Snowfall, travel speed, and seismic lines: The effects of snow conditions on wolf movement paths in boreal Alberta

by

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Abstract

In the winter, snow can present a major challenge to large mammals by impeding locomotion, limiting food availability, and imposing additional energetic costs during travel. This thesis examines the effects of snow conditions on the fine-scale movement patterns of grey wolves (*Canis lupus*) in a boreal forest ecosystem in northern Alberta. In my first chapter, I use traditional snow tracking to quantify the difference in snow depth and sinking depth between wolf travel paths and measurements 1m and 10m off-path. I compare these results to snow depths recorded at a landscape scale using remote cameras that were deployed across my study area. Wolves' choice of shallow snow conditions was not consistent across all spatial scales, as snow depth measured by remote cameras was slightly less than the average snow depth 10m off-path. However, at fine spatial scales, snow depth and sinking depth were consistently lowest on wolf travel paths, and highest 10m off-path. The difference in depth that wolves were able to achieve through travel path choices was highly dependent on substrate type. Linear features, and ploughed linear features in particular, were associated with sinking depths and snow depths that were far lower than any other substrate type. Whereas sinking depth for travel paths on natural, uncompacted substrates was 1.1cm less than measurements 1m away, sinking depth for travel paths on ploughed linear features was 4.5cm less than measurements 1m away. Thus, travelling on ploughed linear features may be highly advantageous for wolves, especially as local snow conditions increase. Based on published leg length measurements, we estimated that wolves would start to become impeded by snow conditions when sinking depth reached 18cm (equivalent to 50% sternum height). Over our study, these high sinking depths were encountered 37% of the time. As most of these sinking depths were recorded when wolves were travelling on natural substrates, linear features may provide energetic advantages, especially when wolves are

covering large distances or travelling at high speeds. However, although the effects of ploughed linear features may be important in deep snow environments with high levels of industrial or recreational activity, they are unlikely to have an overwhelming impact on locomotion or energetics in the moderate snow conditions that are characteristic of where most wolves in North America are found.

In my second chapter, I use remote cameras to identify localized snowfall events, and examine the effects of these events on wolf movements. The effects of snowfall were most noticeable the night of a snowfall event. Relative to my controls, travel speed decreased from 28.1m/min to 20.6m/min the night of a snowfall event. Similarly, the proportion of time spent travelling decreased by 30% compared to controls, from 0.35 to 0.24. The effect of snowfall on movement did not translate into a significant reduction in daily distance travelled; however, relative to controls, wolves travelled nearly 4km less on days of a snowfall event. Because I did not find evidence for persistent effects, I propose that wolves reduce their movements during a snowfall because it is more difficult for them to detect prey, as snowfall can affect wolves' ability to detect odour trails, in addition to limiting visibility and insulating sound.

This thesis furthers our understanding of the grey wolves' winter ecology in a boreal forest ecosystem that is representative of a large part of their geographic distribution in North America. To my knowledge, this is also the first time that a study has investigated the effects of snowfall events on animal movement in a natural setting. Understanding wolves' response to snow is important not only for wolf biology, but also for predator-prey interactions. Through their influence on predator movements, snow conditions have the potential to influence encounter rates, predation risk, and kill rates.

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General introduction

In the winter, snow can present major challenges to large mammals (Telfer and Kelsall 1984). Snow limits food availability, impedes locomotion, and imposes high energetic costs on movement and foraging (Parker et al. 1984, Nelson and Mech 1986, Adamczewski et al. 1988). In the boreal forest, snow persists for more than 7 months of the year. Snow depth averages 30 to 120cm, and snowfalls are light and frequent (Sturm et al. 1995, Pruitt 2005). And, unlike the windswept, hard-packed snow of the tundra, snow in the boreal remains "light" and "fluffy" for most of the winter (Pruitt 1960, Sturm et al. 1995). This soft snow means animals sink to greater depths as they try to move across the landscape, and this has energetic implications. For both ungulates and carnivores, energetic costs increase exponentially with sinking depth (Parker et al. 1984, Crête and Larivière 2003). To survive the winter therefore requires behavioural and morphological adaptations as animals must not only avoid predation and find forage, but also maintain energetic costs at acceptable levels (Pruitt 1960, Murray and Boutin 1991).

In Alberta, the boreal forest of the 21st century is distinctly industrialised and this, too, shapes how animals move around the landscape. As of 2012, 767km^2 of land in Alberta's Athabasca Oil Sands Region was cleared or disturbed as a result of oil sands development (Government of Alberta 2014). A network of linear features, largely in the form of seismic lines used for exploration purposes, now criss-cross the landscape at an average density of 1.5km/km^2 (Lee and Boutin 2006). These linear features have had a documented impact on the abundance, distribution, and behaviour of wildlife (Dyer et al. 2001, Bayne et al. 2005, Tigner et al. 2014). For cursorial carnivores such as grey wolves (*Canis lupus*), these features provide entry into hard-to-access areas, potentially increasing wolves' encounter rates with prey (James and Stuart-Smith 2000, Whittington et al. 2011). Wolves also travel faster on these features than they do on natural substrates (Dickie 2015), and such benefits may be especially pronounced in the winter when activities such as plowing and snowmobiling remove snow and increase compaction.

The grey wolf relies heavily on movement to locate and chase prey. Indeed, wolves travel an average of 7.1km/day, though distances as high as 70.4km/day have been reported (Kolenosky 1972, Dickie 2015). In Banff National Park, Alberta, wolves chased elk (*Cervus elaphus*) for an average of 262m, with some chases exceeding 1km (Hebblewhite et al. 2005). Because of snow's effect on movement, the ways in which wolves and ungulates are affected by snow has implications for predator-prey interactions (Telfer and Kelsall 1984). In severe winters, wolves travel less frequently and cover shorter distances than in mild winters (Fuller 1991). However, they also kill more ungulate prey in deep snow (Peterson and Allen 1974, Nelson and Mech 1986, Post et al. 1999). One proposed reason for this increase in hunting success is morphological: because wolves sink less in deep snow than ungulates (i.e. have a smaller foot-load), it is easier for them to chase down prey (Telfer and Kelsall 1984). Wolves may also rely on behavioural adaptations, such as hunting in larger packs in severe winters, leading to an increase in hunting efficiency (Post et al. 1999).

Despite snow's influence on boreal landscape ecosystems, the fine-scale effects of snow on large mammals remains understudied. Most studies have focused on broad-scale patterns such as migration or regional distribution (e.g. Mladenoff et al. 1995, Nicholson et al. 1997). Predator-prey studies have largely focused on inter-year comparisons between mild and deep snow winters (e.g. Nelson and Mech 1986, Post et al. 1999). Although some studies have successfully analysed the fine-scale effects of snow (e.g. Murray and Boutin 1991, Serrouya et al. 2007), these remain rare. Perhaps a major limiting factor is the coarse resolution at which snow data are available. Indeed, most studies obtain information on snow conditions in one of three ways: 1.

Climate indices, such as the North Atlantic Oscillation index, or winter severity measures, 2. Point data from weather stations, or 3. Large resolution climate models e.g. SNODAS or CMC. The allure of these data is that they are free and easily accessible online. The problem is that they offer no insights into local snow conditions. In reality, local snow conditions are highly variable, changing significantly even over short distances of 50 to 100m (Neumann et al. 2006). As broad-scale snow data is inadequate for capturing such fine-scale heterogeneity (Ossi et al. 2015), how can we better our understanding of the fine-scale effects of snow? What fine-scale methods are available to us?

Fine-scale studies on the effects of snow often rely on snow tracking to obtain data on local snow conditions (Murray and Boutin 1991, Crête and Larivière 2003, Serrouya et al. 2007). A common objective in these studies is to compare snow conditions on animal paths to unused areas. Studies have shown that carnivores such as coyotes (*Canis latrans*), Canada lynx (*Lynx canadensis*), and grey wolves consistently travel in areas where sinking depth is less than the local environment (Murray and Boutin 1991, Crête and Larivière 2003, Chapter 1). This fine-scale selection of favourable snow conditions can help mitigate the costs associated with locomotion in the snow. For example, it is estimated that coyotes can decrease energetic costs by ~5% by travelling in areas with shallower, more compacted snow (Crête and Larivière 2003). Other ways in which animals can decrease the costs of moving in deep snow include consciously decreasing travel speed and using compacted paths such as snowmobile trails and game trails (Parker et al. 1984, Murray and Boutin 1991).

While snow tracking provides us with local snow data, it is a costly and labour-intensive method. How else, then, might we monitor local snow conditions? Perhaps a more palatable approach is the use of remote cameras. Remote cameras have largely been used to monitor biotic variables – anything from the presence or behaviour of animals, to human traffic on hiking trails. Remote cameras are typically programmed to take a picture (or a set of pictures) when they are triggered by heat or by movement. However, they can also be programmed to take a picture at the same time each day, providing us with a snapshot of local conditions at that time. When collated over multiple days and multiple locations, we can obtain information on snow conditions across a given area. As remote cameras are already being used in many biodiversity monitoring studies, programming these cameras to also take daily snapshot pictures would also provide researchers with data on environmental conditions such as precipitation and temperature. Information on localized weather conditions can then be used in conjunction with other data such as telemetry data or demographic information to answer questions about how local environmental conditions affects animal populations. Recently, remote cameras have been successfully used to study the effects of rainfall on nestling survival, which suggests that these devices can be used for studying short-term, extreme weather events such as heavy rains and snowstorms (Fisher et al. 2015).

In the first chapter, we use traditional snow tracking to compare animal travel paths to local snow conditions. We collected data on snow depth and sinking depth along 115 1km wolf travel paths, taking measurements every 100m. We repeated these measurements 1m and 10m perpendicularly away from wolf tracks, and compared differences in snow conditions across these 3 groups (i.e. on-path, 1m off-path, and 10m off-path). We sought to answer the following questions: 1. Does the documented selection for shallow snow persist in systems with only moderate amounts of snow? Most snow tracking studies were conducted in deep-snow areas (>60cm), but travelling in shallower or more compact snow might be unimportant in medium- or low-snow systems such as the boreal forest, which comprise most of the grey wolf's current distribution (Jedrzejewski et al. 2001). 2. Is the difference in depth between on-path and off-path biologically significant? We use published body measurements to examine the biological relevance of travelling in shallower snow.

In the second chapter, we use remote cameras to obtain localized data on snow depth and snow accumulation. We then examine the effects of snowfall events on the movements of grey wolves by relating snow conditions to telemetry data. Because the effects of snowfall have not been previously investigated, our main objective for this chapter is to provide qualitative data and preliminary analyses on this topic. We do so by answering the following questions: 1. Do wolves move slower during a major snowfall event? 2. Do wolves move less during a major snowfall event? 3. Do these effects persist for the days following a snowfall event?

Taken together, these two chapters help further our understanding of the grey wolf's winter ecology in a boreal forest ecosystem. Specifically, we examine wolves' fine-scale movement patterns in response to typical snow conditions and to more extreme snow conditions brought about by snowfall. Understanding wolves' response to snow is important not only for wolf biology, but also for predator-prey interactions, as snow conditions influence hunting success, kill rate, and predation risk (Nelson and Mech 1986, Fuller 1991, Nicholson et al. 1997).

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Chapter 1: The difference in snow conditions between wolf travel paths and the local environment

Abstract

Snow conditions restrict locomotion and impose important energetic costs on wildlife. Animals can respond by taking advantage of snow's spatial heterogeneity, and this can be done across multiple spatial scales. We snow-tracked grey wolves (*Canis lupus*) near the town of Fort McMurray, in northeastern Alberta, over two consecutive winters, and quantified the difference in snow depth and sinking depth along wolf travel paths to measurements 1m and 10m off-path. At fine spatial scales of 10m or less, wolves consistently travelled in areas with less sinking depth and less snow depth than the local environment. The difference in depth between wolf travel paths and off-path measurements was highly dependent on substrate type. Linear features, and ploughed linear features in particular, were associated with sinking depths and snow depths that were far lower than any other substrate type. Whereas sinking depth for travel paths on natural, uncompacted substrates was 1.1cm less than measurements 1m away, sinking depth for travel paths on ploughed linear features was 4.5cm less than measurements 1m away. Thus, travelling on ploughed linear features may be highly advantageous for wolves, especially as local snow conditions increase. Based on published leg length measurements, we estimated that wolves would start to become impeded by snow conditions when sinking depth reached 18cm (equivalent to 50% sternum height). Over our study, these high sinking depths were encountered 37% of the time. As most of these sinking depths were recorded when wolves were travelling on natural substrates, linear features may provide energetic advantages, especially when wolves are covering large distances or travelling at high speeds.

Introduction

In the winter, snow conditions can restrict locomotion and impose important energetic costs on large mammals (Parker et al. 1984, Crête and Larivière 2003). To mitigate these effects, animals may take advantage of environmental heterogeneity in snow conditions. For example, ungulates such as mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) may migrate to wintering areas where snow is shallower, and where it is easier to forage and escape from predators (Boyce 1991, Nicholson et al. 1997). Similarly, predators such as Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) preferentially travel in areas with less snow depth and less sinking depth than the local environment (Murray and Boutin 1991, Crête and Larivière 2003). Heterogeneous snow conditions can occur naturally, caused by differences in canopy cover, wind exposure, or elevation (Neumann et al. 2006). Anthropogenic activities such as snow ploughing or snowmobiling may also lead to fine-scale heterogeneity in snow conditions (Pruitt 2005). The shallow, highly compacted snow conditions associated with these human features can have ecological implications on animal movements, predator-prey interactions, and interspecific competition, especially in areas with high levels of industrial or recreational activities (Crête and Larivière 2003, Kuzyk et al. 2004, Dowd et al. 2014).

Oil sands development in the Athabasca Oil Sands Region in northeastern Alberta, Canada, has led to an extensive network of linear corridors, largely composed of seismic lines used for exploration purposes by the oil and gas industry. Seismic lines and other linear features impact the abundance, distribution, and behaviours of many animals including ovenbirds (*Seiurus aurocapilla)*, caribou (*Rangifer tarandus caribou*) and black bears (*Ursus americanus*) (Dyer et al. 2001, Bayne et al. 2005, Tigner et al. 2014). Moreover, linear features allow carnivores to travel faster and potentially expend less energy when travelling (James and Stuart-Smith 2000, Dickie 2015); they also provide access into otherwise hard-to-reach areas, which may in turn increase hunting efficiency (James and Stuart-Smith 2000). In the winter, the role of linear features as travel routes may be especially important if these features are ploughed or otherwise compacted, as this would lead to an increased difference in snow or sinking depth between these features and the local environment (Latham et al. 2011, Dowd et al. 2014; but see Kolbe et al. 2007). As our human activities expand into even the most remote areas, the impact of human disturbances remains a key issue in wildlife management and conservation biology (Weaver et al. 1996).

Differences in snow conditions between animal travel paths and local conditions have been documented for Canada lynx and coyotes in montane and temperate climates, where average snow depth is high (>60cm) (Murray and Boutin 1991, Crête and Larivière 2003, Dowd et al. 2014). However, most studies have not considered the degree to which selection of paths actually leads to a reduction in snow depth and sinking depth (but see Murray and Boutin 1991). The magnitude of difference between on-path and off-path snow conditions may not be biologically significant when placed in context of an animal's morphology. Moreover, selection for favourable snow conditions may not be as pronounced in low- to moderate-snow areas, where animal movements are not necessarily impeded by snow conditions (Jedrzejewski et al. 2001).

The grey wolf (*Canis lupus*; hereafter wolf) is a suitable species for investigating large mammals' adaptations and responses to snow conditions. As a cursorial predator, it relies heavily on movement to find and kill ungulate prey, and is well-adapted to harsh winter conditions (Mech 1970). Indeed, wolves experience higher kill rates in severe winters when snow is deep, than in mild ones (Nelson and Mech 1986, Fuller 1991). A number of factors contribute to this increase in hunting success, including morphological and behavioural adaptations, and increased prey vulnerability (Peterson and Allen 1974, Telfer and Kelsall 1984). Compared to most of their prey, wolves have a light foot-load (ratio of body mass to foot surface area), which means they sink less in deep snow (Telfer and Kelsall 1984, Nelson and Mech 1986, Fuller 1991). In deep snow years, wolves also adapt their behaviour by hunting in larger packs and favouring single-file travel; in some instances, they may preferentially prey on juvenile ungulates, which are vulnerable to predation in deep snow (Peterson and Allen 1974, Post et al. 1999). However, wolves may be disadvantaged by low snow density; these conditions are typically associated with fresh snow and ecosystems such as the boreal forest, which experience frequent snowfalls and low levels of snow crusting (Peterson and Allen 1974, Sturm et al. 1995).

The grey wolf has a circumpolar distribution; though it was once more widespread, it has been extirpated from much of its southern, historic range as a result of habitat destruction and human persecution. In North America, there are currently between 50 000 to 60 000 wolves in Canada, and 12 000 in the United States (U.S. Fish & Wildlife Service 2007). Small wolf populations exist in the Great Lakes and St. Lawrence regions, the Rocky Mountains, and along the western coast of Alaska and British Columbia (Mech 1995, U.S. Fish & Wildlife Service 2007). However, the largest population of wolves is found on the northern mainland of Canada and Alaska, where they inhabit boreal, taiga, and Arctic ecosystems (U.S. Fish & Wildlife Service 2007).

