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Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features

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Although travel in deep snow imposes high energetic costs, animals can mitigate these costs through behavioural adaptations. For example, they can select habitats with shallower or more supportive snow. It is less well-known however, if animals select for favourable snow conditions at the scale of the step, i.e. along the travel paths themselves. We snow-tracked grey wolves (*Canis lupus* L., 1758) over 187 km, and used a paired design to compare snow conditions on travel paths to snow 1 m and 10 m away. Snow on travel paths was 3.2 cm shallower than measurements 1 m away, except when wolves travelled on linear features recently compacted by humans. In those cases, the average difference in snow depth increased to 17.5 cm. Our analyses suggest that, under natural snow conditions, wolves are limited in the fine-scale differences they can achieve along their travel paths. By creating areas with highly favourable snow conditions, anthropogenic activities drastically change the winter landscape, with potential implications for energetics and predator-prey dynamics.

Key words: Adaptations, boreal, *Canis lupus*, grey wolf, carnivore, least cost, morphology, movement path, seismic lines, snow, winter.

In northern regions, the winter season presents particular challenges for wildlife as food becomes scarcer and as thermoregulation and locomotion become costlier. For mammals restricted to life at the snow surface, the cost of moving through deep snow is especially important (Parker et al. 1984; Crête and Larivière 2003). Indeed, in both ungulates and canids, the cost of locomotion increases exponentially as animals sink deeper into the snow (Parker et al. 1984; Crête and Larivière 2003). Adaptations are therefore crucial if animals are to mitigate the costs associated with living in snowy environments (Pruitt 1978; Telfer and Kelsall 1984). Two morphological adaptations are thought to be especially relevant: foot-load and leg length, because both these traits help determine how deep an animal will sink in the snow (Telfer and Kelsall 1984; Murray and Larivière 2002). In addition to morphological adaptations, animals can modify their behaviour, for example by reducing travel speed, by changing their gait, or by choosing favourable habitats or travel paths (Moen 1976; Murray and Boutin 1991; Dowd et al. 2014).

Selection for favourable snow conditions can be expressed at various spatial scales. For examples, ungulates in alpine areas select windswept slopes or move to valley bottoms where snow is shallower and forage is more accessible (Shannon et al. 1975; Whittington et al. 2005). Coyotes (*Canis latrans* Say, 1823) and red fox (*Vulpes vulpes* L., 1758) have also been associated with shallow or compact snow areas (Gese et al. 2013; Pozzanghera et al. 2016). Even within their home range or territory, animals may reduce energetic costs by choosing snow conditions at the scale of the step, i.e. along a specific travel path. Coyote travel paths are found in shallower, more compact snow than areas a few meters away (Murray and Boutin 1991; Crête and Larivière 2003; Kolbe et al. 2007). Similarly, the paths of the Canada lynx (*Lynx canadensis* Kerr, 1792) occur in snow that is more supportive than conditions a few meters away (Murray

and Boutin 1991), even though Canada lynx are more commonly associated in fluffy snow habitats at the territory scale (Pozzanghera et al. 2016). Selection at the path level has not often been considered, but provides valuable insight into animals' habitat choices and movement behaviours, and is also highly relevant when considering the effects of human-created linear features. Grey wolves (*Canis lupus* L., 1758) cover greater distances and achieve faster speeds when travelling on linear features such as roads and seismic lines (Dickie et al. 2016). Trails that have been compacted from human use may also enable animals to travel long distances and access new areas while minimizing energetic costs (James and Stuart-Smith 2000; Crête and Larivière 2003).

We investigated travel path selection in grey wolves (hereafter wolves) by comparing snow conditions along their travel paths to local, off-path snow conditions. Wolves are cursorial predators that rely heavily on long-distance movements to find prey (Mech 1970). Compared to other northern species, grey wolves have a relatively high foot-load (Telfer and Kelsall 1984; Murray and Larivière 2002). However, their long legs and behavioural plasticity make them well-adapted to winter environments (Mech 1970; Telfer and Kelsall 1984). Indeed, wolves have been shown to experience higher ungulate kill rates in deep snow years (Nelson and Mech 1986; Fuller 1991), and in deep snow areas (Huggard 1993). Still, the cost of locomotion in deep snow is likely significant given their wide-ranging movements and the exponential relationship between energy expenditure and snow depth (Crête and Larivière 2003). Fine-scale movement choices that exploit heterogeneity in snow conditions may mitigate some of these costs (Crête and Larivière 2003). Our objectives were to determine if wolves reduced costs by selecting favourable snow conditions at the scale of individual steps. To do so, we snow tracked grey wolves over 187 km for two consecutive winters in a highly industrialized, boreal forest

