple animals were at the carcass, we multiplied the number of animals with the length of the visit ("animal hours").

2.6 Data analysis

For statistical analyses, we used R 3.2.3 (RStudio Team 2015) with the interface RStudio (version 0.99.484) To compare available biomass at carcasses and elevation of carcass sites among seasons, we applied one-way ANOVAs.

For our main hypotheses regarding time to first visit, number of visits and time spent at carcasses by wolves and wolverines (Table 3) we did not include cameras that were set up more than 9 days after date of death. In this way, we excluded carcasses with unknown visiting history. Additionally, we only included cameras that were either visited by wolf (n=18) or wolverine (n=20), a total of 22 cameras. This was based on the ability to test wolf and wolverine together without reducing sample size, by this we included n=4 absence cameras for wolf and n=2 absence cameras for wolverine, because a combination of either two species was present at these carcasses.

Both time lapse pictures and motion pictures was used to test these hypotheses. We used linear regression models for the log-transformed responses Time to first wolverine visit, Time to first wolf re-visit, and Time spent at carcass by wolf and wolverine (Table 3). Because number of visits is a count, we applied a GLM with poisson link (Table 3). The relatively small sample size (n = 22) did not allow us to enter combinations of more than two predictors into the models. Correlated predictor variables were not entered into the same models. Since most of the variables were correlated, we ended up with entering them one by one. Because we were interested to test hypotheses rather than to compare different models, we used an alpha-level of 0.05 to find significant relations between predictor and response, instead of AIC-model selection (see Appendix I).

To describe the diurnal pattern of carcass use by wolverine and wolf, for each combination of season and time of day, we calculated the proportion of only time-lapse (TP) pictures with presence of wolverine and wolf. We used chi square statistics to test if the number of wolf and wolverine pictures per time of day deviated from an equal distribution across the day.

To evaluate the camera method, we included all 24 cameras that were set up within 9 days of time of death with both time lapse pictures and motion pictures. We tested for seasonal biases regarding camera distance to carcass and camera height over ground with one-way ANOVA. We applied generalized linear models with Poisson link to relate the number of visits by

wolves and wolverines to camera distance and height (Table 3). In addition, we tested the first visit, and revisit for wolf and wolverine to time to camera set up as a predictor, to give an estimate of influence and timing of camera placing (Table 3.)

Table 3. Explanatory variables included in the models to predict time to first visit, number of visits, and time spent at carcass for wolverines and wolves.

Predictors	Description	Time to first visit (log)		Number of visits GLM with Poisson link		Time at carcass (log+1)	
		Linear Model		link		Linear model	
		Wolverine	Wolf	Wolverine	Wolf	Wolverine	Wolf
Season	Summer, Fall, Winter	x	x	x	x	x	x
Biomass	Continuous (kg)	x	x	x	x	x	x
Elevation	Continuous (masl)	x	x	x	x	x	x
Wolf visit prior to wolverine	Binary 0-1	x		x		x	
N of wolf visits	Count			x		x	
Wolf time at carcass	Continuous					x	
Wolf pack size	Binary 1, > 1			x		x	
Wolverine visit prior to first wolf revisit	Binary 0-1						x
N of wolverine visits	Count					x	
Wolverine time at carcass	Continuous (sec)						x
Camera height	Continuous (cm)	x	x	x	x	x	x
Camera distance	Continuous (cm)	x	x	x	x	x	x
Death date camera placed	Continuous (days)	x	x				

3 Results

3.1 Carcasses, biomass and elevation

A total of 33 cameras was placed at wolf-killed ungulates, 32 were moose and 1 red deer. The age distribution of kills was 45% new born moose calves (neonates) (n=15), 45% moose calves (n=15), 3% yearling moose (n=1), 3% adult moose (n=1), and 3% adult red deer (n=1). There was on average 32.6 kg (\pm SE = 11.4 kg) biomass at carcasses. However, the available biomass varied with season (Fig. 2a, $F_{(2,21)} = 9.41$, $p < 0.001$, $R^2 = 0.47$). The highest available biomass at carcasses was in the winter period, while biomass per carcass was lowest in the summer period. The elevation of the carcass sites averaged 434.1 m (\pm SE = 33.9). Elevation of carcasses varied with seasons (Fig. 2b, $F_{(2,19)} = 11.08$, $p < 0.001$, $R^2 = 0.54$), with the highest elevation in the fall period and the lowest elevation in the winter period.

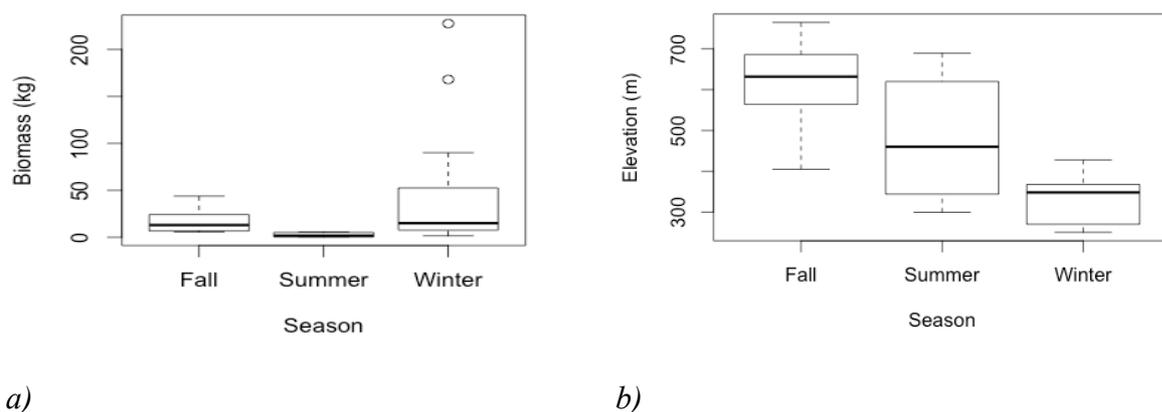


Figure 2. Seasonal variation of biomass per carcass (a) and elevation of carcass sites (b). The boxplot indicates the median, 25, and 75% percentiles with the whiskers indicating the range of values.

3.2 Carcass visitors

Among the more than 377.000 taken pictures at the 33 carcasses, we found presence of mammals or golden eagle on 162.879 pictures (43% of all pictures). Red fox showed up at 78% of all carcasses, followed by wolverines (66%) and wolves (60%) (Table 4). Golden eagles were only present at 21% of the kills, mostly in winter. This species however was observed most frequently at the kills, with 4.01% of all time lapse (TL) pictures (Table. 4). With 464 TL-pictures (1,23%), wolverine was the third most frequent visitor, while wolves returned to carcasses in 0,27% of the time (Table 4).

Table 4. The relative occurrence of different mammalian species and golden eagle spent at 33 wolf-killed ungulates in the Julussa wolf territory, expressed as the number of visited carcasses and the proportion of time lapse-pictures (TL) per season.

Species	Fall (n=5)		Summer (n=15)		Winter (n = 13)		Total (n=33)	
	N carcasses	% TL	N carcasses	% TL	N carcasses	% TL	N carcasses	% TL
Golden Eagle	1	0.65	1	0	5	3.36	7	4.01
Red fox	3	0.02	10	0.06	13	1.89	26	1.97
Wolverine	5	0.17	4	0.02	13	1.04	22	1.23
Wolf	4	0.02	3	<0.01	13	0.25	20	0.27
Brown Bear	0	<0.01	0	0	1	0.11	1	0.11

Wolverine visited all 5 carcasses during fall, while only 4 carcasses were visited by wolf. In summer, wolverine visited 4 of the 15 carcasses (27%). Only one of these 4 carcasses was revisited by wolf. Wolf revisited 3 carcasses (20%), while 60% of the carcasses were not visited by neither wolf nor wolverine. During winter both species visited all carcasses (Fig. 3). For wolverines, we observed only single individuals at carcass, and for wolves, we observed both single and a maximum number of four individuals at the same time revisiting a carcass.

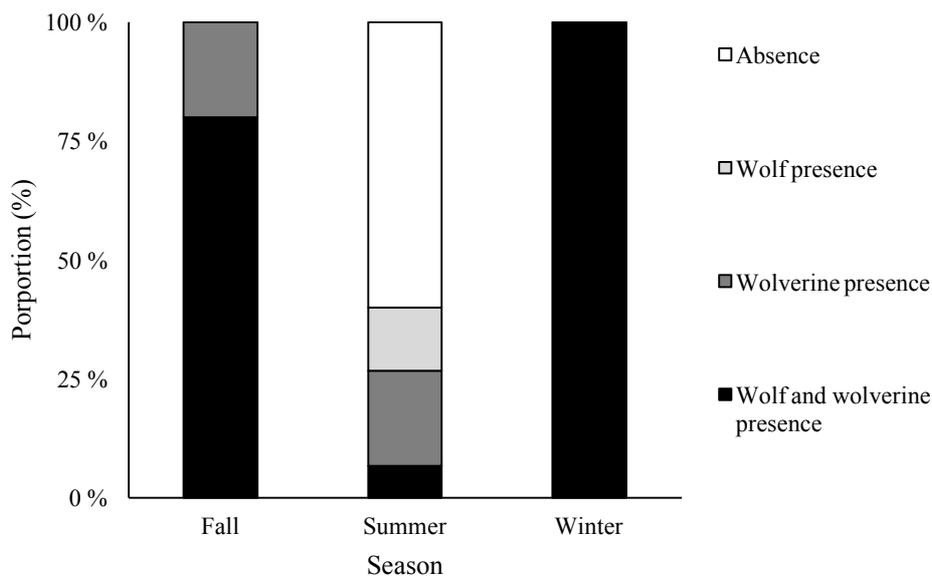


Figure 3. Proportion (%) of carcasses (n=33) that had presence of both wolverine and wolf (black), wolverine only (dark grey), wolf only (light grey), or none of these two species (white).