We wanted to investigate travel path choices in a low- to moderate-snow system that is representative of grey wolves' current range. Our main objectives were to: a) quantify differences in snow conditions between wolf travel paths and the local environment; b) examine how these differences were influenced by substrate type and cover type along wolf travel paths;

and c) contextualize our findings in relation to wolves' body measurements and geographic distribution. To meet these objectives, we snow tracked wolves over 187km from January to March 2013 and 2014, in northeastern Alberta, Canada. At every 100m along wolf travel paths, we measured snow depth and sinking depth, and conducted similar measurements along unused paths 1m and 10m away. We then used linear, mixed effects models to analyse how the difference in snow depth and sinking depth between on-path and off-path conditions were influenced by environmental and anthropogenic variables.

Methods

Study area

Our study area covers 8759km^2 and is located in in the Athabasca Oil Sands Region in northeastern Alberta, Canada (56.4°N, 111.1°W) (Figure 1). It is within the central mixedwood sub-region in the boreal forest, and is characterized by treed wetlands and upland deciduous and mixedwood forests (Natural Regions Committee 2006). Dominant tree species include aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*). The terrain is mainly flat, with some rolling hills; elevation ranges from ~245m to 550m above sea level. Winters are long and cold, with average January temperatures of -17°C and yearly snowfall of 134cm, most of which falls from November to March (based on climate data from 1981 to 2010; Environment Canada 2015). The most common large mammals are moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), grey wolves, and black bears.

Our study area is influenced by the presence of the oil and gas industry. As of 2012, approximately 6.5% (571km^2) was covered by oil sands surface mines. Roads are mostly found in the southern part of our study area, in a ~70km^2 area around the town of Fort McMurray (Figure 1). The road network includes one major highway (Highway 63), as well as secondary roads that include winter roads, truck trails, and gravel roads. Industry-related linear features such as seismic lines and pipelines are much more prominent and widespread than roads, achieving an average density of 1.63km/km^2 (based on 2012 Alberta Human Footprint Map, Alberta Biodiversity Monitoring Institute; Figure 1). The most common are conventional seismic lines, which are 5 to 8 m wide and cleared of overhead vegetation. Narrower, low-impact seismic lines are rare and only present at the eastern edge of our study area (Figure 1).

Capture and radio-collaring of wolves

As part of an affiliated research program, we captured and radio-collared wolves from 2011 to 2013 (Boutin et al. 2015). The objective of the wolf collaring program was to collar at least 1 individual from every wolf pack in our study area (Figure 1). We first began to capture and collar wolves in winter 2011. All captures were conducted by experienced crew and followed standard capture protocols (University of Alberta Animal Care protocol and Alberta Wildlife Animal Care Committee Class protocol #009). Wolves were equipped with Iridium GPS collars weighing ~750g (Lotek Wireless Inc., Newmarket, Ontario, Canada) that were programmed to drop off after 2 years.

In 2012, we used the telemetry data we had previously collected to evaluate whether we had collared at least 1 individual from each pack. When looking at the data, we noticed two large gaps: one to the west of the Athabasca River, between Fort McMurray and the Syncrude mine site, and the second east of the river and directly south of Shell operations (Figure 1). We searched each area by helicopter for one entire day. While we did see some tracks, indicating that wolves had moved through the areas, we could not find any signs that wolves were using these areas as territories. Based on our extensive search efforts, we are confident that we collared at least 1 individual from every pack in our study area.

In total, we collared 41 wolves from 10 different packs, and one lone wolf (Figure 1). This wolf was never seen with other wolves in the first year of collaring; however, by the second year, it appeared to have joined one of the existing packs. Collars were replaced when they failed and new wolves were captured when individuals died. By the end of our research program in 2014, all collars were either removed or had fallen off.

Collar fix rates schedules

Collars were initially programmed to collect one location every 3 hours, but this frequency was increased for certain collars during our study period, which took place from January to March 2013 and 2014. In winter 2013, 9 collars were programmed to take a location every 30 minutes; one of those collars lasted until March 2014. Meanwhile, in winter 2014, 8 collars operated on a 10-minute fix rate. Only collars with 30- or 10-minute fix rates were used for these analyses, because these faster fix rates made it possible for us to isolate wolf travel paths from resting behaviours.

Snow tracking

From January to March 2013 and 2014, we snow tracked 187 1km wolf travel paths, and recorded information on snow depth, sinking depth, substrate type, and cover type along these paths, as well as 1m and 10m perpendicularly away.

Isolating wolf travel paths from GPS data

Travel paths were initially identified using GPS data from radio-collared wolves with fix rates of 30 minutes or less. Each morning, we selected recent GPS locations (<12 hours), identified travel (or movement) paths, and chose which paths to track. Travel paths were identified by ignoring GPS clusters, which are typically associated with rest sites and/or kills (Webb et al. 2008). Once clusters were removed, we further isolated travel paths by considering only individual wolves that had at least three evenly spaced and consecutive GPS points, which meant that a wolf had been moving at the same average speed for at least 30 minutes. Restricting paths to a minimum of 3 GPS points ensured that the wolf had moved far enough to allow us to track the wolf for 1km, which was the chosen length of our sampling paths.

We aimed to sample three paths every day; we found that this was the maximum number of paths we were able to track in one day given the number of daylight hours, the time it took to sample each path, and the time required to drive to and from our sampling paths. On rare occasions when we could not find three paths that matched our selection criteria, we included GPS locations up to 24 hours old. We also tried to sample at least one path from each pack every week. However, because we were limited to sampling paths that were accessible by ground transportation, some packs were sampled less often than others. Over our two years of study, we managed to sample all packs except for the Grand Rapids pack (Figure 1), whose territory was at the southern edge of our study area and was inaccessible by vehicle or snowmobile.

Field data collection and study design

Once we had chosen which paths to sample, we drove, either by truck or snowmobile, to the middle GPS point out of the three (or more) that made up the consecutive movement bout. Once we had located the selected wolf track in the field, we snow-tracked the wolf for 500m in either direction, for a total path length of 1km (Figure 2). At every 100m along the wolf path, we measured snow depth, track sinking depth, and estimated sinking depth. We measured snow depth by pressing a metre stick through the snowpack until it hit the ground or could not be pushed any further, and measuring the height of the snow to the nearest millimetre. To measure track sinking depth, we located the nearest wolf print to every 100m measurement interval and measured, to the nearest millimetre, the depth at which the wolf's paw print sunk in the snow. Measurements were made from the surface of the snow to the base of the print. Lastly, because we were interested in comparing sinking depth on-path to off-path conditions where the wolf had not stepped, we estimated sinking depth using a 355 millilitre metal can that was 11.4 centimetres high and 6.0 centimetres wide. The can was filled with sand to weigh 225 grams, and was dropped widthwise into the snow from a height of 1m. The weight of the can and the height at which it was dropped was meant to mimic the sinking depth of a wolf track, and was based on previously published estimates for estimating sinking depths of lynx and coyote tracks (Murray and Boutin 1991). Estimated sinking depth was measured in millimetres from the top of the can to the top of the snow layer. If the can sank only partly into the snow, we assumed that wolves would have been fully supported by the snow layer, and considered estimated sinking depth as being zero. We added 6.0cm to all non-zero measurements to account for the width of the metal can.

To compare these on-path data to the local environment, we collected similar data 1m and 10m off-path, with the exception of track sinking depth, which could only be measured on the wolf path (Figure 2). 1m and 10m measurements were made perpendicular to on-path measurements, and alternated between the left and right side of the wolf path (Figure 2),. All on-path and off-path measurements along a 1km wolf path were considered as one transect, and were given a unique transect ID.

In addition to measuring snow conditions, we also recorded information on habitat and substrate type. Habitat was described every 100m for both on-path and off-path measurements, but substrate type was only described on-path. We used the Alberta Vegetation Inventory classification scheme to describe habitat (Table 1; Alberta Sustainable Resource Development 2005); we later reclassified habitat into open or closed cover types (see: Statistical analyses). Substrate type was classified into one of the following categories: clearing, forest, game trail, frozen river, road, 3D seismic line, conventional seismic line, or groomed trail. We also noted whether the wolf path had been recently used by humans (skidoo, snowplough, truck or no human use). We subsequently reclassified substrate type into 5 general categories for analysis.

Remote cameras

From January to March 2013 and 2014, we deployed remote cameras (Reconyx PC900, Reconyx Inc., Holmen, Wisconsin) to monitor snow depth and snow accumulation. The location of the remote cameras was limited to areas that were easily accessible by ground transportation. In 2013, we deployed twenty-five cameras along a north-south gradient to account for potential latitudinal differences in snow depth (Figure 1). Twenty-two cameras followed a paired design, with one camera placed in open cover and the other placed in nearby closed cover (<100m away). In 2014, we deployed twelve cameras but did not repeat the paired design (Figure 1). In both years, cameras were active for variable lengths of time as they were moved to different locations in the study area.

Cameras were programmed to take one picture every day at noon. They were aimed at a pole that was planted in the ground and marked every ten centimetres. Upon deployment, we measured initial snow depth by plunging a metre stick in the ground. Using this measurement as a starting point, we used the 10 centimetre markers to visually estimate snow depth.

Statistical analyses

We limited our analyses to 1 transect per pack per day to minimize pseudo-replication; we were left with 115 transects. Statistical analyses were performed in R (R Core Team 2015).

Reclassifying substrate and cover types

In reclassifying substrate type, we distinguished between natural and anthropogenic substrates. We also distinguished between substrates that did not show evidence of previous use, versus those that had previously been used by humans and/or wildlife (Table 1). In doing so, we sought to account for differences in snow depth and in snow compaction caused by human disturbance or by previous use of paths. Thus, we reclassified substrate type into five categories: ploughed linear features, unploughed linear features, game trails, frozen rivers, and uncompacted natural substrates (Table 1). Ploughed linear features included all paths that had been recently used by humans. This category included snowmobile trails, even though these trails might not have been formally ploughed by a snowplough. Most of the paths in this category were on anthropogenic substrates (i.e. roads or seismic lines), but a few were on natural substrates (i.e. forests or clearings). Unploughed linear features included paths on anthropogenic substrates that had no evidence of recent human use. Game trails were paths on natural substrates that clearly showed previous use by large mammals (e.g. fresh tracks, a marked depression in the snow, wildlife damage to vegetation along the trail). The uncompacted natural substrates category was reserved for paths on natural substrates (i.e. forested and open areas) that had not been previously used by either humans or large mammals.

Habitat was reclassified into either open or closed cover type (Table 1). Open cover included deciduous forests, shrubland, and clearings; closed cover was reserved for coniferous and mixedwood forests (Table 1).

On-path conditions

Before pooling our data across years, we performed a *t*-test to evaluate whether snow conditions differed by year. We then described snow depth, estimated sinking depth, and track sinking depth on wolf travel paths. We examined the effect of substrate type on track sinking by using a one-way ANOVA to test whether there were significant differences in track sinking depth as a function of substrate type.

Comparing on-path to off-path conditions at fine spatial scales

We wanted to identify which on-path characteristics led to the greatest difference between off-path and on-path snow conditions, because we assumed that on-path characteristics were driving these differences in snow conditions. Because each on-path measurement was associated with two off-path measurements (i.e. 1m and 10m away), we calculated the difference in a) estimated sinking depth and b) snow depth between each off-path/on-path pairing (i.e. 10m and on-path or 1m and off-path). A positive difference meant that depth was deeper off-path than on-path. We ran separate linear mixed effects models (Pinheiro and Bates 2000) for snow depth and estimated sinking depth, as both variables were correlated ($r = 0.69$).

The on-path characteristics we considered were substrate type and cover type; we also included month and year of sampling to account for potential temporal effects (Table 2). We also included two explanatory variables that were not subject to model selection: distance from path (1m or 10m) and off-path depth (Table 2). We included these variables to account for our two scales of comparison, and because we were interested in whether wolves' choice of snow conditions changed as sinking depth or snow depth in the local environment increased.

To identify the significance of on-path characteristics, we used a backward model selection framework and likelihood ratio tests (Zuur et al. 2009). We began with a full model that included all variables and two interactions: one between substrate type and off-path snow depth, and one between cover type and off-path depth (Table 2). Variables were dropped sequentially until we only had significant variables ($P < 0.05$). Prior to model selection, we centered and scaled our continuous variables (including the response variable) to facilitate with the interpretation of our predictors (Schielzeth 2010). The models also included a random intercept for each transect, to account for multiple measurements taken along the same paths and our paired sampling design. We validated the final models by plotting the standardized residuals and verifying that the assumptions of normality, homogeneity, and independence were not violated (Zuur et al. 2009).

Comparing off-path conditions to remote cameras

We compared snow depth 10m away to snow depth recorded on our remote cameras, as we wanted to see if wolves' choice for shallower snow areas occurred at broader spatial scales (i.e. >10m). For this comparison, we excluded the paired 2013 cameras that were placed in closed cover, as these cameras consistently recorded lower snow depths than their counterparts in open areas. Consequently, we also removed all 10m measurements that were in closed cover. We matched each 10m snow depth measurement to the snow depth recorded on the same day at the nearest remote camera. We used a paired *t*-test to examine whether there was a difference in snow depth between the two spatial scales.

Results

On-path conditions

The average track sinking depth experienced by wolves was 14cm, with a maximum of 52cm. On average, track sinking depth was 4.5cm deeper in 2014 than in 2013 ($t = 6.51$, df = 120, $P < 0.01$). Average on-path snow depth was 27cm, with a maximum recorded depth of 92cm; snow depth did not differ significantly by year ($t = -0.23$, df = 120, $P = 0.82$). There was a strong correlation between track sinking depth and estimated on-path sinking depth ($R^2 = 0.67$; Figure 3), which justified our use of a metal can as a proxy for track sinking depth.

Effect of substrate type on track sinking depth

The substrate type on which wolves travelled had a strong effect on wolves' sinking depth ($F_{4,1146} = 123.67$, $P < 0.001$). Track sinking depth was significantly lower on ploughed linear features than on any other substrate type (Figure 4). On average, sinking depth on ploughed lines was 5.2cm, compared to 15.6cm on unploughed lines and 24cm on uncompacted, natural substrates. Track sinking depth on uncompacted, natural substrates was significantly deeper than sinking depth on all other substrate types, except game trails (Figure 4).

Comparing on-path to off-path snow conditions

Sinking depth

Average estimated sinking depth on-path was 7.6cm, compared to 10.4cm 1m away, and 12.5cm 10m away. The greatest positive difference was +24.5cm; this difference occurred when the wolf was travelling on a ploughed linear feature in closed cover, whereas the off-path measurement was on a natural substrate in closed cover. The greatest negative difference was -

16.3cm. In this case, both on-path and off-path measurements were on natural substrates, but the on-path measurement was in closed cover, while the off-path measurement was in open cover.

Model selection results

Differences in estimated sinking depth between off-path and on-path measurements were highly driven by substrate type (Table 3), with differences being most pronounced when wolves travelled on ploughed linear features (Figure 5). On average, estimated sinking depth on ploughed linear features was 4.5cm less (sd = 6.0) than sinking depth 1m away. In contrast, the difference in sinking depth when travel paths were on uncompacted, natural substrates was 1.1cm (sd = 4.6).

In general, the difference between on-path and off-path conditions increased with off-path sinking depth, but this relationship was dependent on substrate type (Figure 6). The interaction between off-path depth and substrate type was driven by a significant difference between travel paths on ploughed linear features versus paths on uncompacted, natural substrates, with sinking depth on ploughed features remaining relatively small across the range of sinking depth values (Figure 6). Paths on rivers and game trails had very large confidence intervals, which overlapped with the confidence intervals of all other substrate types.

Cover type and month of sampling also had significant effects, with difference in sinking depth being greater in closed cover than in open cover, and greatest in the month of March. Though not subject to model selection, distance from wolf paths was an important explanatory variable. The difference in sinking depth between on-path and off-path measurements was greater with increased distance from wolf paths (Table 4).

Snow depth

Average snow depth 10m off-path was 48.3cm, and was +21.3cm greater than snow depth on wolf travel paths. Average snow depth 1m off-path was 38.4cm, and +11.4cm greater than on-path snow depth.

We recorded a maximum positive difference (i.e. off-path greater than on-path) of +100.8cm. In this instance, the on-path measurement was on a ploughed linear feature in open cover; meanwhile, the off-path measurement was on a natural substrate in closed cover. The greatest negative difference recorded was -37.8cm. The on-path measurement was on an unploughed linear feature in open cover, while the off-path measurement was on a natural substrate in an open cover (recent burn site). Both of these differences occurred at the 10m scale, but the magnitude of difference between 1m off-path and on-path measurements was similar.

Model selection results

The final model identified cover type and substrate type as significant on-path variables in explaining the differences in depth between wolf paths and the local environment (Table 3). Closed cover, ploughed linear features, and frozen water bodies were associated with the largest differences in depth (Table 5). In general, travel paths on these features had less snow depth than paths in open cover, or on uncompacted substrate types. However, as with our sinking depth model, the effect of substrate type depended on off-path snow depth (Figure 7). When off-path snow depth was minimal, snow depth on wolf paths was similar across all substrate types. But as off-path snow depth increased, snow depth for travel paths on manmade linear features remained relatively shallow, especially if these linear features were ploughed (Figure 7). Similar to our sinking depth model, distance from wolf paths (either 1m or 10m away) was also an important explanatory variable, with greater differences in depth at the 10m scale of comparison (Table 5).