ecosystem in northeastern Alberta, Canada. We collected data on snow depth and snow hardness along wolf travel paths, and repeated these measurements 1 m and 10 m away from the paths. We also examined the magnitude of advantages gained when travelling on human-created linear features with and without recent human activity.

MATERIALS AND METHODS

Study area. — Our study took place over two consecutive winters from January to March 2013 and 2014. Our study area encompassed 8759 km² of central mixedwood boreal forest in northeastern Alberta, Canada (56.4°N, 111.1°W) (Fig. 1). Winters are long and cold, with average January temperatures of -17°C and a yearly snowfall of 134 cm (based on climate averages from 1981 to 2010; Environment Canada 2015). Human-created linear features are widespread, achieving an average density of 1.63 km/km² (Fig. 1). The most common are conventional seismic lines, which are 5 to 8 m wide and cleared of vegetation. In our study area, conventional seismic lines represent almost 60% of the total kilometres of human linear features, and 83% of all seismic lines (the remaining being low-impact seismic lines).

Capture and radio-collaring wolves. — From 2011 to 2013, we captured and radio-collared 40 wolves from ten different packs, as well as one lone wolf (“City”; Fig. 1). Captures were conducted by experienced crew and followed the Canadian Council on Animal Care protocols. Protocols were approved by the University of Alberta and by the Government of Alberta Wildlife Animal Care Committee (Class Protocol #009). Wolves were equipped with Iridium GPS collars weighing ~750 grams (Lotek Wireless Inc., Newmarket, Ontario, Canada). Collars were initially programmed to collect one location every three hours. For some, this frequency was increased to 30 minutes in winter 2013 ($N = 9$), and to 10 minutes in winter 2014 ($N = 8$).

Isolating wolf travel paths from telemetry data. — We identified travel paths using data from radio-collars with locations taken every 30 minutes or less. We defined travel paths as GPS segments that had at least three consecutive evenly-spaced GPS points (indicating directional movement), and ignored GPS clusters. We only considered GPS locations that were less than twelve hours old to obtain snow conditions that closely reflected what wolves had experienced at the time of travel. Once these criteria had been applied, we were usually left with 2 to 4 candidate paths, which is the maximum we could sample in one day. We opportunistically sampled wolves, but tried to sample packs evenly by sampling at least one path per pack per week. Some packs were sampled less than others because their territories were difficult to access.

Once we had selected a path for sampling, we drove or snowmobiled to the middle GPS point that made up the travel path, located the wolf tracks and followed the tracks for 500 m in either direction, for a total path length of 1 km (Fig. 2). We used a paired design to compare wolf paths (“on-path”) to off-path conditions. At every 100 m along paths, we recorded information on snow conditions, habitat and substrate.

Measuring snow conditions. — Snow measurements were taken on the wolf path, and perpendicular to the path at distances 1 m and 10 m away (Fig. 2). We took three different snow measurements: 1) snow depth, 2) estimated sinking depth, and 3) wolf sinking depth. We measured snow depth by pressing a meter stick through the snowpack until it hit the ground or could not be pushed any further. We estimated sinking depth by dropping a weighted metal can into the snow from a height of 1 m. The can had a weight/surface area of 107 g/cm^2 , and was intended to mimic the foot pressure of an adult male wolf, which ranges from 89 to 114 g/cm^2 (Formozov 1946; Nasimovich 1955). If the can sank fully into the snow, we measured sinking

depth by measuring from the top of the snow layer to the top of the can, and added 6.0 cm to account for the length of the can. Wolf sinking depth was a direct measure of how deep the wolf sank in the snow, and was obtained by measuring the depth at which the wolf's paw print sunk in the snow, from the surface of the snow to the base of the print. Wolf sinking depth was used to correct estimated sinking depth values by applying a linear transformation¹ (Haefner 2005). We used these transformed values when reporting summary statistics. Post-hoc analyses indicated that sinking depths less than 6.0 cm (the height of the can) poorly represented wolf sinking depth, and were excluded from analyses.