3.3 Wolverine utilization of carcasses

3.3.1 First visit at carcass

It took on average 5.47 days (\pm SE = 0.88) for wolverines to show up at a carcass after time of death. This time to first wolverine visit depended on if wolves revisited a carcass before their arrival (Fig. 4, $F_{(1,18)} = 16.82$, $p < 0.001$, $R^2 = 0.48$). If a carcass was not re-visited by wolves, wolverines came to the carcass on average after 3.2 days (95% CI = 2.4 – 4.2). Wolverines came on average 5,7 days later if wolfs were back at the carcass (mean number of days to first visit = 9.0, 95% CI = 5.9 – 13.7). We did not find any effect of season ($F_{(2,17)} = 1.92$, $p = 0.177$, $R^2 = 0.18$), biomass of carcass ($F_{(1,18)} = 0.01$, $p = 0.997$, $R^2 = 0.01$) or elevation ($F_{(1,18)} = 0.57$, $p = 0.462$, $R^2 = 0.03$).

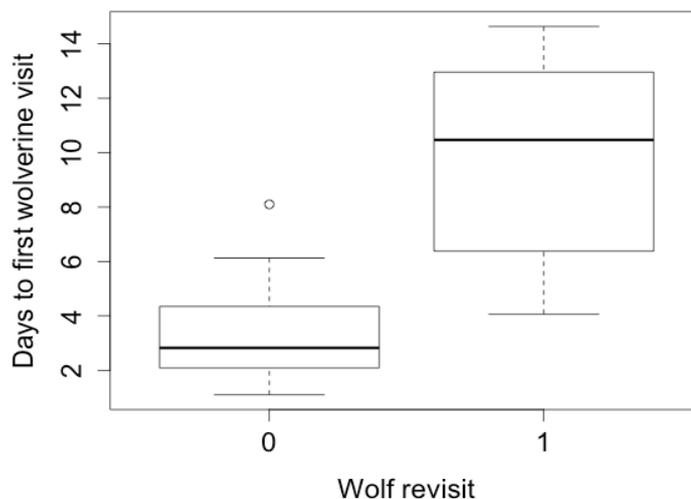
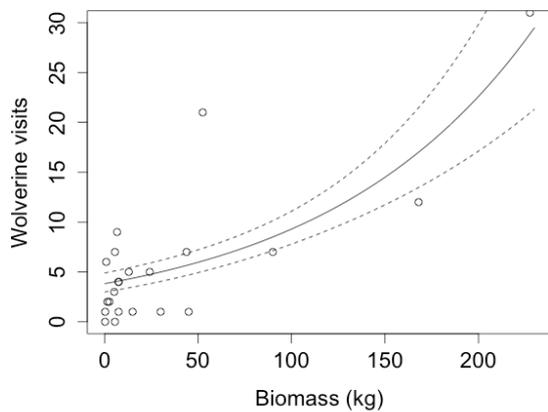


Figure 4. Number of days between time of death of the wolf-killed ungulate and the first visit by a wolverine visit. Time to first visit depended on if wolves had returned to the carcass before the wolverine arrived (1), or if the wolves returned later or never returned (0). The boxplot show median, 25, and 75% percentiles with the whiskers indicating the range of values.

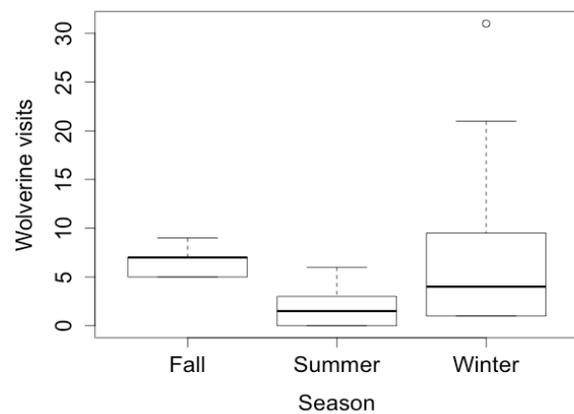
3.3.2 Number of visits

Wolverines visited wolf-killed carcasses on average 6.50 times (\pm SE = 1.68). Number of wolverine visits depended on available biomass at the carcass (Fig. 5a, $\chi^2_{(1,20)} = 77.67$, $p < 0.001$) Carcasses with a higher amount of biomass were more frequently visited by

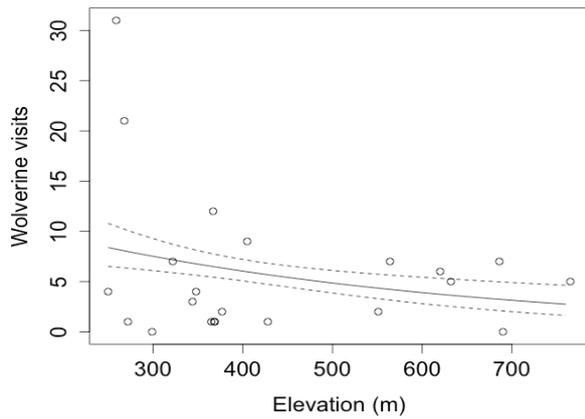
wolverines than carcasses with low biomass. Number of wolverine visits varied also with season (Fig. 5b, $\chi^2_{(2,19)} = 26.90$, $p < 0.001$). Wolverine had a lower visiting rate in the summer period compared to fall and winter. Visit rate increased from summer to fall and was highest in the winter. Wolverine visit rate was also related to elevation (Fig. 5c, $\chi^2_{(1,20)} = 12.28$, $p < 0.001$). Wolverines visited more frequently carcasses at lower than at higher elevation. We also found a slight tendency that wolverine visit rates were lower at carcasses where wolves had spent much time (Fig. 5d, $\chi^2_{(1,20)} = 3.76$, $p = 0.052$). However, we found a strong positive effect between number of wolverine visits and number of wolf visits at a given carcass (Fig. 5e, $\chi^2_{(1,20)} = 9.16$, $p < 0.002$). Carcasses that were more frequently visited by wolves were also more frequently visited by wolverine. We also found a strong effect with less wolverine visits at carcasses where wolves had revisited the carcass before the wolverines' first visit (Fig. 5f, $\chi^2_{(1,20)} = 13.39$, $p < 0.001$). Presence of multiple wolves at a given carcass however was not related to number of wolverine visits ($\chi^2_{(1,19)} = 1.10$, $p = 0.290$).



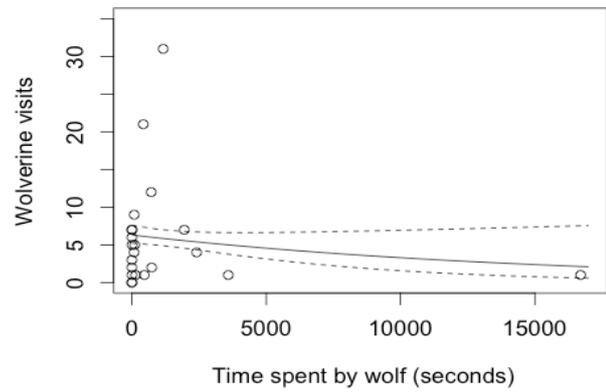
a)



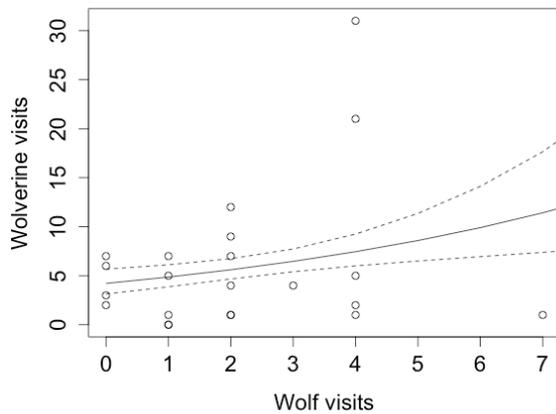
b)



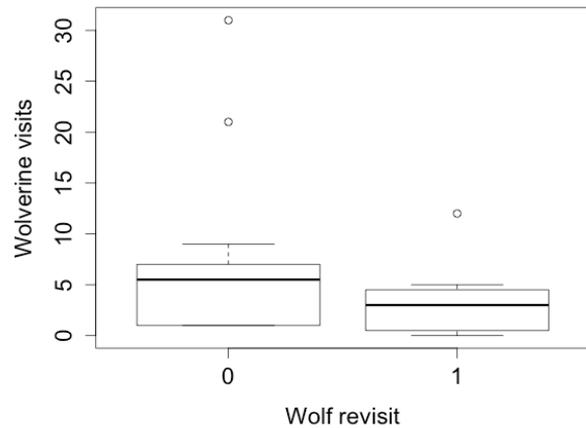
c)



d)



e)



f)

Figure 5. Number of wolverine visits in relation to biomass (a), season (b), elevation (c), time spent at carcass by wolves (d), number of wolf visits (e), and if wolves revisited the carcass before the first wolverine visit (f). Dots in a),c),d),e) are observed values, solid lines are predicted values and stippled lines are the 95% CI. Boxplots in b) and f) show median, 25%, and 75% percentiles with the whiskers indicating the range of values.