Comparing snow tracking to remote camera sites

According to our remote cameras, snow depth in 2013 and 2014 averaged 48.6cm and 44.5cm, respectively. However, in 2013, roughly 10 centimetres of snow accumulated from January to February (Figure 8), whereas snow depth remained relatively constant in 2014.

When compared to snow depth from our 10m off-path measurements, snow depth as measured by our remote cameras was, on average, 3.1cm shallower (t=3.49, df=405, $P < 0.001$); however, this difference was highly variable (sd=17.8).

Discussion

Our study revealed that the use of favourable snow areas by wolves is scale-dependent. We found that wolves did not travel in areas with less snow depth, when compared to what was available to them at the extent of the study area. At larger spatial scales, the decision of where to travel was likely motivated by prey, rather than snow conditions. Indeed, within their territories, wolves have been shown to hunt in areas of higher prey densities, and in open areas and edge habitat where prey might be more susceptible to predation (McPhee et al. 2012). However, at fine spatial scales of 10m or less, considerations for snow conditions becomes important as wolves consistently travelled in areas that had less snow depth and less sinking depth than off-path measurements.

Sinking depth (or the depth to which an animal sinks in the snow) is regarded as being the most important determinant of snow's effects of animal locomotion and energetics, with heart rate increasing exponentially with sinking depth in both cervids and canids (Parker et al. 1984, Crête and Larivière 2003). In ungulates, locomotory costs double when sinking depth reaches at least 50% brisket (sternum) height (Fancy and White 1987). If similar thresholds apply to canids as well, then wolves would be impeded when they sink at least 18 centimetres in the snow, roughly equivalent to the top of their tibia (Bertram and Biewener 1990). Wolves in our study encountered track sinking depths of at least 18 centimetres 37% of the time; the vast majority (77%) of these instances occurred when wolves travelled on natural substrates.

The difference in depth between wolf paths and off-path measurements was largely dependent on the substrate type wolves' travelled on (Figure 5). Linear features, and ploughed linear features in particular, were associated with lower sinking depths and snow depths than other substrate types. Whereas sinking depth for travel paths on natural, uncompacted substrates was 1.1cm less than measurements 1m away, sinking depth for travel paths on ploughed linear features was 4.5cm less than measurements 1m away. Thus, travelling on ploughed linear features may be highly advantageous for wolves, especially as local snow conditions increase, because these features remain relatively free of snow (Figure 6; Figure 7). In the winter, the distance that wolves cover in a day is positively correlated with the time they spend travelling on linear features (Dickie 2015); we propose that the snow conditions wolves' experience on these linear features enables them to cover greater distances, while maintaining reasonable energetic costs (Crête and Larivière 2003).

High variability within substrate types prevented us from identifying significant differences in sinking depth between unploughed linear features, rivers, and game trails. Unploughed linear features likely differed in the amount of time since they had last been ploughed, and the amount of snow that had fallen since then, and this likely contributed to the high variability within this substrate type. Rivers and game trails were undersampled relative to the other habitat types; using a random sampling design stratified by substrate type would increase our ability to detect differences between these categories.

The moderate snow depths encountered in our study area are similar to conditions that wolves would encounter across much of their geographic range in North America. Snow depth in our study area is representative of snow depths throughout the boreal forests of northwestern Canada, and taiga and tundra ecosystems in northern Quebec, the Northwest Territories, and Nunavut (Figure 8). Most studies on carnivores' fine-scale use of favourable snow conditions have been conducted in high-elevation or temperate areas with high (≥60cm) annual snowfall (Crête and Larivière 2003, Kolbe et al. 2007); that predators living in areas with more moderate snow conditions also exploit areas of lesser snow and sinking depths suggests that the ability to find and use areas of favourable snow conditions is not specific to one species or one region, but is likely an evolutionary adaptation shared by many year-round residents in northern areas (Telfer and Kelsall 1984). Our results between on-path and off-path are similar to studies conducted on coyotes (Murray and Boutin 1991, Crête and Larivière 2003); similar results between coyotes and wolves are expected given that these species have comparable footloads (Murray and Larivière 2002).

Snow conditions have wide-ranging implications on wildlife, affecting energetics, locomotion, and foraging efficiencies of both predators and their prey (Parker et al. 1984, Huggard 1993). Animals can mitigate these impacts behaviourally, by reducing their travel speed, changing their gait, or by using areas that have less snow depth and less sinking depth than the local environment (Parker et al. 1984, Murray and Boutin 1991). Ploughed linear features can offer a drastic improvement for travel, but the benefits wolves can derive from these features is restricted to deep snow conditions, which were not commonly encountered over the course of our study.

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Tables

Table 1 Reclassification of habitat into cover type for use in our statistical models. Information on habitat type was collected in the field and was loosely based on categories from the Alberta Vegetation Inventory (AVI). We used this habitat information to categorize wolf paths as being in either open or closed cover type. Open cover included anthropogenic and non-vegetated areas, as well as deciduous forests. Closed cover was associated with coniferous or mixedwood forests, and treed (coniferous) wetlands.

Habitat	**Cover type reclassification**
Forested	
Mixedwood	Closed
Conifer	Closed
Dry, open	Open
Deciduous	Open
Recent burn	Open
Wetland	
Treed	Closed
Shrubby	Open
Marsh	Open
Graminoid	Open
Water	
River	Open
Creek	Open
Riparian	Open
Anthropogenic	
Seismic line	Open
Cutblock	Open
Industrial	Open

Table 2 Variables included in our mixed effects models to explain differences in snow depth and sinking depth between on-path and off-path measurements. Our interest was in identifying which on-path variables contributed most to creating a large difference between on-path and off-path snow conditions. Variables were collected in the field from January to March 2013 and 2014 by snow tracking grey wolves, which were radio-collared. Prior to analysis, we scaled and centered continuous variables.

Variable	Definition	Type
diff	Difference in depth between off- and on-path measurements (cm)	Continuous response variable; centred around mean
dist	Distance from path	Nominal explanatory variable with 2 levels (1m or 10m)
depth	Snow condition off-path (cm)	Continuous explanatory variable; centred around mean
month	Month of sampling	Nominal explanatory variable with 3 levels (Jan., Feb., or Mar.)
year	Year of sampling	Nominal explanatory variable with 2 levels (2013 or 2014)
subs	Type of substrate on path	Nominal explanatory variable with 5 levels (ploughed linear feature, unploughed linear feature, frozen river, game trail, or natural uncompacted)
cover	Cover type on path	Nominal explanatory variable with 2 levels (open or closed)
ID	Transect ID	Random effect with 115 unique IDs. A unique ID was given for each 1km wolf path; off-path measurements had the same ID as the wolf path they were taken near.

Table 3 Results from our model selection process for explaining differences in sinking depth **(top)** and snow depth **(bottom)** between off-path and on-path measurements. We began with a full model that included all variables and two interactions. Each model also included a random intercept for transect ID. Interactions and variables were dropped sequentially until all variables were significant. Distance from path and off-path snow depth were included in the final model, but not subject to model selection. On-path cover type, substrate type, and an interaction between cover type and off-path depth were found to be significant for both models. In addition, we identified month of sampling as a significant variable for our sinking depth model.

df = degrees of freedom; LL = log-likelihood; L. ratio = likelihood ratio.

#	**Model**	**Drop**	**df**	**LL**	**Test**	**L. ratio**	***p*-value**
1	dist+month+year+cover+subs+depth+ depth:subs+depth:cover		18	-2234.95			
2	dist+month+year+cover+subs+depth+ depth:subs	Inter. #1	17	-2236.71	1 vs. 2	3.52	0.07
3	dist+month+year+cover+subs+depth	Inter. #2	13	-2347.97	2 vs. 3	222.52	<0.01
4	dist+month+cover+subs+depth+depth: subs	Year	16	-2236.78	2 vs. 4	0.13	0.71
5	dist+cover+subs+depth+depth:subs	Month	14	-2240.60	4 vs. 5	7.65	0.02
6	dist+month+subs+depth+depth:subs	Cover	15	-2241.42	4 vs. 6	9.28	<0.01

#	**Model**	**Drop**	**df**	**LL**	**Test**	**L. ratio**	***p*-value**
1	dist+month+year+cover+subs+depth +depth:subs+depth:cover		18	-1634.74			
2	dist+month+year+cover+subs+depth +depth:subs	Inter. #1	17	-1634.75	1 vs. 2	0.03	0.87
3	dist+month+year+cover+subs+depth	Inter. #2	13	-1714.05	2 vs. 3	158.59	<0.01
4	dist+year+cover+subs+depth+depth:subs	Month	15	-1635.27	2 vs. 4	1.04	0.60
5	dist+cover+subs+depth+depth:subs	Year	14	-1635.29	4 vs. 5	0.04	0.85
6	dist+subs+depth+depth:subs	Cover	13	-1643.83	5 vs. 6	17.09	<0.01

Table 4 Estimates for our final sinking depth model, which explains the difference in sinking depth between off-path measurements and wolf travel paths. The final model identified substrate type, cover type, and month of sampling as significant explanatory variables. Travel paths on manmade linear features (both ploughed and unploughed) had much smaller sinking depths, relative to off-path measurements, than paths on natural substrates. Closed cover, and travel path sampled in March, were also associated with greater differences in sinking depth, with wolf paths being less deep than off-path measurements. Lastly, as off-path sinking depth increased, wolf paths on ploughed linear features had much smaller sinking depths than the local environment, whereas path conditions on natural and unploughed substrates remained similar to off-path conditions.

Fixed effects	**Estimate**	**SE**	**t-value**	***p*-value**
Intercept	-0.56	0.12	-4.66	<0.001
Distance - 1m	-0.06	0.02	-2.91	<0.01
Cover type – closed	0.11	0.04	3.07	<0.01
Month – February	0.20	0.15	1.38	0.17
Month – March	0.48	0.17	2.76	<0.01
Substrate – game trail	-0.14	0.12	-1.12	0.26
Substrate – river	0.08	0.11	0.80	0.42
Substrate – unploughed linear features	0.24	0.05	4.89	<0.001
Substrate – ploughed linear features	0.84	0.05	17.74	<0.001
Depth, off-path	0.57	0.03	20.70	<0.001
Depth:game trail	-0.26	0.12	-2.20	0.03
Depth: river	0.02	0.10	0.16	0.87
Depth:unploughed	0.09	0.04	2.12	0.03
Depth:ploughed	0.45	0.03	13.45	<0.001
Random effects	**Intercept**	**Residual**		
Transect ID, std. dev	0.66	0.54		

Table 5 Estimates for our final snow depth model, which explains the difference in snow depth between off-path measurements and wolf travel paths. The final model identified cover type and substrate as significant explanatory variables. Travel paths on manmade linear features and on frozen rivers had much shallower snow depths, relative to off-path measurements, than paths on game trails or uncompacted natural substrates. Closed cover was associated with shallower snow than open cover. At low snow depths, wolf paths had snow depths that were comparable to those off-path, regardless of substrate type. However, as off-path snow depth increased, manmade linear features had relatively shallow snow, whereas snow depth on natural substrates and game trails remained similar to off-path conditions.

Fixed effects	**Estimate**	**SE**	**t-value**	***p*-value**
Intercept	-0.54	0.054	-9.89	<0.001
Distance - 1m	-0.09	0.02	-4.81	<0.001
Cover type – closed	0.12	0.03	4.14	<0.001
Substrate – game trail	0.18	0.09	1.87	0.062
Substrate – river	0.64	0.08	7.95	<0.001
Substrate – unploughed linear features	0.46	0.04	11.89	<0.001
Substrate – ploughed linear features	1.05	0.04	28.49	<0.001
Depth, off-path	0.42	0.03	14.81	<0.001
Depth:game trail	-0.06	0.13	-0.47	0.64
Depth: river	0.40	0.11	3.69	<0.001
Depth:unploughed	0.23	0.03	6.60	<0.001
Depth:ploughed	0.37	0.03	12.16	<0.001
Random effects	**Intercept**	**Residual**		
Transect ID, std. dev	0.49	0.43		

Figure legends

Figure 1 Map of our study area in the Athabasca Oil Sands Region in northeastern Alberta, Canada. Our study area is characterized by the presence of manmade linear features, such as roads and seismic lines, and oil sands surface mines. From 2012 to 2014, we captured and radio-collared 41 wolves from 10 packs, and 1 lone wolf (“City”). The winter territories of these packs are shown using 95% kernel density estimates. From January to March 2013 and 2014, we snow tracked 187 1km wolf paths; the centre of each path is shown here. We also deployed remote cameras (25 in 2013 and 12 in 2014) to monitor snow depth and snow accumulation.

Figure 2 Study design used to compare snow conditions on wolf travel paths to the local environment. A focal wolf track (circled) was located using GPS data. The wolf’s track was followed for 500m in either direction, for a total of 1km. At every 100m along this path, snow depth and sinking depth were measured using a metre stick and a weighted metal can. Information on substrate type and travel group size was also recorded. For comparative purposes, the same information was recorded 1m and 10m perpendicularly away from each track.

Figure 3 Scatter plot with original data points and 1:1 line in red, showing the relationship between estimated on-path sinking depth and associated value of track sinking depth. Although estimated sinking depth underestimates track sinking depth, the positive relationship between the two metrics suggests that estimated sinking depth is a satisfactory measure of relative sinking depth.

Figure 4 Average track sinking depth on wolf travel paths across different substrate types. Substrate types were described during field collection, and later classified into categories. Track sinking depth was defined as the depth at which the wolf’s paw sunk, from the top of the snow layer to the base of the paw print. Error bars represent 95% confidence intervals. Wolves experienced significantly smaller sinking depths when travelling on ploughed and unploughed linear features, than when travelling on uncompacted natural terrain.

Figure 5 Average snow depth **(top)** and estimated sinking depth **(bottom)** along wolf travel paths (0m), as well as 1m and 10m away. Error bars represent 95% confidence intervals. Snow depth and estimated sinking depth were measured every 100m along a 1km path. Detailed information on substrate type was recorded in the field, and was later reclassified into 5 categories for analytical purposes. For both snow depth and sinking depth, on-path averages were significantly lower than off-path when wolves were travelling on ploughed and unploughed linear features (e.g. roads, seismic lines, snowmobile trails). In contrast, there was no difference in sinking depth for wolf paths on rivers, game trails, and uncompacted, natural substrates, compared to off-path measurements.

Figure 6 Interaction between on-path substrate type and sinking depth 1m away, based on population-level predictions from our mixed effects model. Open cover type and the month of January were used as references. Original data points are shown for all substrate type categories. The straight line of points arises when sinking depth is 0cm on-path, but >0cm off-path, as the metal can we used to estimate sinking depth had to sink fully into the snow (a width of 6.0cm) before being considered as a non-zero measurement (see: Methods). The predicted slopes and 95% confidence intervals are shown only for the three substrate types that had non-overlapping CIs: ploughed linear features, unploughed linear features, and uncompacted natural substrates.

Figure 7 Interaction between on-path substrate type and snow depth depth 1m away, based on population-level predictions from our mixed effects model. Open cover type and the month of

January were used as references. Original data points are shown for all substrate type categories. The predicted slopes and 95% confidence intervals are shown only for the three substrate types that had non-overlapping CIs: ploughed linear features, unploughed linear features, and uncompacted natural substrates.

Figure 8 **Top:** Average snow depth measured by remote cameras from January to March. Red points symbolize 2013 data; blue points are 2014. 25 cameras were deployed in 2013; 13 were deployed in 2014. Snow depth was visually estimated using remote cameras that were pointed at a marked metre stick and programmed to take 1 picture every 24 hours. Snow was deeper in 2013, and increased by nearly 10cm from January to February. **Bottom:** Average monthly snow depth (in centimetres) across North America from January to March, based on snow depth models from the Canadian Meteorological Centre (CMC). Snow depth in our study area is representative of snow conditions across most of northern Canada, where the majority of wolves in North America are found. Figures are from Brown et al. (2003).