3.3.3 Time spent

Based on data from the number of carcasses either visited by wolverines and or revisited by wolf (n=22), wolverines spent on average 1.38 hours (\pm SE = 0,77) at carcasses. And total of 33 recorded hours on carcasses with wolverine presence (n=20). The time spent at carcass varied with season ($F_{(2,19)} = 5.24$, $p = 0.015$, $R^2 = 0.36$). Wolverines spent less time at carcass in the fall and summer periods and significant more time in the winter period. Time used was also positively related with available biomass of the carcass ($F_{(1,20)} = 11.70$, $p < 0.003$, $R^2 = 0.37$) (Fig. 6a-b). We did not find any effect of elevation ($F_{(1,20)} = 1.05$, $p = 0.318$, $R^2 = 0.05$), the total time spent at carcass by wolves ($F_{(1,20)} = 0.19$, $p = 0.667$, $R^2 = 0.01$), the number of

wolf visits at carcass ($F_{(1.20)} = 0.02$, $p = 0.989$, $R^2 = 0.01$), nor the size of the wolf pack that had visited the carcass ($F_{(1.16)} = 2.94$, $p = 0.106$, $R^2 = 0.155$). We did not find any effect between the total time spent at carcass for wolverines and if the wolves had their first revisit at carcass before the wolverine ($F_{(1.20)} = 1.98$, $p = 0.175$, $R^2 = 0.09$)

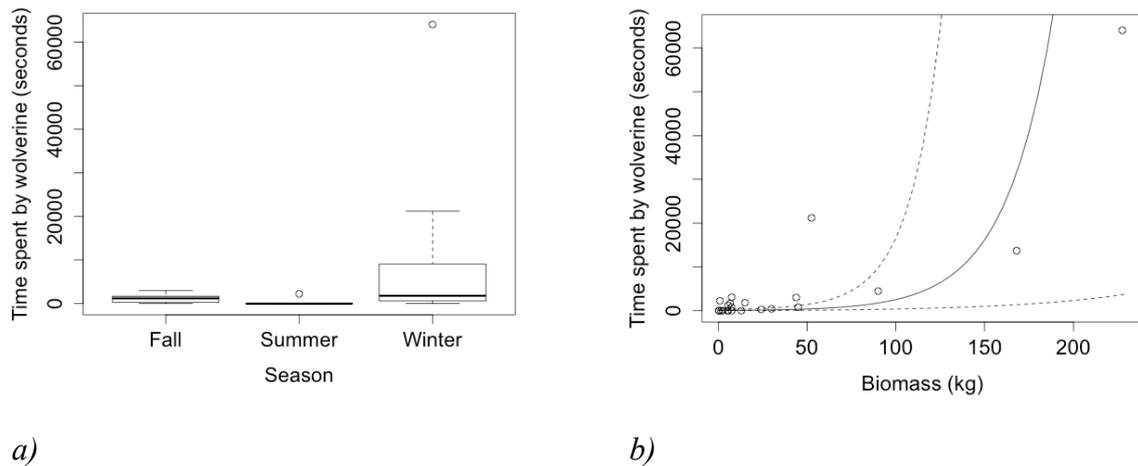


Figure 6. Time spent by wolverine (seconds) at carcass in different seasons (a) Time spent by wolverine (seconds) related to biomass (b) Boxplot (a) show median, 25, and 75% percentiles with the whiskers indicating the range of values. Dots in (b) are observed values, solid lines are predicted values and stippled lines are 95% CI.

3.3.4 Diel activity pattern at carcass

Wolverines showed a distinct diurnal activity pattern in their presence at carcass in all three seasons (summer $\chi^2_{(1.3)} = 14.45$, $p = 0.002$; fall $\chi^2_{(21.3)} = 40.80$, $p < 0.001$; winter $\chi^2_{(1.3)} = 359.46$, $p < 0.001$). They preferred the dark periods, i.e. they were more often than expected at the carcass during night hours in fall and winter, and during dawn and dusk in summer (Fig. 7a-c). The summer period had no night hours. In all seasons, they spent less time than expected during daytime, but also during dawn and dusk in fall and winter.

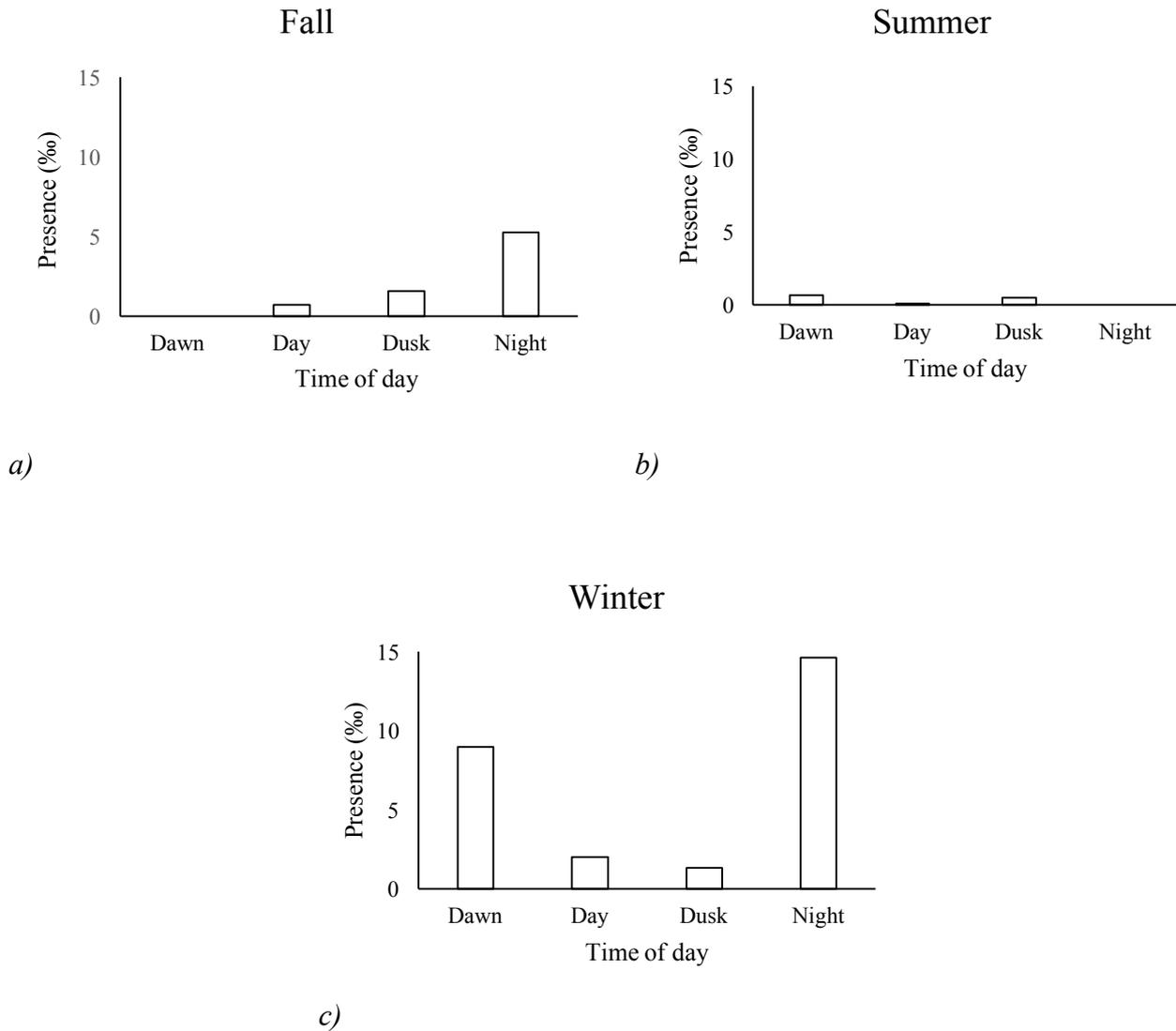


Figure 7. Variation in wolverine presence at wolf kills based on the number of time laps pictures (‰) during dawn, day, dusk and night and in the study periods fall (a), summer (b), and winter (c)

3.4 Wolf utilization of carcasses

3.4.1 First revisit at carcass

It took on average 7.7 days (\pm SE = 1.22) for wolves to revisit at their carcass after time of death. We did not find any effect of season ($F_{(2,15)} = 2.03$, $p = 0.167$, $R^2 = 0.21$), elevation ($F_{(1,16)} = 0.80$, $p = 0.384$, $R^2 = 0.04$), biomass ($F_{(1,16)} = 0.52$, $p = 0.479$, $R^2 = 0.03$) or first visit by wolverine before first revisit by wolf ($F_{(1,16)} = 0.22$, $p = 0.649$, $R^2 = 0.01$).

3.4.2 Number of visits

Wolves re-visited carcasses on average 2.6 times (\pm SE = 0.38). We did find a seasonal effect, i.e between the periods fall, summer and winter ($\chi^2_{(2,19)} = 13.94$, $p < 0.001$). Wolves had a higher re-visitation rate during winter, and a lower re-visitation rate in the fall and the lowest in the summer. Wolves re-visited more frequent on carcass at lower than at higher elevations ($\chi^2_{(1,120)} = 5.49$, $p = 0.019$) (fig. 8 a-b). We found no effect for biomass ($\chi^2_{(1,20)} = 1.48$, $p = 0.224$), number of wolverine visits at carcass ($\chi^2_{(1,20)} = 1.41$, $p = 0.235$) or the total time spent at carcass by wolverine ($\chi^2_{(1,20)} = 1.95$, $p = 0.161$).

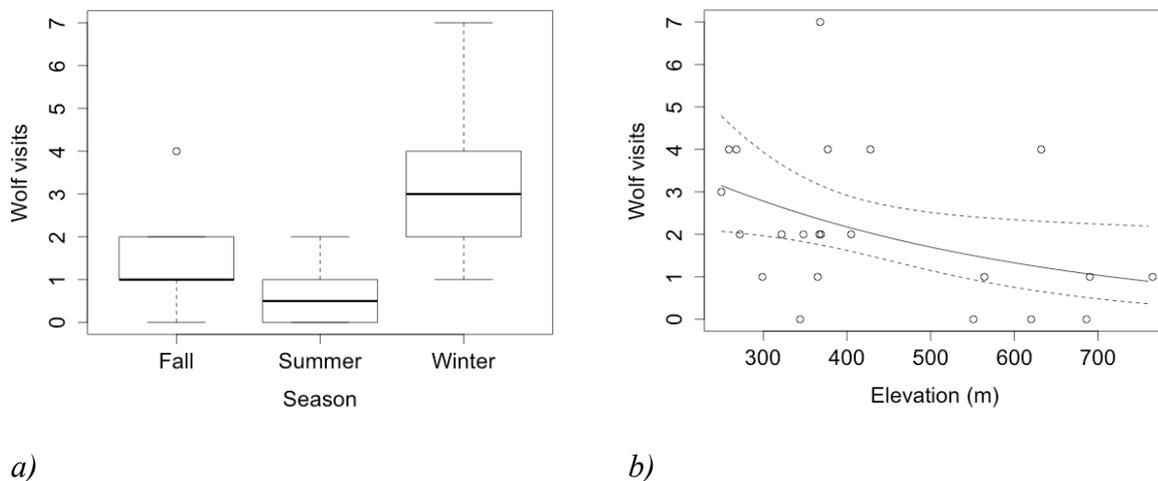


Figure 8. Number of wolf visits in different seasons (a) Number of visits by wolf in relation to elevation (b) The boxplot a) show median, 25, and 75% percentiles with the whiskers indicating the range of values. Dots in b) are observed values, solid lines are predicted values and stippled lines are 95% CI.

3.4.3 Time spent

Based on data from the number of carcasses either visited by wolverines and or re-visited by wolf (n=22) Wolves spent on average 0.38 hours (\pm SE = 0.20) at carcasses. And a total of 8 recorded hours on carcasses with wolf presence (n=18). The time at carcass varied with available biomass ($F_{(1,20)} = 4.55$, $p = 0.045$, $R^2 = 0.19$); wolves spent more time at carcasses with a higher amount of biomass than carcass with low biomass. Consequently, wolves spent more time on carcasses at lower elevation than carcasses at higher elevation ($F_{(1,20)} = 8.31$, $p < 0.009$, $R^2 = 0.29$), and during winter than during fall and summer ($F_{(2,19)} = 39.33$, $p < 0.001$, $R^2 = 0.81$) (fig. 9a-c). We did not find any correlation between the time wolves used at carcass and the time used by wolverines ($F_{(1,20)} = 1.86$, $p = 0.188$, $R^2 = 0.09$) or the number of visits by wolverines ($F_{(1,20)} = 1.19$, $p = 0.289$, $R^2 = 0.06$).

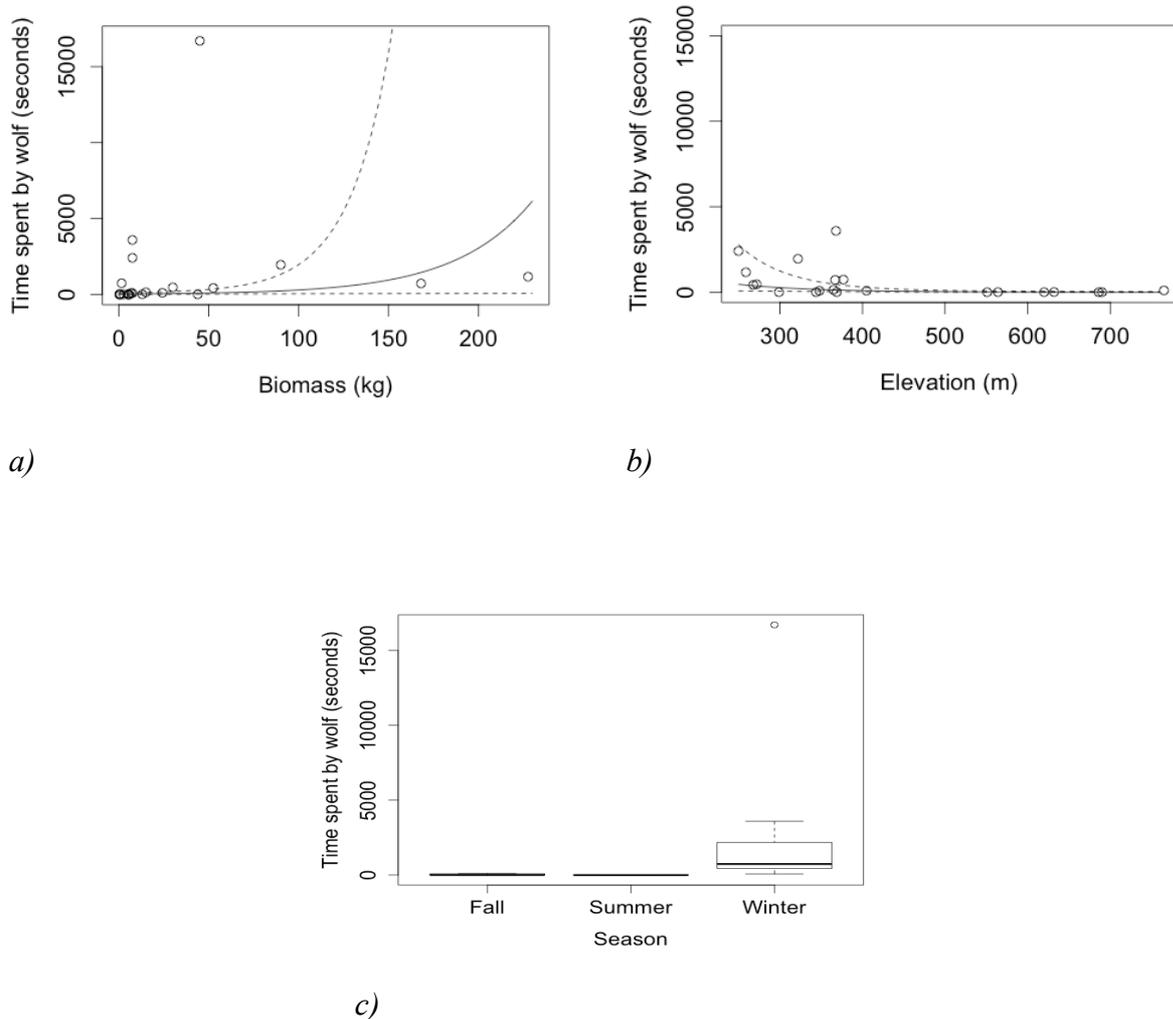


Figure 9. Time spent by wolf at carcass in relation to biomass (a) and time spent by wolf at carcass in relation to elevation (b) Time spent by wolf (seconds) at carcass in the three periods (c) Dots in a) – b) are observed values, solid lines are predicted values and stippled lines are 95% CI. Boxplot c) show median, 25, and 75% percentiles with the whiskers indicating the range of values.