Figures

Figure 1

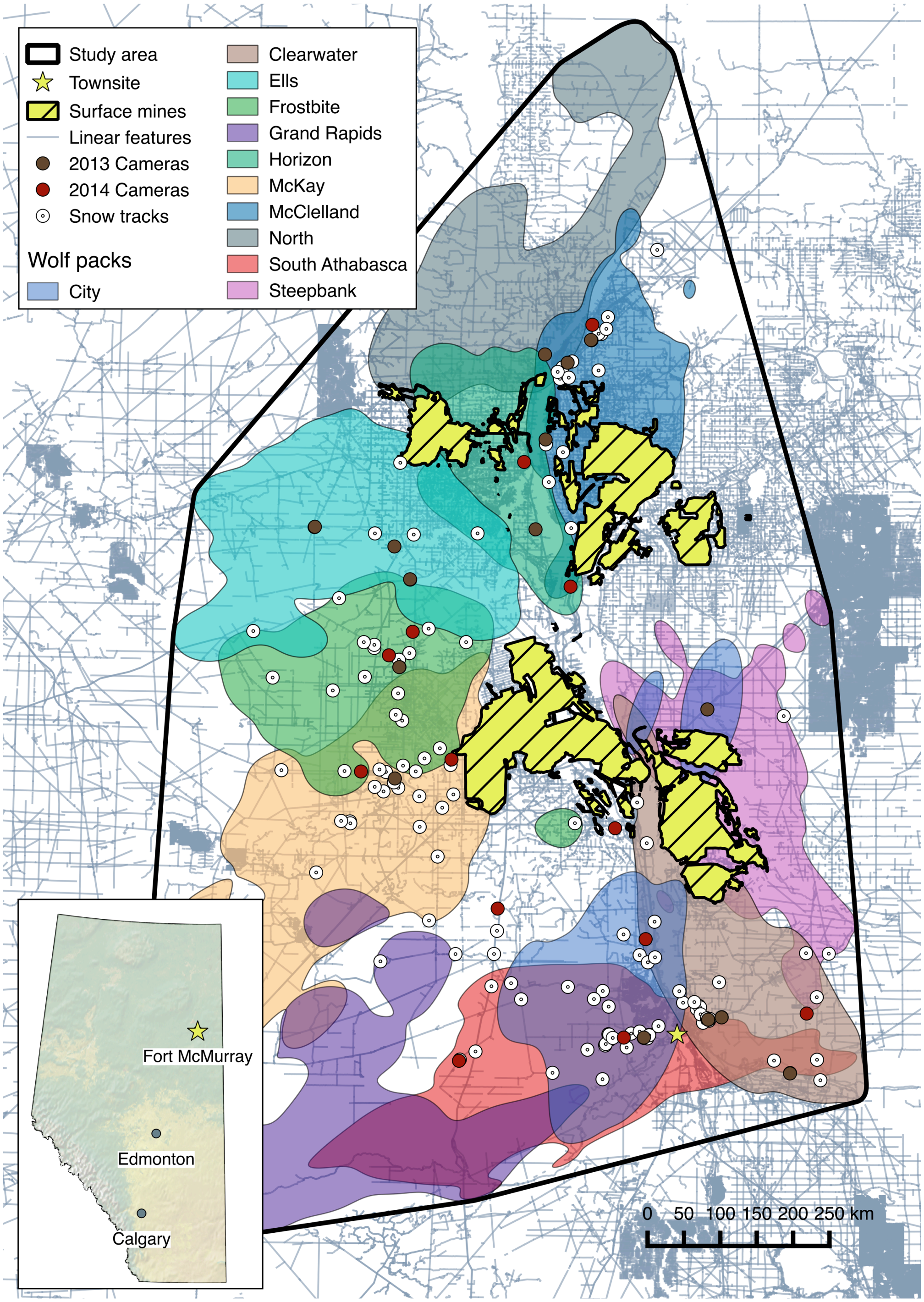


Figure 2

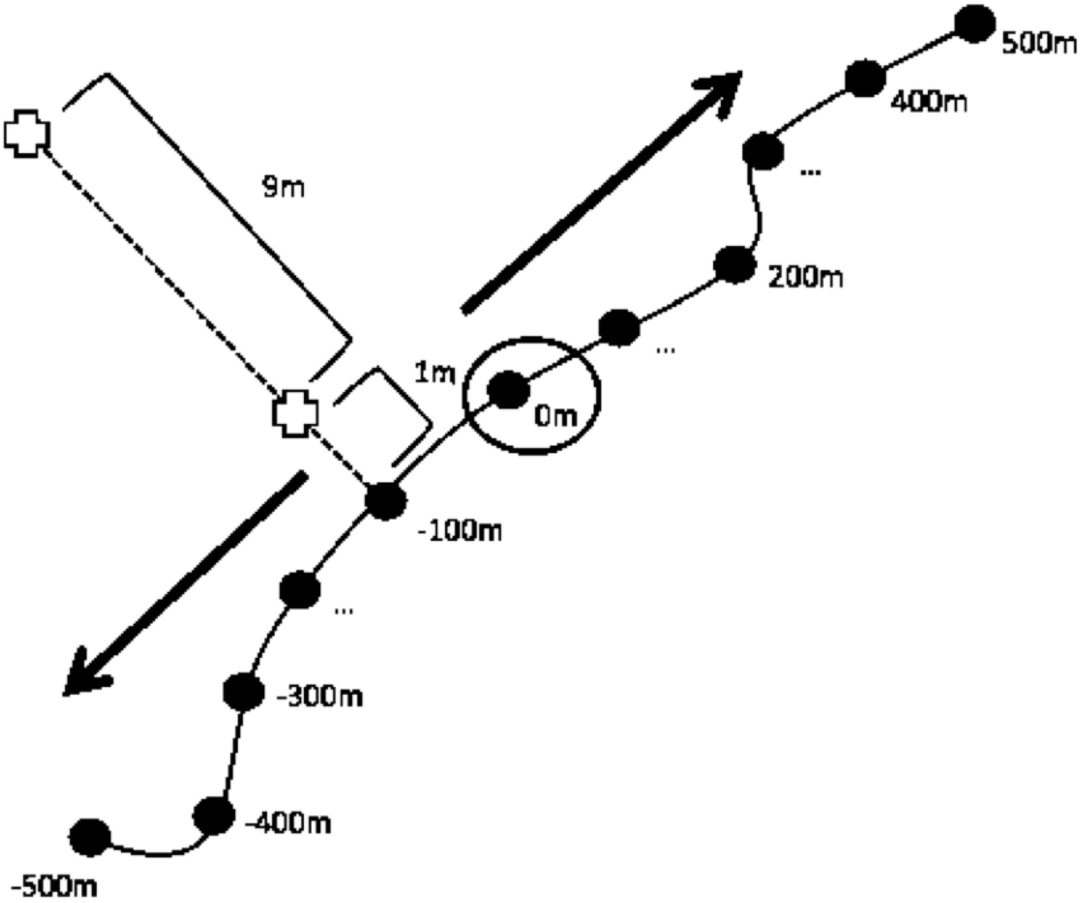
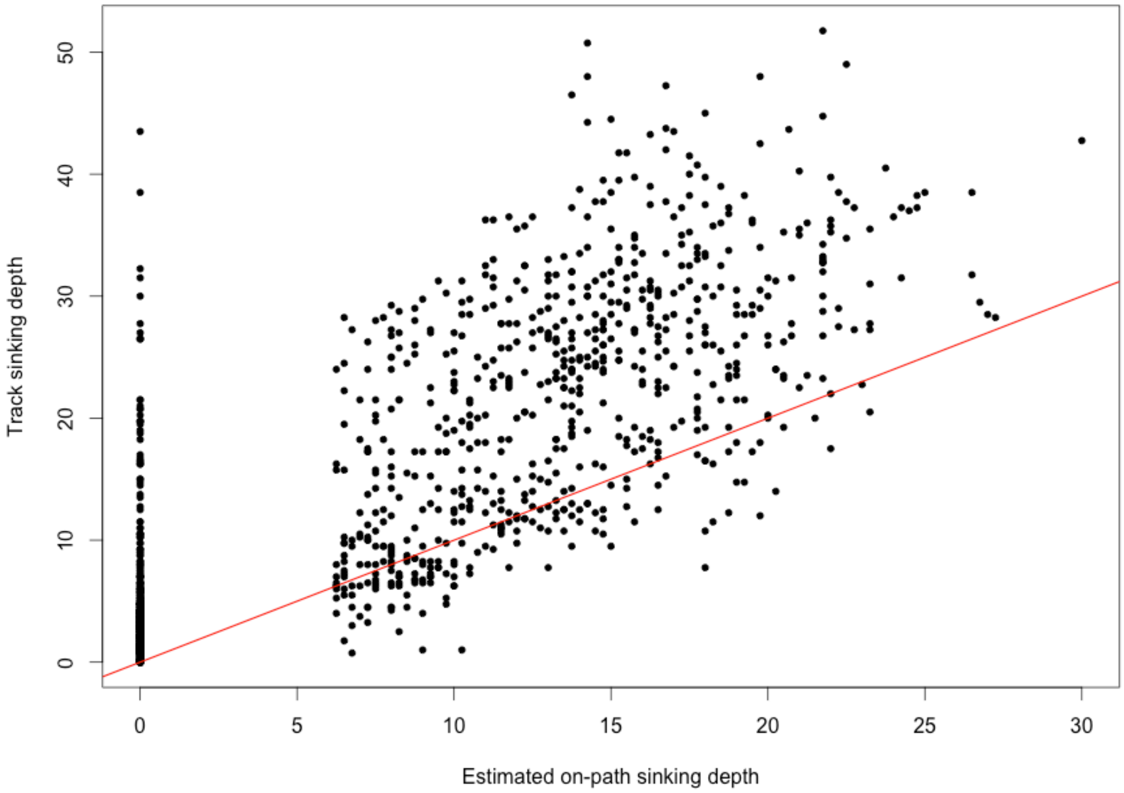


Figure 3



Track sinking depth
0
10
20
30
40
50
0
5
10
15
20
25
30
Estimated on-path sinking depth

Figure 4

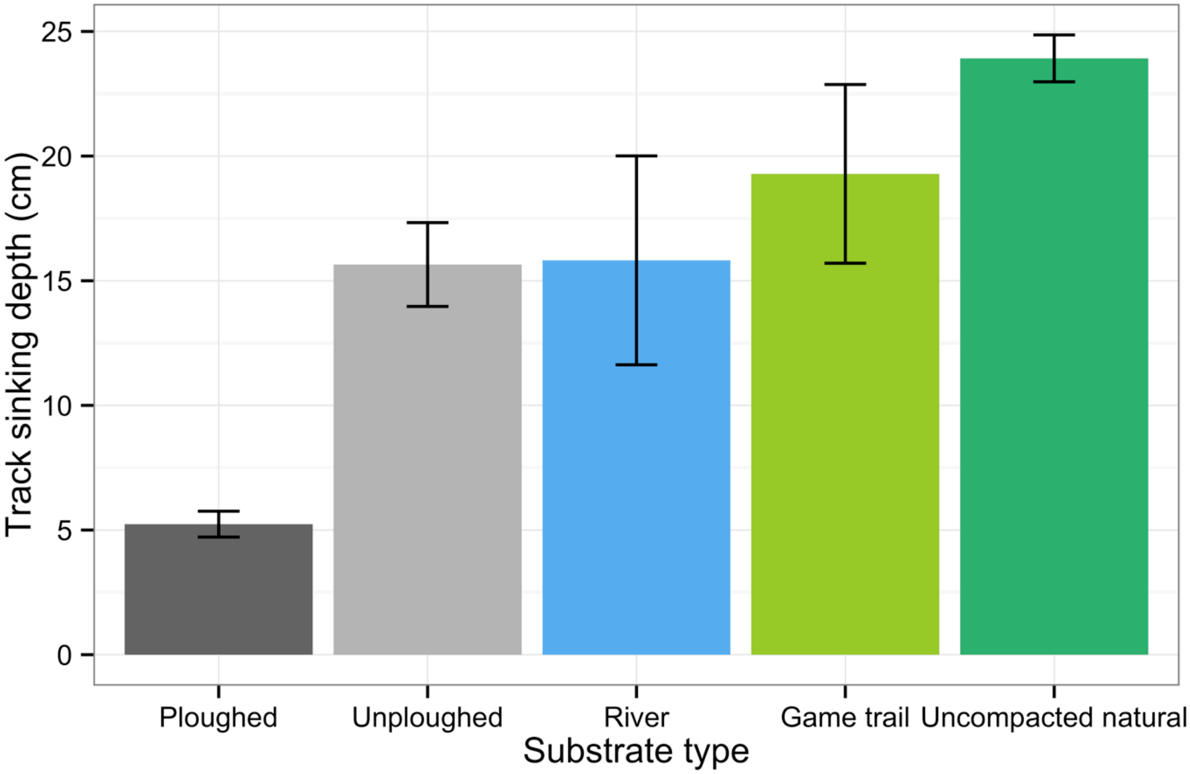

Track sinking depth (cm)
0
5
10
15
20
25
Ploughed
Unploughed
River
Game trail
Uncompacted natural
Substrate type

Figure 5

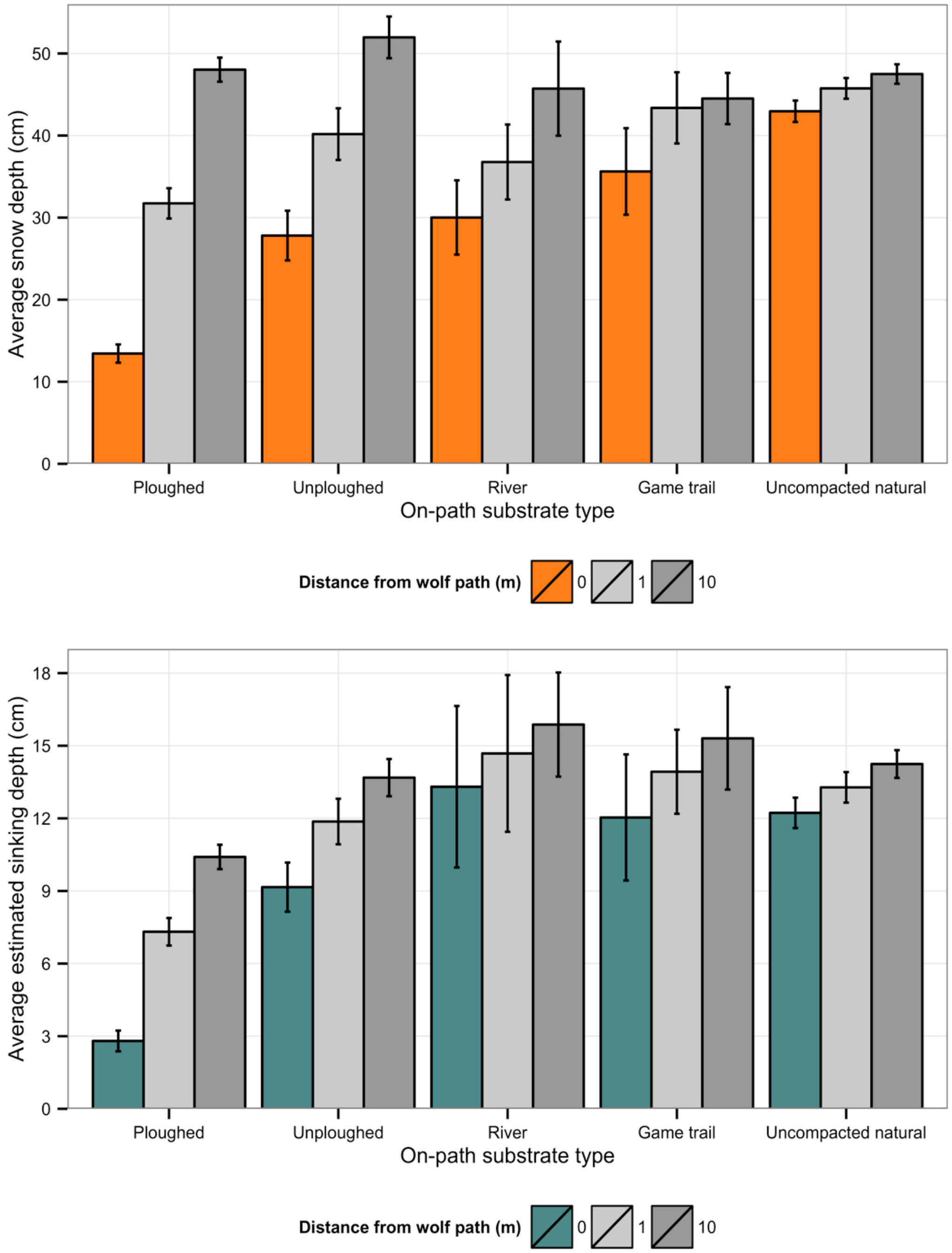

Average snow depth (cm)
0
10
20
30
40
50
Ploughed
Unploughed
River
Game trail
Uncompacted natural
On-path substrate type
Distance from wolf path (m)
0
1
10
Average estimated sinking depth (cm)
0
3
6
9
12
15
18
Ploughed
Unploughed
River
Game trail
Uncompacted natural
On-path substrate type
Distance from wolf path (m)
0
1
10