3.4.4 Diel activity pattern at carcass

Wolves showed a distinct nocturnal pattern of carcass use in the fall period ($\chi^2_{(1,3)} = 2.93, p < 0.001$). For the summer period there were no time lapse pictures of wolves at any of the carcasses. The activity pattern for winter was significantly different from an equal use throughout the day independent of light conditions ($\chi^2_{(1,3)} = 45.61, p < 0.001$). (Fig. 10a-c) Wolves visited the carcasses mostly during dawn (0,27%) and night (0,23%) of all time lapse pictures in winter.

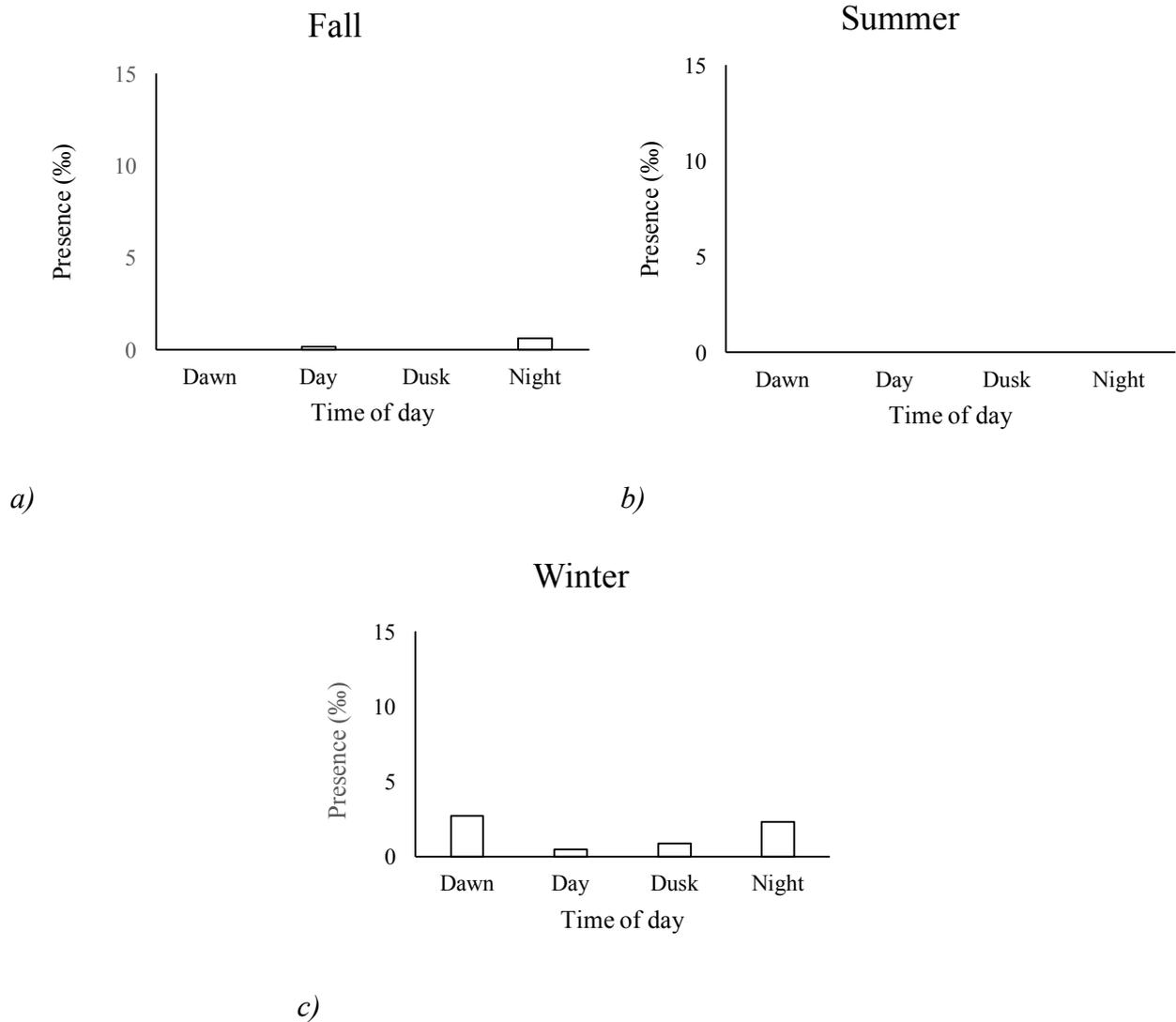


Figure 10. Variation in wolf presence at wolf kills based on the number of time lapse pictures (%) during dawn, day, dusk and night during the different study periods fall (a), summer (b) and winter(c).

3.5 Camera monitoring

While cameras were set up at comparable heights in each season ($F_{(2,21)} = 1.72$, $p = 0.203$, $R^2 = 0.14$), the distance to the carcass was biased ($F_{(2,21)} = 9.28$, $p = 0.001$, $R^2 = 0.46$). The cameras were placed closer to the carcass during summer compared to fall and winter (Fig. 11).

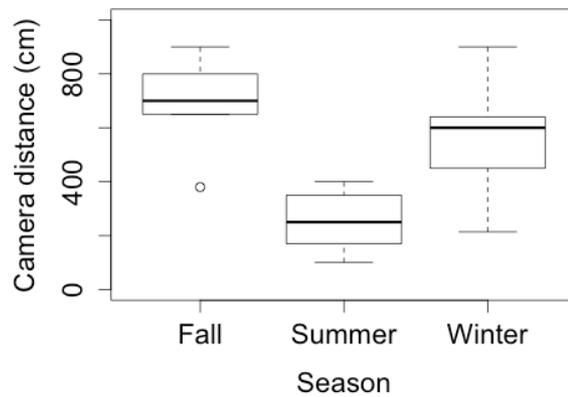


Figure 11. Distance between camera and carcass in the different periods. Boxplot show median, 25, and 75% percentiles. with the whiskers indicating the range of values.

We did not find any relation between the total time spent at carcass and camera distance to carcass, or the height of camera, neither for wolverine ($F_{(2,21)} = 0.78$, $p = 0.471$, $R^2 = 0.07$) nor wolf ($F_{(2,21)} = 1.24$, $p = 0.309$, $R^2 = 0.11$). We found a positive correlation between number of wolverine visits and camera distance ($\chi^2_{(1,22)} = 12.30$, $P < 0.001$) (Fig. 12), but not for camera height ($\chi^2_{(1,22)} = 1.30$, $p = 0.254$). Number of wolf visits was not related to either camera distance ($\chi^2_{(1,22)} = 3.13$, $p = 0.077$) or height ($\chi^2_{(1,22)} = 2.78$, $p = 0.095$).

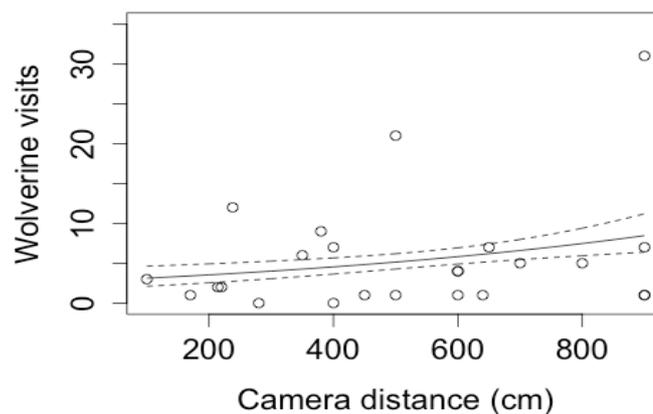


Figure 12. Number of visits by wolverine in relation to camera distance (cm) Dots are observed values, solid lines are predicted values and stippled lines are 95% CI.

We also tested the amount of days elapsed from death date to the date when cameras were placed and how that affected the time to first and second visit by wolverine and the first revisit by wolf. Here we did find an effect with the number of days elapsed between time of death to the date were camera was placed at the carcasses to the first visit by wolverine ($F_{(1,20)} = 9.57$, $p < 0.006$, $R^2=0.32$) (Fig. 13). We did not find any effect for first time revisit by wolf ($F_{(1,17)} = 0.16$, $p = 0.692$, $R^2 = 0.01$) or the second visit by wolverine ($F_{(1,13)} = 0.63$, $p = 0.443$, $R^2 = 0.05$).

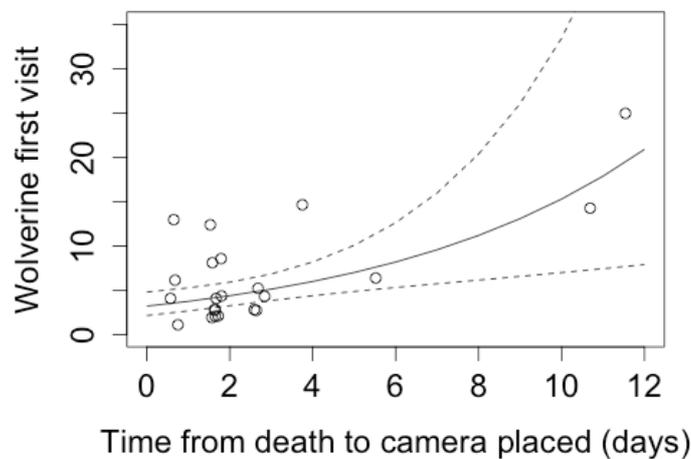


Figure 13. Number of days to wolverine first visit in relation to number of days elapsed from death date to camera placed Dots are observed values, solid lines are predicted values and stippled lines are 95% CI.

3.5.1 Failure index

Time lapse camera failures due to ambient factors showed a seasonal and diurnal pattern of occurrence (fall $\chi^2_{(1,3)} = 1035.56$, $p < 0.001$; summer $\chi^2_{(1,3)} = 5004.38$, $p < 0.001$; winter $\chi^2_{(1,3)} = 318.15$, $p < 0.001$). Failures occurred mostly during night and in the transition phase at dusk and dawn, and least during day (Fig. 14a-c). Success rate and failure rate shown in Table. 5.

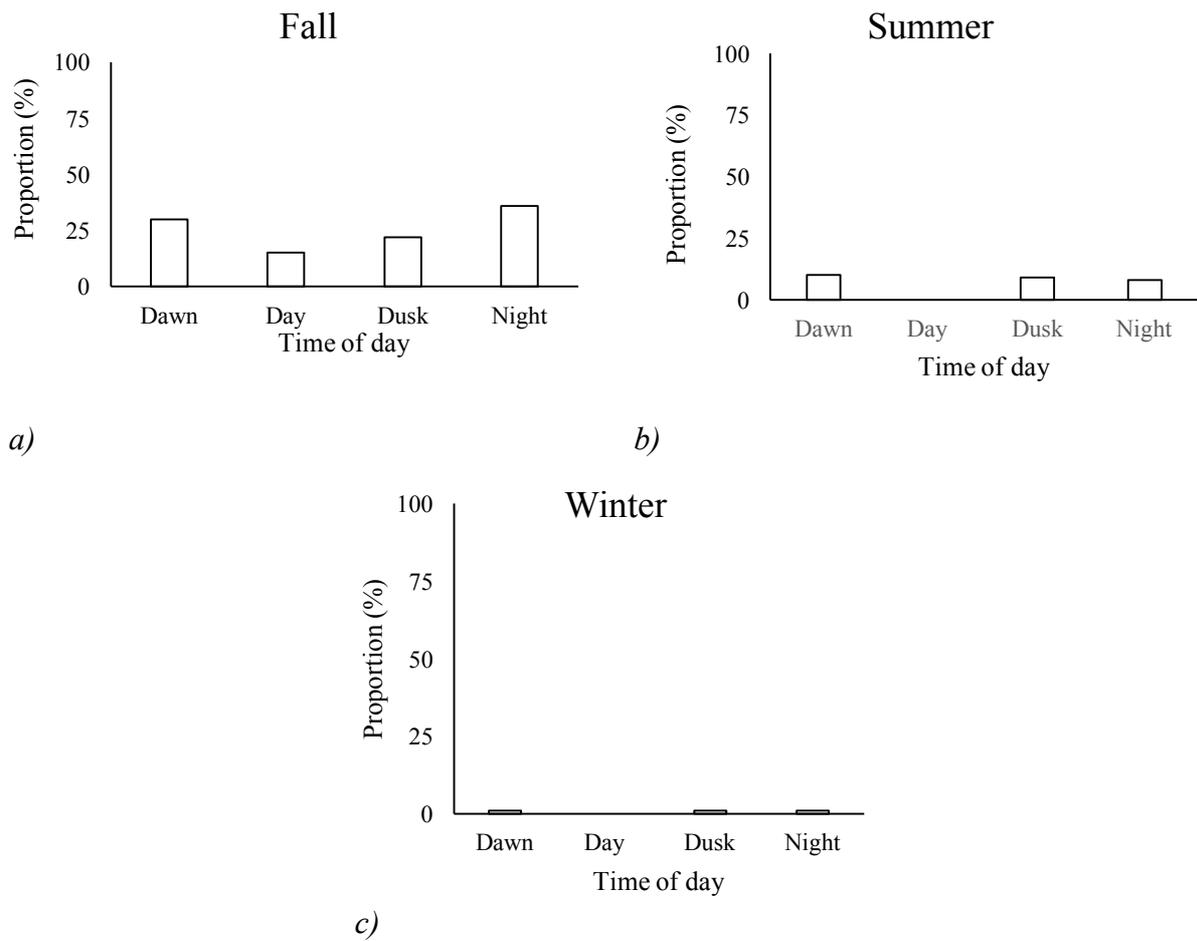


Figure 14. Variation of occurrence of failure pictures (%) in dawn, day, dusk and night during the different study periods fall (a), summer (b) and winter (c).

Table 5. Amount of failures (%) and success rate (%) within the study periods fall, summer and winter. Success rate is calculated on numbers of taken pictures time lapse (TL) and the number of received images. Failure rate is calculated from total failure pictures of both motion picture (MP) and time-lapse pictures impossible to interpret.

Period	Cameras	Motion p. (MP)	Time lapse p. (TL)	Programmed p.	Failure p.	Total p.	Success rate (%)	Failure rate (%)
Fall	5	468	25917	25920	6403	25917	99.9	24.7
Winter	13	15523	65852	67392	1436	71196	97.7	2.0
Summer	6	630	31110	31104	312	65852	100	0.5
Total	24	16621	122879	124416	8151	162965	98.7	5.0

4 Discussion

Our study suggests a temporal diet shift in seasonal foraging by wolverines at wolf-killed moose carcasses. This is indicated by high carcass utilization during winter as opposed to low utilization, and moderate to low utilization, during summer and fall, respectively. We believe that biomass, in respect to the amount of resources available at a specific time of the year, is the main impetus for wolverines' relationship to scavenging at wolf-killed ungulates. We suspect this is because scavenging is most energy efficient during this time, in relation to exploiting food from wolf kills by scavenging, and competition for food in the nested system of scavengers in the boreal forest. In order to compete with other scavengers such as golden eagles, red foxes and ravens, wolverines need to act quickly, and therefore must trade off risk and gain of scavenging carefully. We propose that for wolverines, as an opportunistic facultative scavenger, living sympatrically with wolves poses great opportunities but also possible risks. Intra-guild interactions are to be avoided but must be balanced within the optimal foraging strategy of wolverines (e.g. elevation and visit rate). The presence of wolves (i.g. revisit rate) to a certain extent could imply increased biomass of food resources, but a greater amount of wolf presence (i.e. time spent by wolf) could increase risk of encounter. Alternatively, the opposite is also possible, where wolf presence may indirectly imply less food as the carcass is being consumed by wolves themselves and may not be energetically worth the risk.

4.1 Seasonal variation of resource availability shapes the foraging behavior of wolverines

The age distribution of the wolf-killed carcasses found in our study corresponded to that found in previous predation studies of the Scandinavian wolf population (Sand *et al.* 2005; Sand *et al.* 2008; Sand *et al.* 2012; Zimmermann *et al.* 2015): wolves prefer to kill moose calves throughout the year. Since neonate moose calves are still small in summer, the biomass left at these kills after the first exploitation by wolves is very limited. As calves grow throughout summer and fall, biomass of wolf-killed ungulates increases. During late winter, adult moose can also, to a limited degree, be killed by wolves (Zimmermann *et al.* 2015), as also shown in our study. We therefore found a strong seasonal change of available biomass of wolf-killed ungulates, which was paralleled by a changing foraging pattern of both wolf and wolverine. Wolf revisited 100% of their own kills during winter, 80% during fall and only

20% in the summer periods. Wolverine visited 100% of all monitored carcasses during winter and fall, but only 26% of carcasses during summer. Number of visits per carcass and time spent at a given carcass changed correspondingly with the seasonally changing biomass at carcasses for both wolf and wolverine.

Generalist predators switch prey as a functional response to changing prey availabilities, as for example shown for red fox predation on roe deer fawns during the short summer period (Panzacchi *et al.* 2008). Correspondingly, we expect also facultative scavengers to switch from predation to scavenging depending on the availability of prey and carcasses. It is a result of optimal foraging; if the net gain of scavenging outweighs that of predation, the facultative scavenger will rather switch to scavenging. The net gain is merely a function of the time used to search for prey or carcasses, the time used for handling, the costs associated with inter- and intraspecific interactions at a kill or carcass, and the nutritional value of the kill or carcass.

Which foraging strategy is used by wolverines (predation or scavenging) switches depending on the variety of resource availability (Landa *et al.* 1997), and prey choice is coupled to hunting success and energy expenditure (Haglund 1966; van Dijk *et al.* 2008a). A similar relationship between foraging strategy and temporal resource availability is reported for badger (*Meles meles*) (Loureiro *et al.* 2009). The summer and winter diet has been reported as equally important for wolverine (Inman *et al.* 2012). However, diet choice during summer is less documented (Haglund 1966; van Dijk *et al.* 2008a). It is known that wolverines have the ability to subsist on a wide spectrum of food elements (Landa *et al.* 1997). In the boreal forest of our study area, the prey spectrum could include everything from rodents, small game, and possibly neonate moose calves. Wolverines are capable of killing wild neonate ungulates; during the calving season of woodland caribou, wolverine were the main predator (Haglund 1966; Gustine *et al.* 2006; Mattisson *et al.* 2011). During winter, prey availability is probably lower due to snow cover, while the biomass of wolf-killed ungulates is high. Based on our findings, we hypothesize that wolverines in our study area, to a large extent, depend on these carcasses during winter, while switching to other food sources in summer.