Figure 6

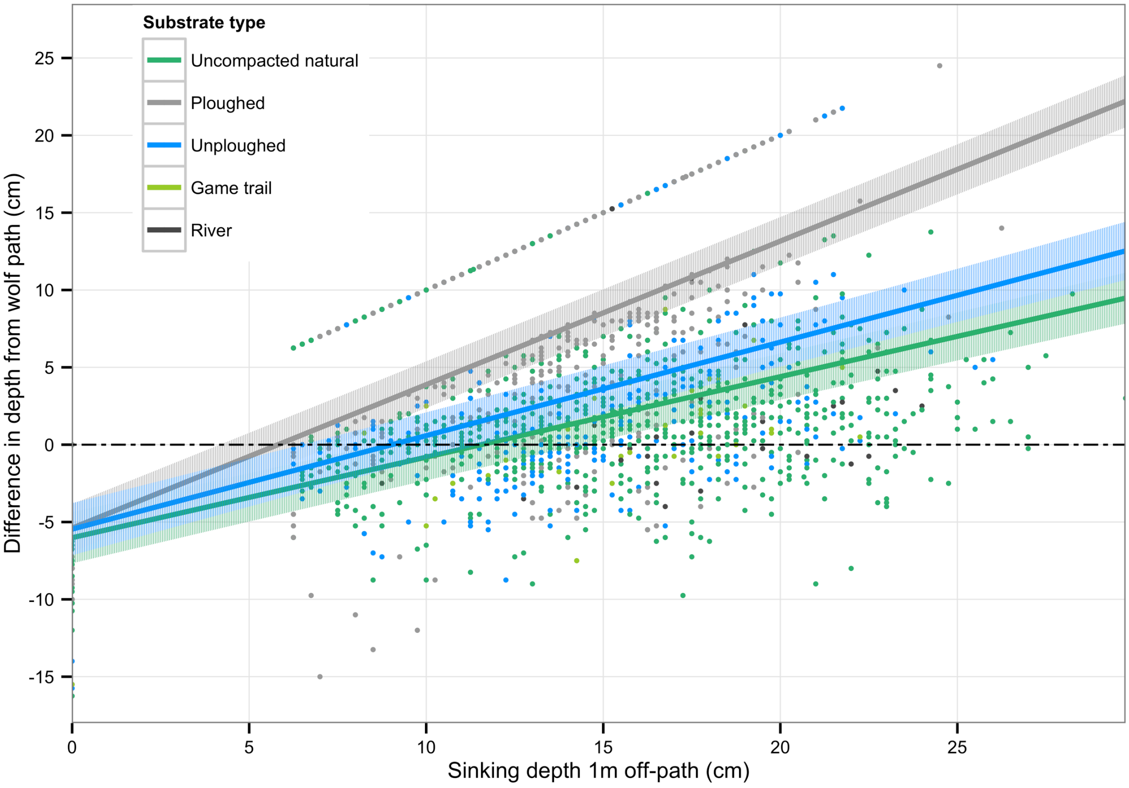

Substrate type
Uncompacted natural
Ploughed
Unploughed
Game trail
River
Difference in depth from wolf path (cm)
Sinking depth 1m off-path (cm)
25
20
15
10
5
0
-5
-10
-15
0
5
10
15
20
25

Figure 7

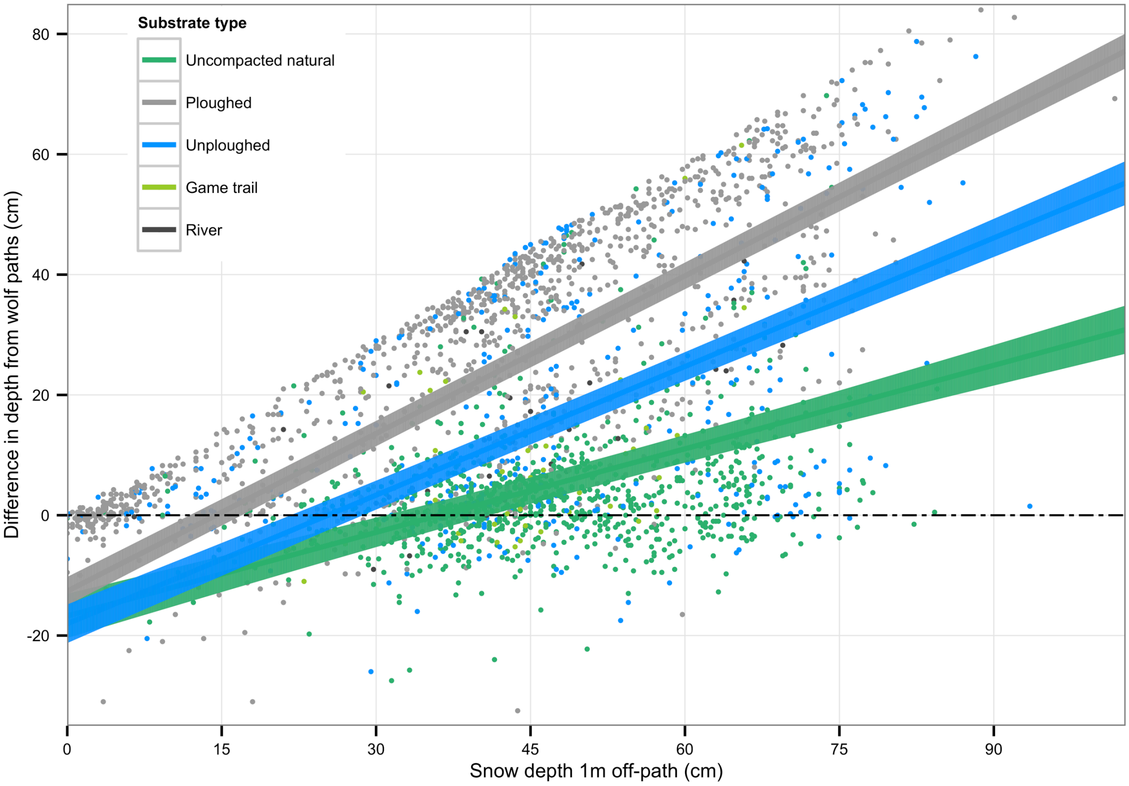
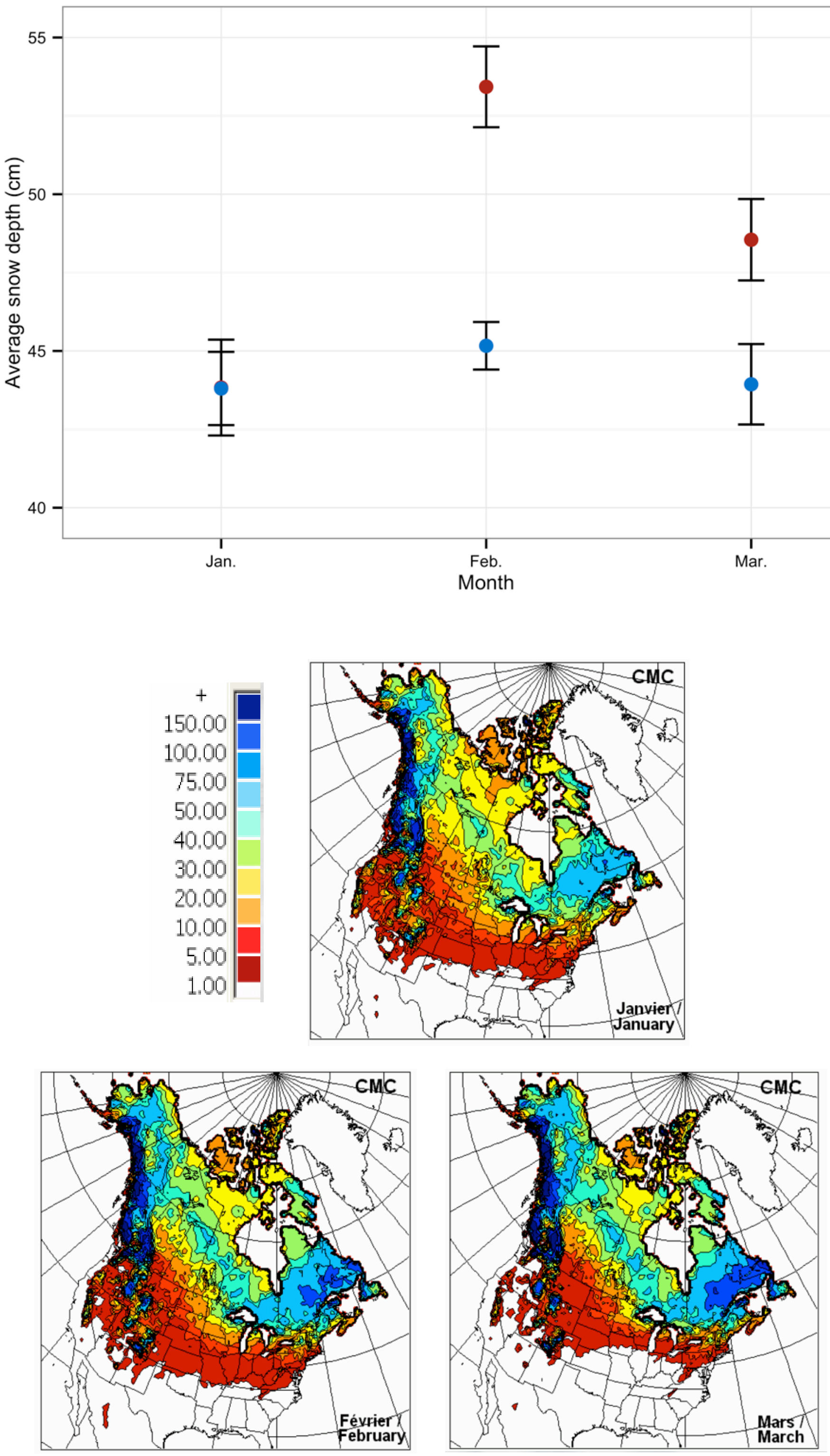

Substrate type
Uncompacted natural
Ploughed
Unploughed
Game trail
River
Difference in depth from wolf paths (cm)
80
60
40
20
0
-20
0
15
30
45
60
75
90
Snow depth 1m off-path (cm)

Figure 8



55
50
45
40
Average snow depth (cm)
Jan.
Feb.
Mar.
Month
+
150.00
100.00
75.00
50.00
40.00
30.00
20.00
10.00
5.00
1.00
CMC
Janvier /
January
CMC
Février /
February
CMC
Mars /
March

Chapter 2 The calm during the storm: Snowfall affects the movement and behaviour of grey wolves

Abstract

Although behavioural responses to snow have been well-documented over large spatial and temporal scales, little is known about the effect of snowfall. We investigated the effects of snowfall on the movement of grey wolves (*Canis lupus*) in northeastern Alberta, Canada. We used remote cameras to identify major snowfall events, which we defined as an accumulation of at least 5 centimetres of snow in 24 hours. We used 30-minute GPS telemetry data from 10 radio-collared wolves to discretize step lengths into travelling and resting behaviours, and calculated travel speed, proportion of time spent travelling, maximum speed, and daily distance travelled. We hypothesized that wolves' response to snowfall would be mainly driven by energetic considerations; in response to increased snow depth and sinking depth, we predicted that wolves would decrease their travel speed and the proportion of time spent travelling during snowfall events, and for a few days afterwards. On the night of a snowfall event, wolves decreased the proportion of time spent travelling by 30%, from 0.35 to 0.24, and their travel speed from 28.1m/min to 20.7m/min, compared to our control category. As well, the daily distance travelled by wolves was 3.5 kilometres less during a snowfall event than during controls. However, the absence of longer term effects (i.e. one to three days after an event) suggests that wolves' response to snowfall events is driven by factors other than energetic considerations. We propose that wolves' immediate, but short-term response to snowfall events may be influenced by what their prey are doing, and to less efficient hunting brought about by a decline in their sensory perceptions as a result of snowfall's effect on olfaction.

Introduction

In the winter, snow presents a major challenge to large mammals by affecting movement costs, predation risk, and foraging ability. In response, animals have developed many behavioural and physiological adaptations to mitigate these effects. Individuals travel slower, or in areas of shallower snow, to reduce the high energetic costs of travel in deep snow (Parker et al. 1984, Murray and Boutin 1991). Similarly, some populations migrate to areas where snow is shallower and forage is more readily accessible (Boyce 1991). Snow conditions also affect predator-prey interactions by modulating hunting success and predation risk. In severe winters, grey wolves (*Canis lupus*) form larger packs, which may not only decrease the energetic costs of travel, but may also increase hunting success (Fuller 1991, Post et al. 1999).

Though behavioural responses to snow have been well-documented over large spatial and temporal scales (e.g. Adamczewski et al. 1984, Boyce 1991, Post et al. 1999), little is known about the effect of snowfall events. Snowfall events are short-term weather events that change the landscape that animals must deal with. For one, fresh snow has little supportive capacity for moving animals. But snowfall events also likely affect animals' ability to see, hear, and smell. Falling snow cleans the air of chemical molecules, which produce scent, and covers up tracks; as well, fresh snow is an effective sound insulator (Attenborough 1988, Kyrö et al. 2009). The effects of winter precipitation on an animal's sensory perceptions may, in turn, affect whether an animal chooses to move around and search for food, or sit still and wait for foraging and hunting conditions to improve.

The grey wolf (hereafter wolf) is a year-round resident of many northern regions, including Canada's boreal forest. Wolves are well-adapted to travel in the snow, having a relatively low foot-load (ratio of body mass to foot surface area) that enables it to sink less in deep snow than most of its prey (Telfer and Kelsall 1984). When hunting, wolves detect prey primarily by picking up on its scent (Mech 1970). Wolves sense of smell is particularly important in forested habitats such as the boreal forest where visual detection of prey is limited (Mech 1970). Moreover, as a cursorial predator, wolves rely heavily on movement to find prey. By searching large areas, wolves increase the likelihood that they will detect or encounter prey.

We used remote cameras and GPS telemetry to identify snowfall events and examine their effect on wolf behaviour and movement. Our hypothesis was that wolves' response to snowfall events would be mainly driven by energetic considerations as a result of increased snow depth and sinking depth. We predicted that wolves would respond to this increased cost of movement by decreasing their travel speed and the proportion of time spent travelling during a snowfall event. Moreover, we predicted that this reduction in movement would persist for a few days until snow settled and became easier for travel. But the effect of snowfall events on wolves' movements may also be driven by hunting considerations. If hunting success is higher during (or shortly after) snowfall events, wolves should increase their movement over the time period where hunting is improved. However, if hunting is worse during a snowfall event, because of factors not directly related to an increase in snow depth (i.e. reduction in sensory perception), then wolves should decrease their movements, but this effect may not persist beyond the duration of the snowfall event.

Methods

Study area

Our study area was located north of Fort McMurray in the Athabasca Oil Sands Region in northeastern Alberta, Canada (Figure 1). The area is within the central mixedwood sub-region of the boreal forest ecosystem (Natural Regions Committee 2006). The most common vegetation types are treed wetlands, deciduous forests, and mixedwood forests; dominant tree species include aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and white spruce (*Picea glauca*). Mean yearly temperature is 1.0°C, with average January temperatures of -17°C (Environment Canada 2015a). Yearly snowfall is 134cm (based on averages from 1981 to 2010), falling mostly from November to March (Environment Canada 2015a). Our study area is also characterized by heavy industrial development from the oil and gas sector; notably, there is a vast network of human-created linear features, including seismic lines, pipelines, and electrical transmission lines. In addition, as of 2012, approximately 6.5% (571km^2) of our study area was covered by mines for oil extraction. See Chapter 1 for more details.

Telemetry data

Capturing and radio-collaring wolves

As part of an affiliated research program, we captured and radio-collared wolves from 2011 to 2013 (Boutin et al. 2015). Captures were conducted by experienced crew and followed the Alberta Wildlife Animal Care Committee Class Protocol #009 (Alberta Environment and Parks 2015). Collars weighed ~750g and were programmed to drop off after two years. From 2011 to 2013, we collared 41 wolves from 10 different packs. We also collared one lone wolf just north of Fort McMurray. Collars were replaced when they failed and new wolves were captured when individuals died. By the end of our research program in 2014, all collars were either removed or had fallen off. More information can be found in Chapter 1.

Collar fix schedules

Collars were initially programmed to collect one location every 3 hours, but this frequency was increased at different times over the course of our study. From November 11th to November 22nd 2012, the fix rate on 12 collars was increased to one location every 15 minutes. This schedule was repeated in November 2013 for three collars. From January to March 2013, fix rates were set at 30-minute intervals for nine collars; one of those collars lasted until March 2014. From January to March 2014, eight collars operated on a 10-minute fix rate. In this analysis, we only included data from January to March 2013 and 2014, because that is the time period for which we had local snow data. We focus on wolves equipped with collars which had fix rates of 30 minutes or less (Table 1). We excluded three individuals from our analysis because of collar failure. To ensure a sufficient sample size, we analysed data from 2013 and 2014 together; to do so, we rarefied our 2014 data from 10 to 30 minutes.

Identifying travel behaviour

We calculated step length for each individual and for each pair of consecutive telemetry location points (ordered by date and time). Step length is the distance covered from one consecutive telemetry point to the next. We then divided step length by the exact duration between each telemetry fix to obtain speed (expressed in m/min). After calculating speed, we categorized telemetry data into two distinct behaviours, resting and travelling, by following an approach similar to the one outlined by Dickie (2015). The frequency distribution of the log-transformed speed values revealed a bimodal distribution (Figure 2), suggesting that wolf movements occur in at least two distinct phases: slow and fast (Dickie 2015). We used the *mixtools* package in R to fit two normal distributions to the data, and used the intersection point of the two distributions to separate our data into resting and travelling behaviours (Figure 2). We estimated the breakpoint at 0.5, which corresponds to 1.65m/min**.** All steps with speeds less than 1.65m/min were classified as “resting”; all steps with speeds of at least 1.65m/min were classified as “travelling”. We restricted our analyses to travelling behaviours only, because we expected snowfall events to have the greatest effect when wolves are moving.

Classifying data into day and night

We separated telemetry locations into “day” and “night” based on sunrise and sunset times in Fort McMurray for the middle of each month, rounded to the nearest hour (National Research Council Canada 2015) (Table 2). We analysed day and night separately because wolves may behave differently during these two parts of the day (Hebblewhite and Merrill 2008). As well, because most snowfall events in our area occurred after sunset, we expected the effect of snowfall to be stronger at night than during the day (A. Droghini, unpublished data).