4.2. Spatial variation of resource availability

We found a strong correlation between elevation of the carcass sites and season in our study: wolf kills were situated at low altitudes in winter, and at higher altitudes in summer and fall. This pattern is a result of the seasonally changing space use of moose: Moose migrate to

valley bottoms during winter because of higher snow depths at upper elevations, while during summer moose spend more time in higher elevation ranges (Cederlund, Sand & Pehrson 1991; Gundersen 2003; Sand *et al.* 2008; Eriksen *et al.* 2011) to exploit the increased energy content of late-growing plants (Bischof *et al.* 2012).

It has been previously illustrated how the wolverine exploits and scavenges at wolf-killed ungulates by moving down into the valley bottoms (van Dijk *et al.* 2008b). After utilizing a carcass, it is suggested that wolverines return to higher altitudes to avoid interactions with wolves. Our study showed that wolverines utilizing carcasses at lower elevations increased their rate of visits, rather than spending additional time at the carcasses. This movement pattern and behavior coincides with what has been previously hypothesized (van Dijk *et al.* 2008b). Whether this is a result of avoidance of wolves or of human activity at lower elevations, where impacts of infrastructure seems to be important to wolverines (May *et al.* 2006), is hard to say. It could actually just be an effect of higher biomass availability per carcass in winter, see 4.1.

4.3. Intra-guild interactions between wolf and wolverine

It took less than a week, 5.5 days on average, from the time of kill to the first visit by wolverine. This is a considerably shorter timespan than the average of 14 days reported in an earlier study (van Dijk *et al.* 2008a). The authors suggested avoidance of wolves as the main reason for the wolverines to postpone their first visit. Our data supports the hypothesis of wolverines avoiding intra-guild interactions with wolves: If a carcass was not re-visited by wolves, wolverines arrived on average already 3.2 days after time of death. If wolves revisited a carcass before a wolverine, it took wolverines on average 8.9 days to arrive. Another indication of avoidance of intra-guild interactions was the negative correlation between number of wolverine visits and the total time wolves spent at a carcass. This may be a result of risks associated with interference competition, or of indirect resource competition; less food is available at carcasses that are exploited more by wolves.

Interestingly, we found the number of wolverine visits to increase with the number of wolf visits at carcass. We propose that wolverines could use the presence of wolves as a strategy to locate carcasses, with the presence of wolves, to a certain extent, associated with a possible food source. Such phenomenon has been found with raven and wolf at wolf-killed ungulates

(Kaczensky, Hayes & Promberger 2005). The mechanism behind this dynamic is however uncertain and most likely complex, especially when wolf revisits only depended on lower elevations and season. If it is the case that wolverines are using wolf re-visits at carcasses as a part of their strategy to locate carcasses it would imply that the wolverines are also locating carcasses randomly regardless of biomass. As an opportunistic scavenger this is possibly the most efficient way of finding resources killed by wolf. Even so, this is in coherence with our findings that wolverine first visit was not related to biomass, and was only delayed by wolf visit. Conversely, another explanation for increasing wolverine visits with wolf visits is that wolverines increase their rate of visits due to the rate of revisits by wolf as a strategy to avoid encounter.

Wolf kill rates in Scandinavia during winter have been estimated at 0.22 moose kill/day/pack (Sand *et al.* 2008; Zimmermann *et al.* 2015), i.e. the time span between consecutive kills was on average 4.6 days. This is less than the time to first revisit by wolf at carcass observed in this study (mean 7.7 days), and the first visit by wolverine (mean 5.5 days). This may indicate that the wolverine “waits” for the wolves to make a new kill before they exploit a wolf-killed carcass, and that the scavenging behavior therefore is a function of wolf kill rates.

In summary, our data indicate that wolves may both facilitate and hamper the scavenging activity of wolverines. Considering the fact that wolverines easily can escape intraguild predation by wolves by climbing trees in the coniferous forest (Grinnell 1926; White *et al.* 2002), risk of mortality is probably small. Interspecific killing of wolverines by wolves has however been documented (Palomares & Caro 1999; White *et al.* 2002; Berger & Gese 2007). A strategy for the subordinate species to avoid interference competition at a common resource is to shift the diurnal activity pattern. We did not find any segregation between wolverine and wolf in relation to time of the day. We conclude that the wolverine deliberately utilizes and exploits wolf kills, and presence of wolves could either be associated with food or danger. The extent of one or the other is the impetus for the efficiency and rate of utilization of wolf kills by wolverine.

4.4 Potential effects of wolverine scavenging on wolf-kill rates

The total time spent at a carcass averaged 1.38 hour for wolverines (33 hours total), compared to 0.38 hours for wolves after camera set-up (8 hours total). Such high utilization rates of scavengers can have effects in relation to higher kill rate by the main predator. Increased kill rates as a response to scavenging has been reported. Ravens were found to promote a possible increased kill rate by wolves on their prey (Kaczensky, Hayes & Promberger 2005). Increased kill rates have also been seen between lynx and bear (Krofel, Kos & Jerina 2012). In a system where there may be high competition at carcasses by a variety of scavenging species, it is believed that increased utilization could increase the kill rates of the main predator (Mattisson *et al.* 2011). However, this also helps sustain the possible predation from the facultative scavenging, when available resources of food increases by coexisting and exploiting from others (Mattisson *et al.* 2011; Lopez-Bao *et al.* 2016). We hypothesize that the high utilization of carcasses by wolverines during winter, in addition to competition from all the other facultative scavengers could possibly increase wolf kill rates, however this is uncertain and should be investigated further.

4.5 Remote camera method, possible biases and sources of error

By evaluating our method of using remote cameras we found a potential, though weak bias of camera placement on the number of wolf and wolverine visits. This could lead us to believe that the camera distance and even height can be a factor of disturbance and should be accounted for in the interpretation of observations. On the other hand, this could also be related to other more logical aspects of detection by monitoring with camera traps. One possible explanation could be that with a longer distance the detection angle is wider, and the detection range is longer which makes observations easier detected and interpreted. We suggest that using remote cameras could have impact for possible biases depending on species, even when using stealth cameras with covert IR diodes.

By testing how many days between date of death and camera was placed we found that we may have missed the first time visit by wolverine, especially if the camera is placed > 5 days after time of kill. This should be taken into consideration when describing the average first time visit at carcasses for wolverine, and their use of wolf-killed ungulates, which could be even more extensive than we report. In our case, we did not find any correlation between time

of camera placement and time to first visit/revisit by wolverine and wolf. We propose that the timing of disturbance at carcasses, by setting up camera traps, had little effect on the species behavior, but timing could possibly influence observations because of the consumption rate and available biomass is a likely impetus for.

Using relative non-invasive methods like remote camera monitoring can have drawbacks. We suspect possibly 4-5 individual, or more, wolverines caught on camera, where it was possible to tell individuals apart by size and markings on chest, and ribbons on the back. However, we have no guarantee regarding sex or age of these wolverines. Proposing that within our predator guild wolverines utilizing carcasses may be breeding females, solitary adult males or roaming juvenile wolverines of both sexes, the spatial use and foraging strategy could be age- and sex-dependent. An additional concern is our sample size. The fall season had a lower sample size and higher failure rate compared to larger sample sizes in summer and winter season, as shown in the relative failure index. In relation to season we also had two carcasses with high amount of biomass, which bias our observations, and this should be taken into consideration when interpreting results. Lastly, how unique visits are defined (here minimum 30 minutes interval between presence pictures) plays an important role for the outcome of the analyses.

4.6 Conclusion, and further studies

Many questions are left unanswered regarding the wolverine in the boreal forest ecosystem such as distribution, spatial use, survival, reproduction, abundance as well as interactions with wolves and the impact to prey species such as moose, or predation by wolverines themselves. We know little about the impact of the wolverine's high use of carcasses during winter, though supplemental feeding is reported to increase reproductive rates for females (Persson 2005). We document a seasonal variation where the wolverines tend to rely on wolf-killed ungulates during winter, more than previously reported. The consequences of high utilization rates by wolverines at kills by wolves during winter could be an important factor for wolf utilization, possibly increasing the kill rate during the winter and even in fall, when the time used at carcass by wolf seems dependent on remaining biomass. On the contrary, wolverines' high utilization of wolf-killed moose in the winter to low utilization on the newborn moose calves during summer makes it even clearer that the wolverine's ecological impact should be looked into more in depth, especially to determine whether wolverines are killing newborn calves themselves or not. Surveying and assessing the basic knowledge of wolverine's

ecological role in the boreal forest ecosystem, and especially the compensatory or additive effect of wolverines in relation to wolves in a predator guild should be an important focus point for future research.