Remote cameras

From January to March 2013 and 2014, we deployed remote cameras (Reconyx PC900, Reconyx Inc., Holmen, Wisconsin) to monitor snow depth and snow accumulation. In 2013, we deployed 25 cameras (Figure 1). 22 were paired, with one camera placed in open habitat and the other placed in nearby (<100m away) closed habitat. For each pair, we excluded cameras placed in closed habitats from our analysis, because cameras in closed habitats consistently recorded lower snow depths and had less snow accumulation than their open habitat counterparts (Figure 3), likely as a result of interception from coniferous trees (Peterson and Allen 1974). In 2014, we deployed 12 cameras but did not repeat the paired design. In both years, cameras were deployed for variable lengths of time as they were moved to different sites across the study area.

Cameras were programmed to take one picture every day at noon. Cameras also had an active motion sensor and would take three pictures whenever that sensor was triggered (e.g. by an animal walking by). Cameras were aimed at a pole that was planted in the ground and marked every 10 centimetres (Figure 4). Upon deployment, field technicians measured the initial snow depth by plunging a metre stick in the ground. This measurement, combined with daily pictures, provided us with data on both absolute and relative (i.e. snow accumulation) snow depth (Figure 4).

Assigning cameras and snow conditions to individual wolves

Remote cameras were assigned to individual wolves if they were within a wolf's territory boundary. When more than one camera was within a wolf's territory, we averaged daily snow accumulation and snow depth. Because cameras were deployed for variable lengths of time as they were moved from one site to another, averaging across all cameras in a wolf's territory allowed us to achieve a continuous temporal resolution from January to March. We omitted individuals that did not have any cameras in their territory ($N = 3$).

We defined territory boundaries by using 95% kernel density estimators and winter telemetry data i.e. from November 1st to March 31st (Figure 1; E. Neilson, unpublished data). Telemetry data for kernel estimation was subset to a 3-hour fix rate to minimize the influence of dense clusters associated with kills and bed sites.

Identifying snowfall events

We defined a snowfall event as having occurred if the difference in snow depth from one day to the next was 5 centimetres or more. As a reference, Environment Canada issues a snowfall warning in Alberta when “10 centimetres or more of snow falls within 12 hours or less” (Environment Canada 2015b). We used a more liberal definition because snowfalls of such magnitude were rarely captured on our cameras. Indeed, of all snowfall events of at least 5 centimetres, only 22% had an accumulation of 10 centimetres or more.

Creating time categories around snowfall events

For each individual, telemetry data were classified into seven categories, relative to when they experienced a snowfall event (Table 3). We created 1 snowfall category every 24 hours, from two days before a snowfall event to three days after, for a total of six categories (including the day of the event). Our last category was a control category, for which we selected data from three random days outside of this time window.

Because our cameras took pictures every day at noon, each 24 hour period (hereafter day, for simplicity) spanned from 12PM the previous day to 12PM the day of. Thus, the “day of the snowfall” category included all the data taken after the previous picture (in which no event was detected), and up until the picture that showed the snowfall event. For comparative purposes, the days in the control category were defined in the same way as the other categories i.e. from 12PM to 12PM. Data which did not belong to any of our snowfall categories were excluded from our analyses.

Statistical analyses of movement metrics

Using our seven snowfall categories, we analysed the effects of snowfall on four movement metrics: travel speed, maximum speed, proportion of time spent travelling, and daily distance travelled. Travel speed and the proportion of time spent travelling were analysed with mixed effects models using the *lme4* package in R. For travel speed, we used a linear mixed effects model and log-transformed speed values as our response variable to improve the distribution of our residuals. For our analysis on the proportion of time spent travelling, we used the proportion of travel steps (as a function of the total number of steps) as a proxy. In our case, the proportion of travel steps is a suitable estimate for time spent travelling because the time between two consecutive GPS locations was standardized to 30 minutes (sd = 0.23, range: 26.5 – 34.5 minutes). We analysed the effect of snowfall category on the proportion of travel steps by using a mixed effects logistic regression model with travel steps coded as 1 and resting steps (i.e. all non-travel steps) coded as 0.

We used one-way, repeated measures ANOVAs to analyse maximum speed and daily distance travelled. We proved that our data met the assumptions of normality and sphericity. We did not separate our data into day and night for these analyses, and included both resting and travelling steps. We calculated daily distance travelled by summing the distance covered with each step (i.e. step length). We used the same definition of a "day" that we used when defining our snowfall categories i.e. from 12:00PM to 12:00PM. After looking at our residual plot, we removed 1 outlier and repeated the analysis.

All analyses included a random intercept (or error term) for each individual wolf. We used the control category as our reference category. We used the *lsmeans* package to perform pairwise comparisons and obtain significance values if there was a significant effect ($P < 0.05$) of snowfall categories on movement.

We conducted a t-test paired by individual and by date to determine whether movement metrics were different between day and night. Prior to conducting the test, we ensured our data met the assumptions of normality and homoscedasticity.

Results

Snow depth was higher in 2013 than in 2014, averaging 51.5 centimetres and 44 centimetres, respectively (Figure 5). Snow depth was also more variable in 2013, and increased over the winter as nearly 10 centimetres of snow accumulated from January to February (Figure 5); in contrast, snow depth remained relatively constant in 2014 (Figure 5). Considering additional snowfall categories (e.g. 3+ days before, or 4+ days after) would have proven difficult, as categories would have begun to overlap. The median number of days between "2 days before the snowfall event" and the previous event was 9 days, with a minimum of 4 days. Similarly, the "3 days after" category was separated by the following snowfall event by a minimum of 3 days, with a median of 8 days.

We had camera data for 14 individuals. Each wolf had an average of 1.6 remote cameras in its territory (range: 1-3.8). We identified 15 unique snowfall events across 10 individuals (Figure 6). Of these, 12 (80%) occurred in 2013, with an average frequency of 1 event every 6 days. However, most snowfalls were highly localized and affected only 1 collared individual. Indeed, of the 15 snowstorm events we identified, more than half (67%) were experienced by only 1 individual (Figure 6). We detected only 1 regional snowfall event that affected all individuals that year ($N = 6$). In 2013, each wolf experienced an average of 3.6 snowfall events (range: 2-6; Figure 6). In 2014, all 4 individuals experienced only 1 snowfall event. An additional 4 individuals did not experience any snowfall events and were excluded from further analyses.

Travel speed

Wolves travelled faster at night than during the day, covering an additional 5.8m/min. On control days, wolves' average travel speed was 25.7m/min at night (sd=24.2), versus 19.8m/min during the day (sd=19.7).

During the day, travel speed did not change significantly across snowfall categories (Figure 7). Based on our pairwise comparison test, we did not detect any statistically significant differences in travel speed across snowfall categories. However, a few trends emerged. First, relative to the control category, wolves exhibited a slight increase in travel speed the day before a snowfall event (19.2m/min vs. 23.3m/min; $P = 0.11$). Travel speed on the day of an event, as well as 2 days before, 1 day after, and 3 days after were nearly identical to the travel speed of our control group (Figure 7). The lowest travel speeds were recorded 2 days after the snowfall event, when wolves averaged 17.2m/min.

At night, there was a clear response to snowfall events, as wolves significantly reduced their travel speed from 30.0m/min the night before to 19.6m/min the night of a snowfall event (Figure 7). This decrease in speed on the night of a snowfall event was statistically significant when compared to both control and night before categories ($P < 0.01$ and 0.014, respectively). Travel speed increased to 23.7m/min one night after the event, but we still detected a marginal statistical difference when compared to the control and to the night before ($P = 0.068$ and 0.085, respectively).

Maximum speed

Maximum speed was marginally different across snowfall categories ($F_{4,54} = 1.91$, $P = 0.096$); none of our pairwise comparisons were significantly different from each other. The absolute maximum speed was attained on a control day (144.6m/min); however, on average, individuals attained the highest speeds the day before a snowfall event. While this trend was consistent with our other findings, the pattern with respect to the other categories is less clear. When averaged across individuals, maximum speed was low the day of a snowfall event (72.3m/min), but was similarly low two days before a snowfall event (70.8m/min) and two days after (71.0m/min).

Proportion of time spent travelling

Across all storm categories, the proportion of time spent travelling was lower at night than during the day (31% and 40%, respectively), and this difference was significant (t=2.28, df = 9, $P < 0.05$). During the daytime, there were no differences in the proportion of time spent travelling across snowfall categories (Figure 8). On average, the proportion of travel ranged from 36% to 46%, but did not appear to be in response to time since a snowfall event (Figure 8). At night, however, the proportion of time spent travelling decreased significantly on the night of a snowfall event (Figure 8); this decrease was statistically significant when compared to all other categories except for two days after the event (Table 3 Snowfall categories used in our statistical analyses. Categories were assigned based on when a snowfall event was detected in an individual wolf's territory. After all snowfall events had been identified, we created a control category by choosing, for each wolf, 3 random days that did not belong to any other snowfall category. All other unassigned telemetry data were excluded from our analyses.

Category	**Days since snowfall event**
Control	3 random days, not belonging to any other category
-2	2 days before
-1	1 day before
0	Day of snowfall event

+1	1 day after
+2	2 days after
+3	3 days after

Table 4). Proportion of time spent travelling ranged from 23% to 35%; proportion was highest two days before an event and for our control category.

Relationship to daily distance travelled

There was a high correlation between daily distance travelled and average travel speed (*r* = 0.89). There was also a high correlation between daily distance travelled and the proportion of travel steps, though this relationship was less pronounced (*r* = 0.72). Unsurprisingly, then, the daily distance travelled by wolves followed similar trends to travel speed: on average, distance travelled was lowest the day of a snowfall event and highest the day before, with values of 8.5km and 13.8km, respectively. However, the high distance covered the day before a snowfall event was driven by one instance in which an individual travelled almost 50km in one day. After removing this outlier from our dataset, the control category had the highest average distance travelled (Figure 9). The effect of snowfall category on distance travelled was not statistically significant ($F_{6,157} = 0.89$, $P > 0.05$).

Discussion

We present the first study on the effects of snowfall on animal movement. Snowfall events are pulsed weather events that lead to both an increase in snow depth and in relative sinking depth. Our analyses show that wolves respond to snowfall events by moving less; as well, when they do move, they move at a slower speed (Figure 7; Figure 8). This decrease in speed has been shown in response to deep snow, but only in manipulated trials (Parker et al. 1984). Our study is the first to show that these effects occur in natural settings. Our study also shows that the effect of snowfall events on movement is significant enough to translate into a reduction in daily distance travelled. Indeed, relative to our controls, wolves travelled 3.5 kilometres less on days where snowfall events occurred (Figure 9).

The effect of snowfall on wolf movements was most noticeable on the night of a snowfall event; this is when most snowfall events occurred during our study. We found that snowfall events did not have a significant effect on maximum speed attained by wolves, suggesting that wolves can and do still achieve high speeds even during snowfall events. Additionally, we did not find evidence for a persistent effect on wolf movements, although our data suggest that travel speed and time spent travelling may remain low for several days after a snowfall event. Persistent effects may only be detectable when wolves' experience larger snowfall events e.g. 20 centimetres or more. When snowfall events are light, as in our study, wolves' response to these events may be driven by considerations beyond snow depth and sinking depth.

As nearly all wolf movements are driven by their need to find prey (Mech 1970), wolves may limit movement during a snowfall event because it is harder for them to detect prey. Wolves detect prey primarily through olfaction (Mech 1970). Predators are attracted to specific combinations of chemical molecules, which correspond to a prey's unique olfactory signature (Conover 2007). As scents are comprised of chemical molecules that are suspended in the air, the ability for a predator to pick up on the scent of its prey are enhanced or degraded by atmospheric conditions. For example, high wind conditions increase the distance at which scents can be detected (Cablk et al. 2008). In contrast, precipitation can degrade scent signals (Whelan et al. 1994). Falling snow degrades scent signals because chemical molecules aggregate to ice crystals and snowflakes and precipitate down the vertical column, thereby cleansing the air of chemical molecules (Kyrö et al. 2009). Because wolves rely so heavily on olfaction to detect prey, any process that interferes with their ability to smell is likely to have negative repercussions on their hunting success.

To understand wolves' movement responses during snowfall events also requires information on prey movements, as prey movement rates influence encounter rates (Vander Vennen et al. 2016). Prey can respond to snowfall events in one of three ways: movement rates can either increase, decrease, or stay the same. Unless prey increase their movements during snowfall events, we would expect a decrease in encounter rates, given wolves' decrease in travel speed and time spent travelling. Prey's response to snowfall events may help to establish whether wolves' are responding to a decline in prey movement rates or a reduction in sensory perceptions, though the two options are certainly not mutually exclusive.

Using remote cameras allowed us to estimate changes in snow depth over time, and to identify localized snowfall events, which we would not have been able to do had we relied on broad-scale snow models. Indeed, more than half of the snowfall events in our study area were highly localized (Figure 6), which suggests that data on snow conditions needs to be collected at a fine enough spatial scale to allow for detection of these localized events. Major snowfall events were rare over our study, and especially in 2014; as well, most of the snowfall events we detected ranged in magnitude from 5cm to 16cm, with an average of 7.2cm. Such mild snow conditions made it more difficult for us to detect significant differences across snowfall categories; future studies in areas where snowstorms are more common or more extreme may discover that the effects are even larger than the ones reported here, and may find significant effects on movements beyond just the duration of the snowfall event.

Although snowfall events are short-term events that usually last only a few hours, our study shows that these events are significant enough to induce a decrease in proportion of travel and in travel speed, and a concomitant decline in daily distance travelled. While movement responses to snow are often attributed to snow depth and sinking depth, which impede locomotion and increase the cost of movement, the strong response on the night of a snowfall event, and the absence of longer term effects on movements, suggest that wolves' response to snowfall events is driven by other factors. We propose that wolves' immediate, but short-term response to snowfall events may be influenced by what prey are doing and to less efficient hunting brought about by a decline in their sensory perceptions as a result of snowfall.

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Tables

Table 1 Schedule and number of radio-collars deployed on wolves in the winter that had fix rates of 30 minutes or less. From January to March, collar frequency was increased to 30 minutes in 2013 and to 10 minutes in 2014 for 20 of our collared wolves. Three of these collars failed and were not used in our analyses. Start and end dates represent the earliest and latest dates for which we had fast fix rates.

Year	**Start date**	**End date**	**Fix rate (min.)**	**Deployed**	**Used**
2013	January 10th	March 31st	30	9	9
2014	January 10th	March 31st	30	2	0
2014	January 10th	March 31st	10	9	8

Table 2 Hours that mark the beginning of the day and night for each month. Start times were based on sunrise/sunset times, rounded to the nearest hour, for the middle of each month in Fort McMurray, Alberta, Canada. Telemetry data were classified into "day" and "night" and analysed separately.

Month	**Day**	**Night**
January	9:00	17:00
February	8:00	18:00
March	7:00	19:00

Table 3 Snowfall categories used in our statistical analyses. Categories were assigned based on when a snowfall event was detected in an individual wolf's territory. After all snowfall events had been identified, we created a control category by choosing, for each wolf, 3 random days that did not belong to any other snowfall category. All other unassigned telemetry data were excluded from our analyses.

Category	**Days since snowfall event**
Control	3 random days, not belonging to any other category
-2	2 days before
-1	1 day before
0	Day of snowfall event
+1	1 day after
+2	2 days after
+3	3 days after

Table 4 The movement steps of 10 radio-collared wolves were discretized into one of two behaviours: resting or travelling. Each step was also categorized based on time since the most recent snowfall event: from 2 days before (“-2”) to 3 days after (“+3”). We ran different models for night and day. The results shown here are for nighttime travel only. **Top:** □ coefficients and standard errors from our logistic model, which examined whether the proportion of travel steps was affected by snowfall events. The model includes a random effect for individual wolf. **Bottom:** Pairwise comparison across snowfall categories. Only pairs with significant differences (*P* < 0.05) are shown. On the night of a snowfall event, there was a marked decline in the proportion of travel steps taken by wolves. This decline was statistically significant when compared to all categories except 2 days after.

	Estimate	**SE**	**Z ratio**	***p*-value**
Intercept	-0.629	0.123	-5.103	<0.001
“-2”	-0.008	0.115	-0.070	0.945
“-1”	-0.156	0.113	-1.382	0.167
“0”	-0.516	0.117	-4.417	<0.001
“+1”	-0.139	0.113	-1.228	0.220
“+2”	-0.236	0.114	-2.066	0.039
“+3”	-0.012	0.113	-0.108	0.914

Pairwise comparison	**Estimate**	**SE**	**Z ratio**	***p*-value**
“0” – Control	-0.516	0.117	-4.417	<0.001
“0” – “-1”	-0.360	0.120	-2.997	0.043
“0” – “-2”	-0.508	0.121	-4.182	<0.001
“0” – “+1”	-0.377	0.120	-3.136	0.028
“0” – “+3”	-0.504	0.120	-4.195	<0.001

Figure legends

Figure 1 Map of our study area, located in the Athabasca Oil Sands Region just north of Fort McMurray, in northeastern Alberta, Canada. From January to March 2013 and 2014, we deployed remote cameras at various locations in our study area to measure snow depth and snow accumulation. Cameras were then assigned to radio-collared individual wolves to study how wolf movements are affected by snowfall events. The wolf territories shown here were generated for each individual using 95% kernel density estimators.

Figure 2 Histogram of log-transformed speed values, revealing a bimodal distribution which suggests that wolf movements can be discretized into two distinct phases: slow and fast (Dickie 2015), associated with resting and travelling behaviours, respectively. We modelled the density distribution as two Gaussian curves (shown in red and green) and used the intersection point as the cut-off value: speed values greater than or equal to 0.5 were classified as “travel”, whereas values less than that were classified as “resting”. This breakpoint is equal to 1.65m/min.

Figure 3 Comparison of snow depth in closed versus open habitats in 2013 as measured by remote cameras. Snow depth in open habitats in 2014 is also shown for reference. Relative to open cameras in 2013, closed cameras recorded lower snow depths and fewer snowfall events. As well, there was slightly more variation among cameras in open than in closed habitats.

Figure 4 An example of two pictures taken from the same remote camera on consecutive days (January 23rd and January 24th 2013). Black lines on the pole are spaced 10 centimetres apart. By counting the number of black lines that are visible from one day to the next, we can estimate the amount of snow that has accumulated over that time period. In this example, we estimated a snowfall of five centimetres, with an increase in absolute snow depth from 47 to 52 centimetres. According to our definition, this snow accumulation qualified as a snowfall event.

Figure 5 Average monthly snow depth experienced by wolves in northeastern Alberta from January to March, in 2013 and 2014. Snow depth was recorded using remote cameras, which were deployed throughout our study area in individual wolf territories. In 2013, snow depth was higher and much more variable than in 2014, and increased by nearly 10 centimetres from January to February. Error bars represent 95% confidence intervals.

Figure 6 Number of wolves that experienced snowfall events from January to March 2013 and 2014. Remote cameras were deployed in the territories of 14 wolves in northeastern Alberta, and recorded snow depth and snow accumulation every 24 hours. A snowfall event was defined when at least 5 centimetres of snow fell in 24 hours. Of the 14 wolves for which we had snow data, 10 experienced a snowfall event (6 in 2013 and 4 in 2014). We identified 15 unique snowfall events over our two years of study. 10 of the 15 events occurred at a local scale, affecting only 1 individual. Only one snowfall event occurred at a regional scale, affecting all the wolves in that year of study.

Figure 7 Average travel speed of wolves **a) at night** and **b) during the day** before, during, and after a snowfall event. Relative to the control category, wolves travelled significantly slower the night of a snowfall event. Lower travel speeds persisted up to 48 hours after the event, but were not statistically significant. Error bars represent 95% confidence intervals.

Figure 8 Proportion of time spent travelling **a) at night** and **b) during the day** before, during, and after a snowfall event. Wolves travelled less at night than during the day. On the night of a snowfall event, wolves significantly decreased the proportion of time spent travelling, from 0.35 on control days, to 0.24 the night of a snowstorm. Time spent travelling was not affected by snowfall events during the day. Error bars represent 95% confidence intervals.

Figure 9 Average daily distance travelled, in kilometres, as a function of days since a snowfall event. Wolves travelled the least on days when there was a snowfall event, covering 3.5 kilometres less than on control days.

Figures

Figure 1

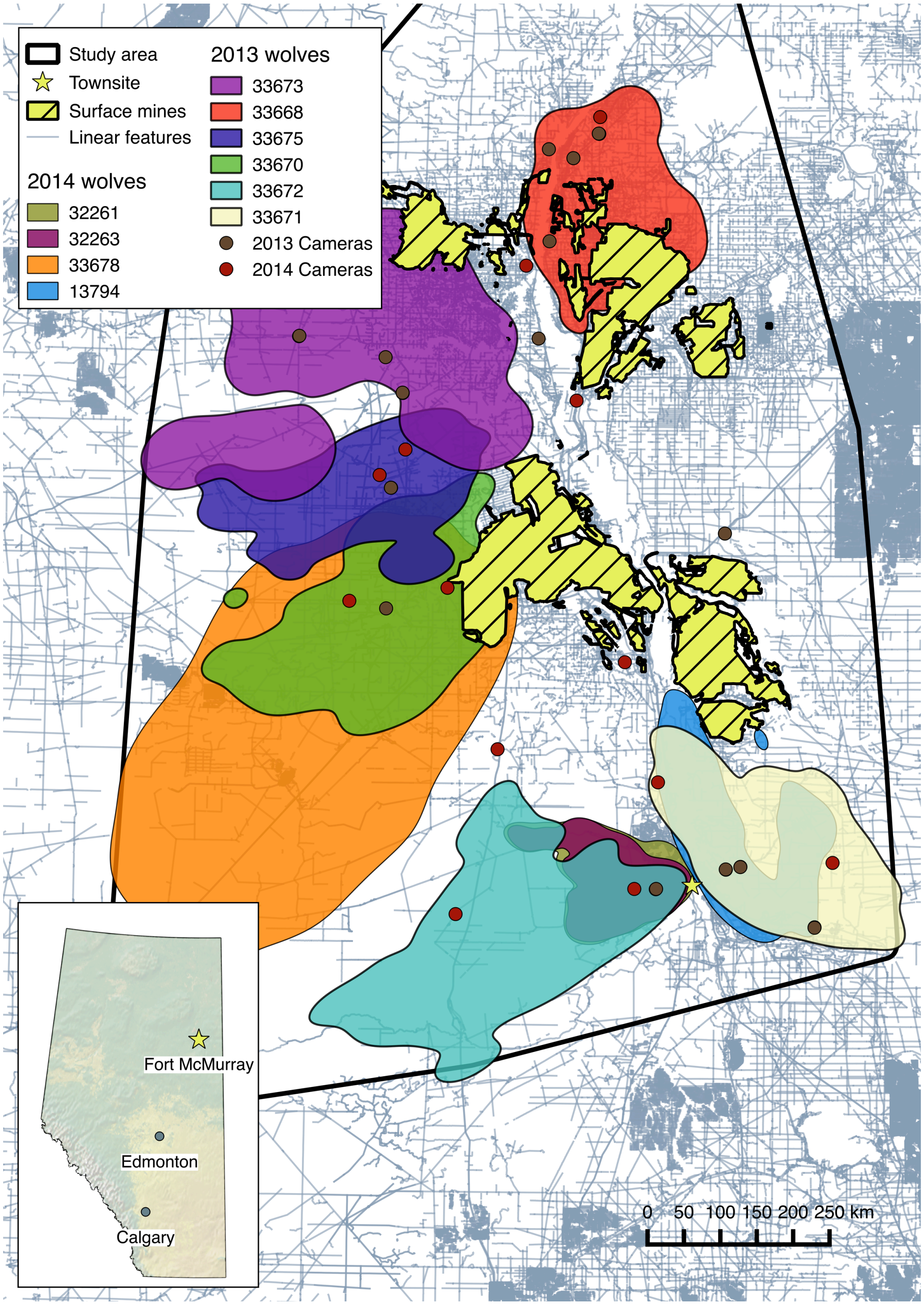


Figure 2

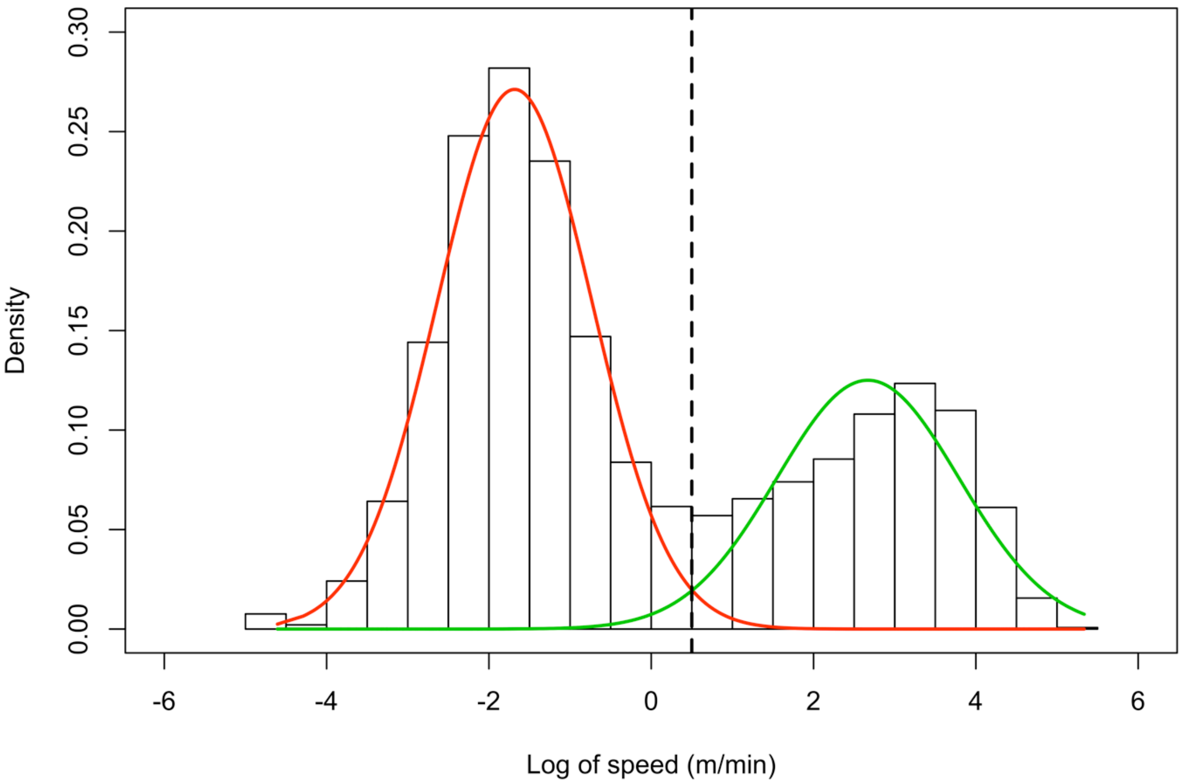


Figure 3

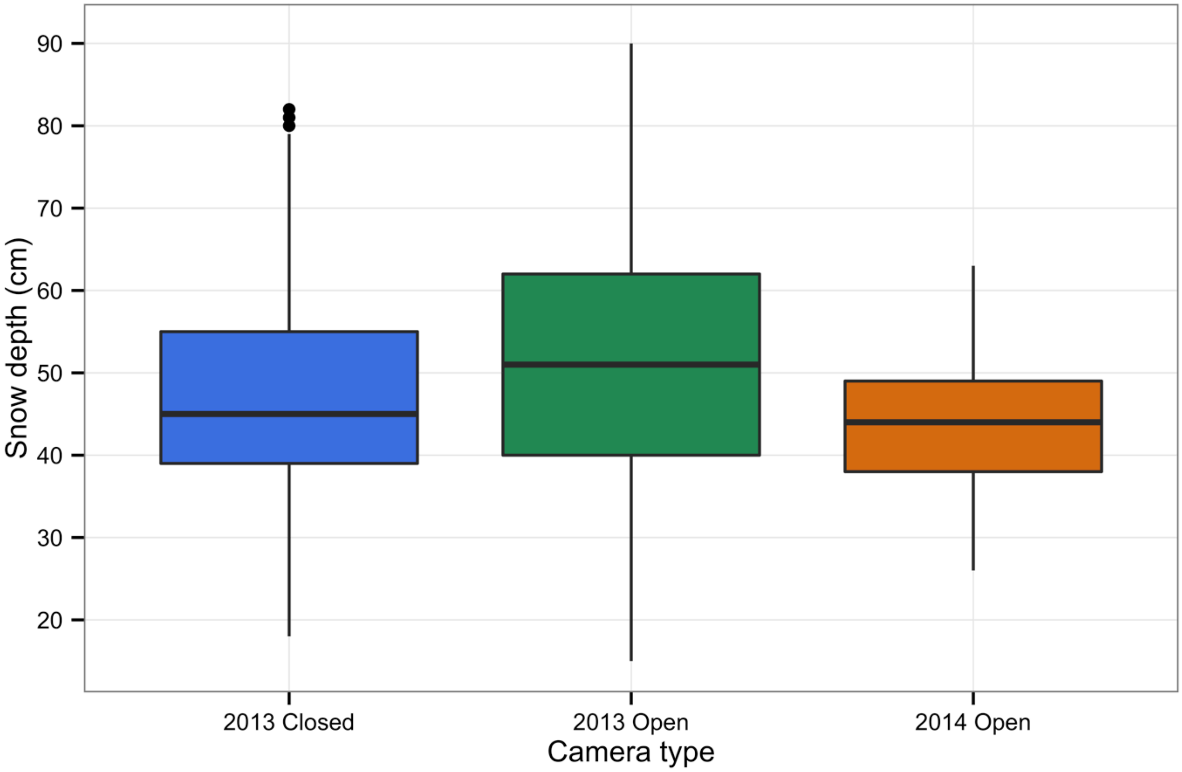
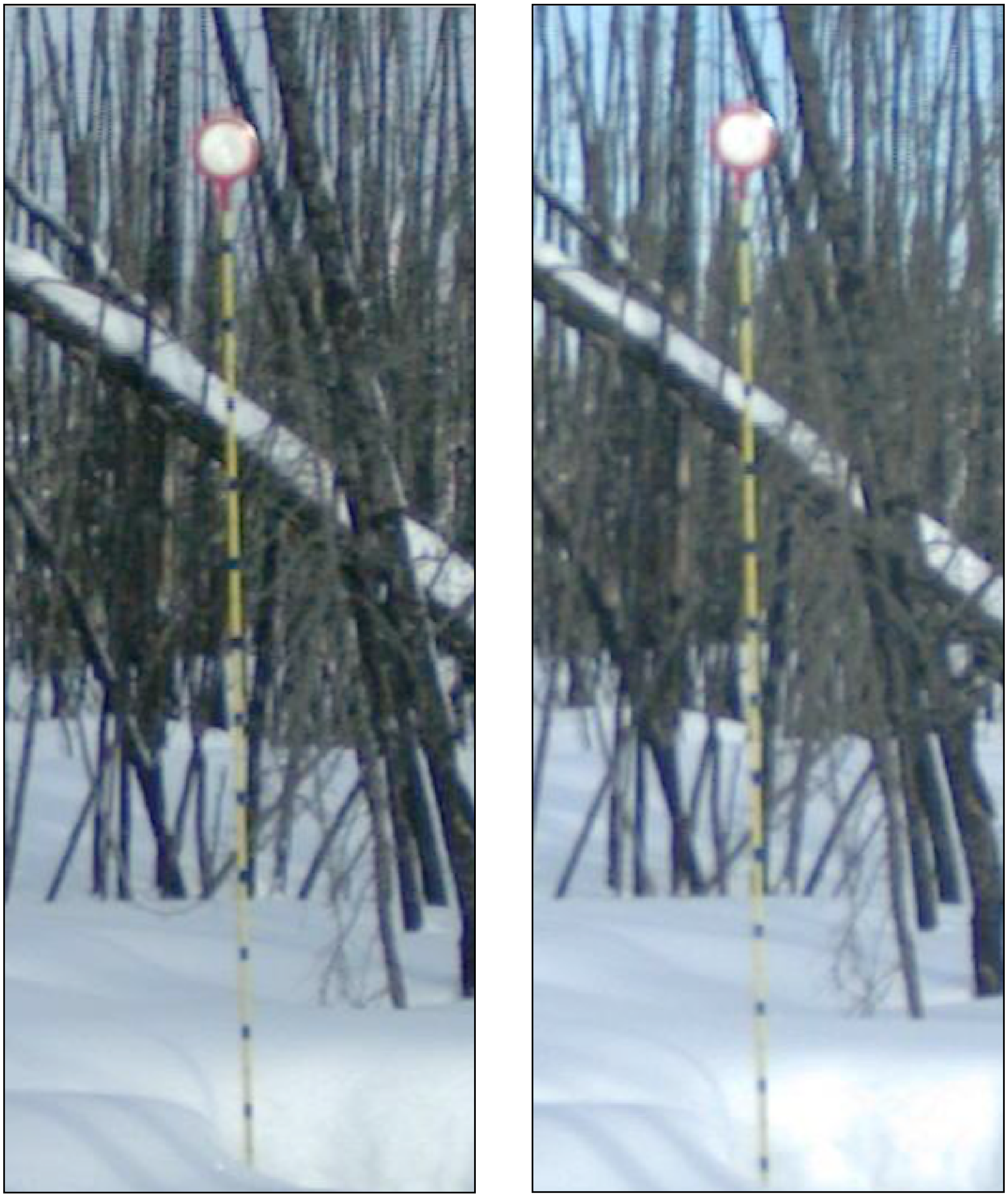

90
80
70
60
50
40
30
20
Snow depth (cm)
2013 Closed
2013 Open
2014 Open
Camera type