4.7 Management implications

Following their recolonization, challenges related to conservation and management of carnivores in Norway has increased. Sources of conflict involve livestock and semi-domesticated reindeer (Mattisson *et al.* 2011), but also cultural conflicts within hunting, competition for game and aspects to human fear (Zimmermann, Wabakken & Doetterer 2001). To accommodate these challenges, management faces problems meeting the needs of the affected user groups while still conserving sustainable populations of large carnivores. Increased knowledge related to interactions of species within the carnivore guild seems important when managing carnivores in general but also their coexistence and impacts in relation to prey species. Carnivore distributions are often anthropogenically restricted to management zones, but this often comes with an uneven distribution of benefits and costs for local societies. Therefore, increased knowledge to such a system, especially a system in development, seems to be an important focus point for the future. Managing forest wolverines within zones where conflicts with domestic sheep and reindeer husbandry are missing or low, might be a good strategic plan. These areas, today, will include a big part of the geographically differentiated management area for wolf, common referred to as the wolf zone where free-grazing sheep and reindeer husbandry is less or has been phased out. But the effects, both negatively and positively, should be investigated and weighted properly before implementing.

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Appendix I

Response variables and combinations of predictor variables in respective models.

Analysis	Response variable	Predictor	estimate	SE	t	P
LM, log	Biomass	Intercept	2.629	0.6142	4.28	0.000
		Season summer	-2.357	0.8317	-2.834	0.011
		Season winter	0.587	0.7408	0.793	0.438
		Intercept	2.981	1.175785	2.535	0.020
		Elevation	-0.002	0.002551	-0.634	0.534

Analysis	Response variable	Predictor	estimate	SE	t	P
LM, log	Wolverine first visit	Intercept	1.156	0.1387	8.335	<0.001
		Wolf revisit before wolverine visit	1.038	0.2532	4.102	<0.001
		intercept	1.468	0.1920	7.646	<0.001
		Biomass	0.000	0.0028	-0.003	0.997
		intercept	1.810	0.4828	3.749	0.001
		Ellevation	-0.001	0.0011	-0.752	0.462
		intercept	1.277	0.2999	4.257	0.001
		Season summer	-0.268	0.4498	-0.595	0.559
		Season winter	0.444	0.3617	1.229	0.236

Analysis	Response variable	Predictor	estimate	SE	z	P
GLM poisson	Number of wolverine visits	Intercept	1.440	0.1478	9.743	<0.001
		Number of wolf re-visits	0.142	0.0455	3.127	0.002
		Intercept	1.841	0.0929	19.83	<0.001
		Time at carcass wolf	0.000	0.0000	-1.655	0.098
		Intercept	1.231	0.1225	10.05	<0.001
		Biomass	0.009	0.0010	9.881	<0.001
		Intercept	1.887	0.1741	10.84	<0.001
		Season summer	-1.194	0.3371	-3.542	<0.001
		Season winter	0.158	0.2051	0.769	0.442
		Intercept	2.673	0.2714	9.848	<0.001
		Elevation	-0.002	0.0007	-3.305	0.001
		Intercept	1.783	0.1588	11.233	<0.001
		Number of wolfs in pack	0.028	0.0772	0.356	0.722
		Intercept	1.986	0.0990	20.057	<0.001
		Wolf re-visit before wolverine visit	-0.733	0.2134	-3.436	0.001

Analysis	Response variable	Predictor	estimate	SE	t	P
LM, log +1	Time at carcass wolverine	Intercept	5.29E+00	8E-01	6.43	<0.001
		Time at carcass wolf	9.64E-05	2E-04	0.436	0.667
		Intercept	3.7509	1E+00	2.766	0.014

		Numbers of wolf in pack	1.1541	7E-01	1.714	0.106
		Intercept	7.573223	2E+00	3.38	0.003
		Elevation	-0.004982	5E-03	-1.025	0.318
		Intercept	4.12999	7E-01	5.739	<0.001
		Biomass	0.03708	1E-02	3.421	0.003
		Intercept	5.39713	1E+00	4.405	<0.001
		Number of wolf re- visits	0.00638	4E-01	0.014	0.989
		Intercept	6.0468	1E+00	4.522	<0.001
		Season summer	-3.9554	2E+00	-2.185	0.042
		Season winter	0.8855	2E+00	0.549	0.589
		Intercept	6.1952	9E-01	6.695	<0.001
		Wolf visit before wolverine visit	2.1572	1.5345	-1.406	0.175

Analysis	Response variable	Predictor	estimate	SE	t	P
LM, log	Wolf first revisit	Intercept	2.225177	0.4537	4.905	<0.001
		Elevation	-0.000935	0.0010	-0.895	0.384
		Intercept	1.921032	0.1896	10.13	<0.001
		Biomass	-0.001872	0.0026	-0.724	0.479
		Intercept	1.734067	0.2817	6.156	<0.001
		Wolverine first visit	0.001975	0.0393	0.05	0.961
		Intercept	1.3623	0.3092	4.405	0.001
		Season summer	0.925	0.4723	1.958	0.069
		Season winter	0.5352	0.3611	1.482	0.159
		Intercept	1.9091	0.2120	9.007	<0.001
		Wolverine visit before wolf	-0.1477	0.3180	-0.465	0.648

Analysis	Response variable	Predictor	estimate	SE	z	P
GLM poisson	Number of wolfre-visit	Intercept	0.47	0.3536	1.329	0.184
		Season summer	-0.8755	0.6124	-1.43	0.153
		Season winter	0.6874	0.3919	1.754	0.079
		Intercept	1.762958	0.4559	3.867	<0.001
		Elevation	-0.002464	0.0011	-2.189	0.029
		Intercept	0.649433	0.1755	3.700	<0.001
		Biomass	0.002771	0.0022	1.285	0.199
		Intercept	0.61936	0.1912	3.239	0.001
		Number of wolverine visits	0.02139	0.0171	1.251	0.211
		Intercept	6.76E-01	0.1608	4.204	<0.001
		Time at carcass wolverine	1.22E-05	0.0000	1.532	0.126

Analysis	Response variable	Predictor	estimate	SE	t	P
LM, log +1	Time at carcass wolf	Intercept	3.33718	0.7293	4.576	0.000
		Biomass	0.02343	0.0110	2.133	0.045
		Intercept	8.824696	1.7232	5.121	<0.001
		Elevation	-0.010778	0.0037	-2.883	0.009

		Intercept	2.5449	0.6550	3.885	0.001
		Season summer	-1.978	0.8869	-2.23	0.038
		Season winter	4.2823	0.7900	5.421	<0.001
		Intercept	3.79E+00	0.7093	5.346	<0.001
		Time at carcass wolverine	6.56E-05	0.0000	1.364	0.188
		Intercept	3.548	0.8665	4.095	0.001
		Number of wolverine visits	0.1013	0.0929	1.09	0.288
Analysis	Response variable	Predictor	estimate	SE	t	P
LM log	Camera height	Intercept	154	19.9100	7.734	<0.001
		Season summer	-55.67	26.9600	-2.065	0.052
		Season winter	-34.54	23.4300	-1.474	0.155
LM log	Camera distance	Intercept	686	89.5100	7.664	<0.001
		Season summer	-432.67	121.2000	-3.57	0.002
		Season winter	-113.54	105.3300	-1.078	0.293
Lm log +1	Time at carcass wolf	Intercept	-433.826	694.8120	-0.624	0.539
		Camera distance	2.312	1.2160	1.902	0.070
		Intercept	172.178	901.9530	0.191	0.850
		Camera height	4.842	6.9540	0.696	0.494
LM log +1	Time at carcass wolverine	Intercept	-2489.05	6339.8600	-0.393	0.698
		Camera distance	14.41	11.0900	1.299	0.207
		Intercept	4548.544	8000.3550	0.569	0.575
		Camera height	3.334	61.6820	0.054	0.957
GLM Poisson	Number of wolf re-visit	Intercept	0.951968	0.8154	1.167	0.256
		Camera distance	0.00211	0.0014	1.479	0.153
		Intercept	0.69535	0.9936	0.7	0.491
		Camera height	0.01109	0.0077	1.448	0.162
GLM Poisson	Number of visits wolverine	Intercept	1.953972	3.3999	0.575	0.571
		Camera distance	0.006868	0.0059	1.154	0.261
		Intercept	4.02579	4.2451	0.948	0.353
		Camera height	0.01215	0.0327	0.371	0.714
LM log	First visit by wolverine	Intercept	1.16427	0.2016	5.776	<0.001
		Interval between death date and camera placing	0.15625	0.0505	3.093	0.006
	Second visit by wolverine	Intercept	1.4547	0.3260	4.462	0.001
		Interval between death date and camera placing	0.1167	0.1474	0.792	0.443
	First re-visit by wolf	Intercept	1.80974	0.2285	7.922	<0.001
		Interval between death date and camera placing	0.02748	0.0682	0.403	0.692