Figure 4



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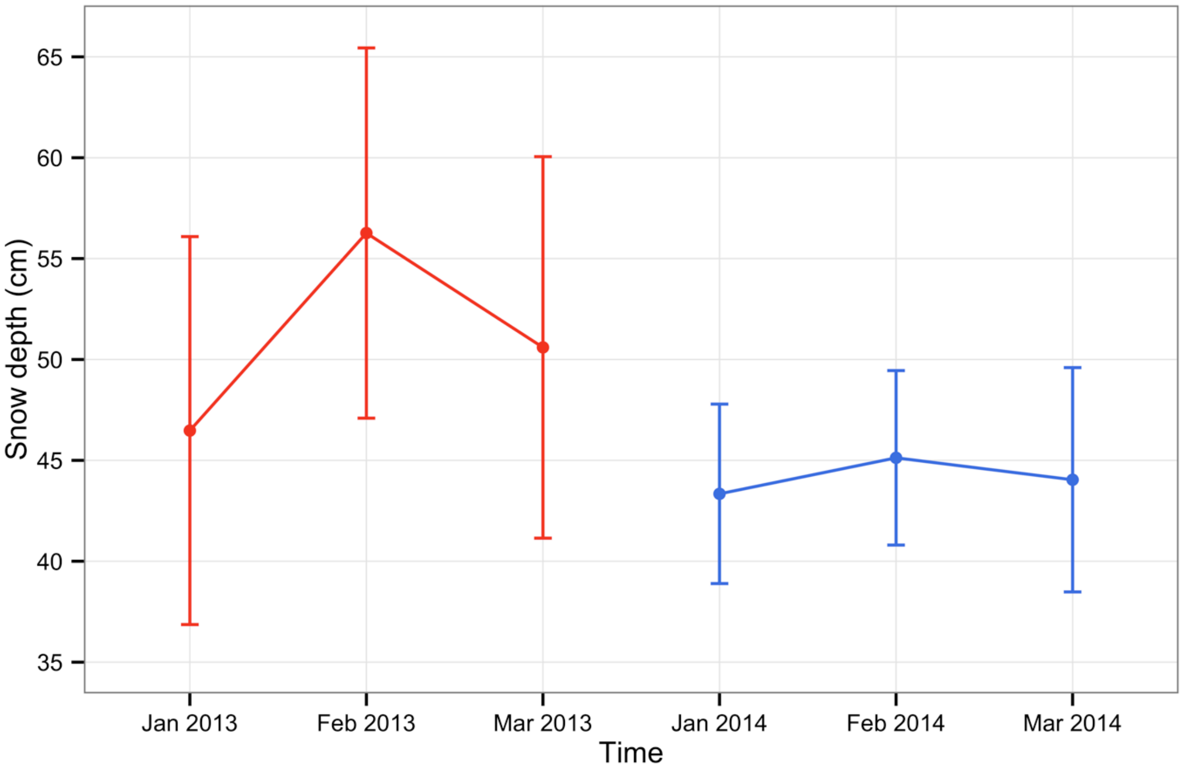


65
60
55
50
45
40
35
Snow depth (cm)
Jan 2013
Feb 2013
Mar 2013
Jan 2014
Feb 2014
Mar 2014
Time

Figure 6

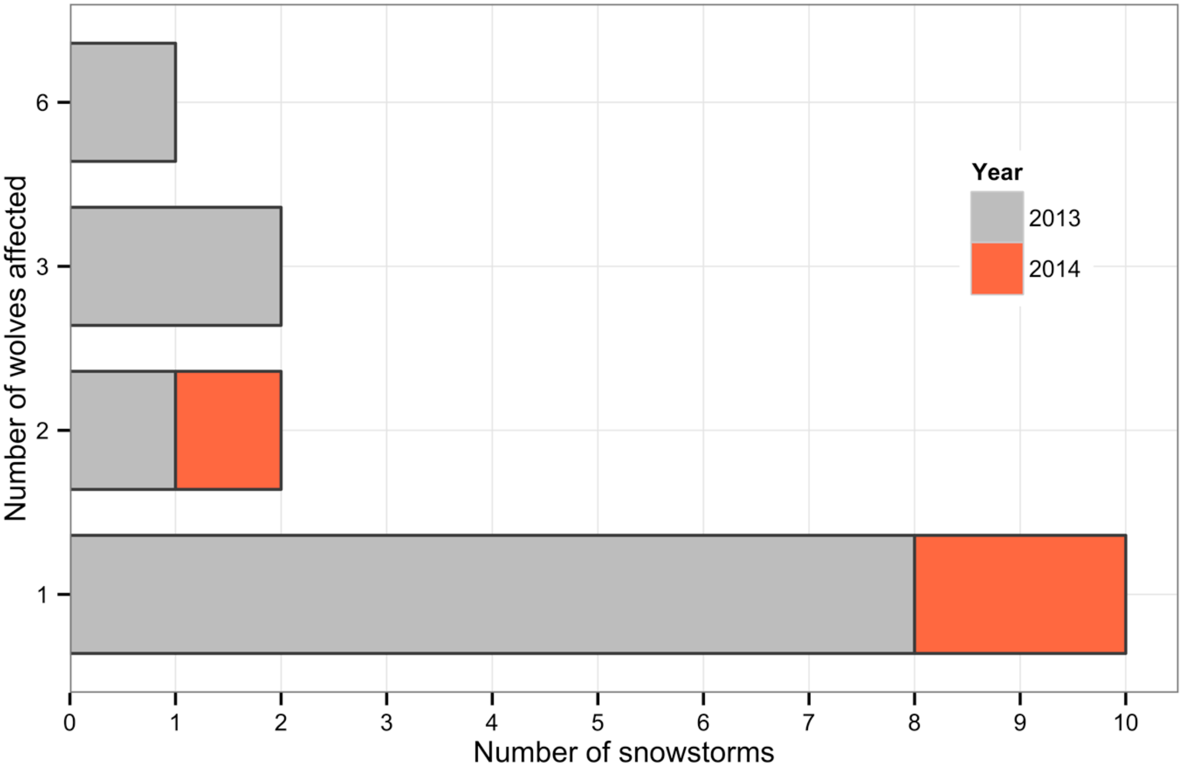

Year
2013
2014
Number of wolves affected
6
3
2
1
0
1
2
3
4
5
6
7
8
9
10
Number of snowstorms

Figure 7

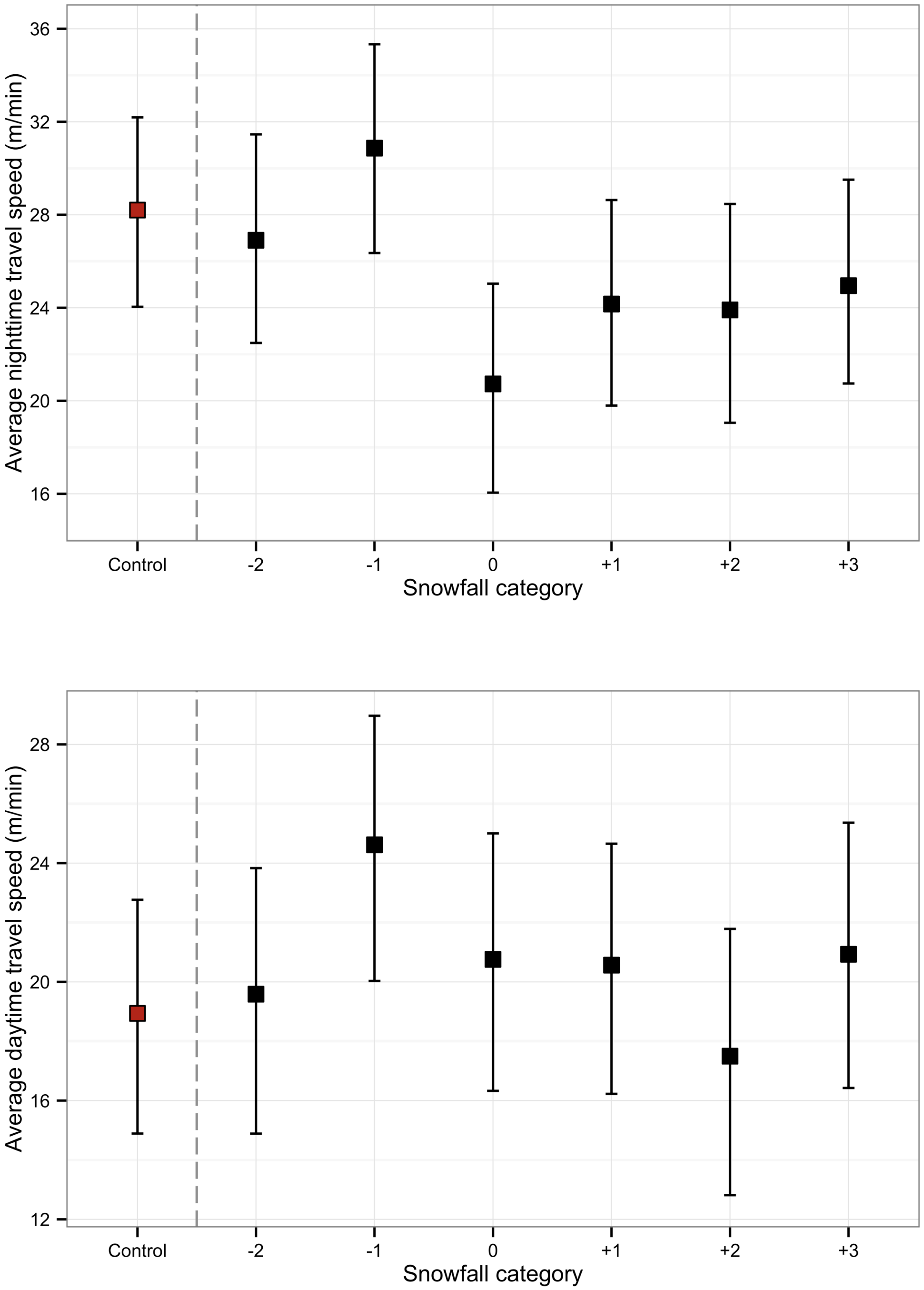
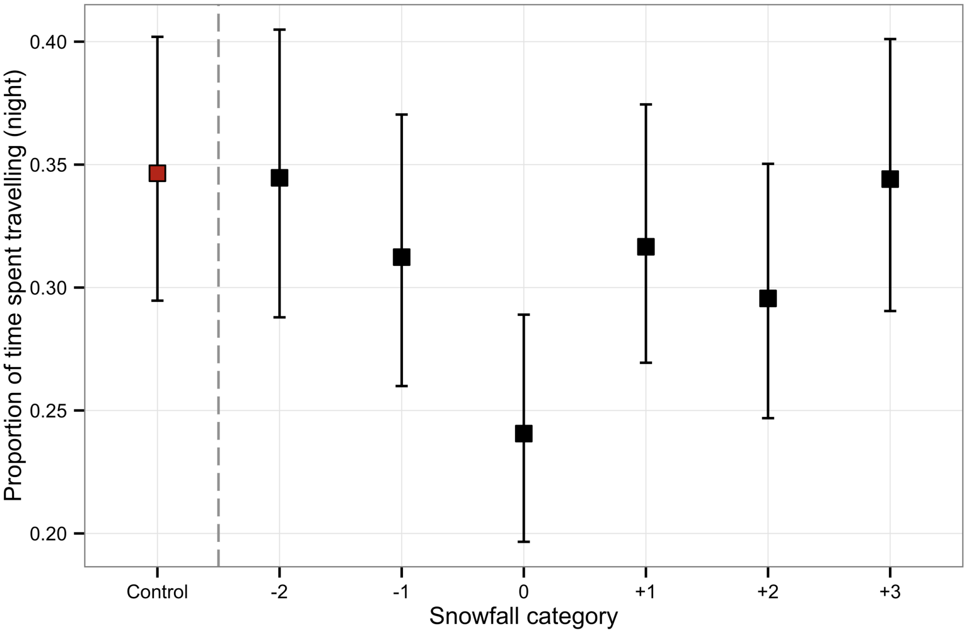

Average nighttime travel speed (m/min)
36
32
28
24
20
16
Control
-2
-1
0
+1
+2
+3
Snowfall category
Average daytime travel speed (m/min)
28
24
20
16
12
Control
-2
-1
0
+1
+2
+3
Snowfall category

Figure 8


Proportion of time spent travelling (night)
0.40
0.35
0.30
0.25
0.20
Control
-2
-1
0
+1
+2
+3
Snowfall category

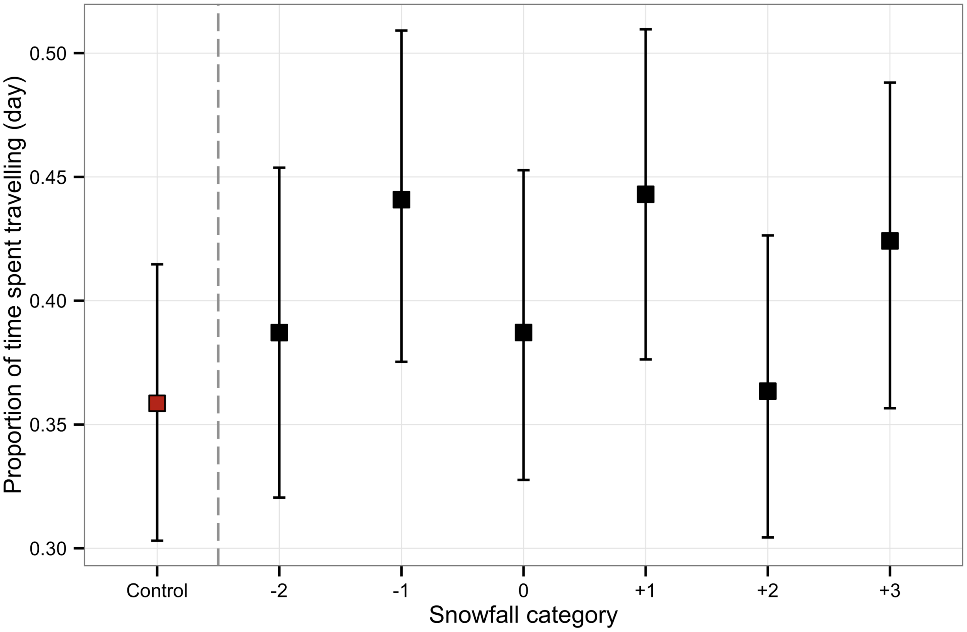
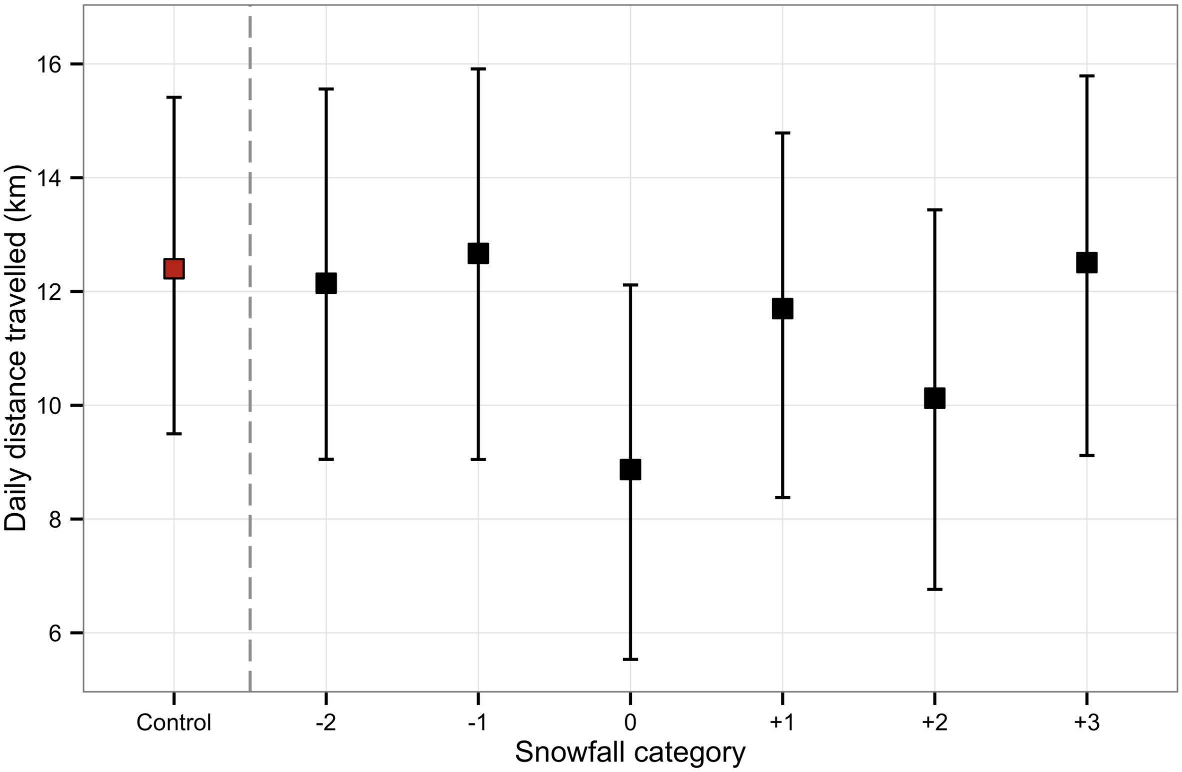

Proportion of time spent travelling (day)
0.50
0.45
0.40
0.35
0.30
Control
-2
-1
0
+1
+2
+3
Snowfall category

Figure 9



Daily distance travelled (km)
16
14
12
10
8
6
Control
-2
-1
0
+1
+2
+3
Snowfall category

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