Environmental variables. — Habitat was categorized in the field using the Alberta Vegetation Inventory classification scheme (Government of Alberta 2005). We later reclassified habitat with respect to canopy cover by categorizing habitats as either open or closed cover type². Substrate was similarly classified by technicians in the field. Substrate was categorized as: natural (no evidence of human disturbance or animal activity), game trail (evidence of animal tracks), frozen river, compacted linear feature (anthropogenic substrate with evidence of disturbance to the snow through clearing or packing by human traffic), and uncompacted linear feature (anthropogenic substrate with no evidence of human disturbance to the snow).

Statistical analyses. — The objective of our statistical analyses was to investigate whether there was a difference between on-path and off-path snow conditions, and to determine which environmental variables contributed to the greatest difference. We ran separate, linear mixed effects models for snow depth and estimated sinking depth using the *nlme* package in R (Pinheiro et al. 2015; R Core Team 2015). We used our entire dataset to build a snow depth

¹ Fig. S1

² Table S2

model. Because snow depth and estimated sinking depth were strongly and positively correlated ($r_s = 0.72$), we used our sinking depth data to analyze whether wolves perceived and responded to misleading or conflicting information between snow depth and sinking depth conditions i.e. if snow was deep, but very supportive. If wolves only discern between differences in snow depth, but not sinking depth, we would expect to find no selection for sinking depth under these conditions. However, if wolves can perceive sinking depth in addition to absolute depth, we would expect path-level selection favouring low sinking depth values to minimize the energetic costs of travel. To identify instances of “mismatched” snow conditions, we calculated the difference between on-path snow depth and wolf sinking depth. We restricted our dataset to measurements for which the difference between the two on-path snow conditions was ≥ 20 cm based on the frequency distribution of our data³ and sample size considerations. Because of these criteria, and because snow conditions changed from one sampling point to the next, not every measurement taken along a 1 km path was included in this analysis.

For both models, our response variable was the difference in snow condition (snow depth or estimated sinking depth) between off-path and on-path measurements, with positive differences indicating that depth was greater off-path than on-path. In following with our paired sampling design, each on-path measurement was associated with its two, corresponding off-path measurements 1 m and 10 m away, and we calculated the difference between each on-path/off-path pair. We followed an AIC model selection framework (Burnham and Anderson 2002) and began with a global model that included the following covariates: substrate, cover type, month and year of sampling, distance from wolf path (i.e. the spatial scale of comparison; either 1 m or 10 m), and off-path depth (Table 1). We included interactions between substrate and off-path

³ Fig. S3

depth, and between cover type and off-path depth to investigate the effect of environmental variables with changing availability in snow conditions. Both models included a random effect for wolf pack. We limited our analyses to one transect per pack per day to minimize within-pack correlation (e.g., if two individuals from the same pack were sampled on the same day). For our snow depth model, each 1 km travel path (comprised of 11 on-path measurements) was given a unique transect ID, which we included as a random effect (Table 1). Transect ID was not used as a random effect in our sinking depth model because we did not use all the measurements along a 1 km sampling path. We standardized all continuous variables, including the response variable (Schielzeth 2010). For both our snow depth and sinking depth analyses, we generated candidate model sets that included all possible permutations of our global models using the MuMIn package (Bartoń 2016). Each set contained 104 models. Models with a $\Delta AIC < 4$ were averaged to obtain final coefficients (Burnham and Anderson 2002). We validated these top models by plotting the residuals of our global models and verifying that the assumptions of normality, homoscedasticity, and independence were met (following Zuur et al. 2009).

RESULTS

On-path conditions. — Average on-path snow depth was $27.0 \text{ cm} \pm 20.2 \text{ (SD)}$, with a maximum recorded depth of 92.0 cm. Average wolf sinking depth was $14.0 \pm 12.2 \text{ cm}$, with a maximum of 51.8 cm. Substrate type had a significant effect on wolf sinking depth ($F_{4,1146} = 123.67$, $P < 0.001$): average wolf sinking depth was lowest on compacted human linear features ($5.2 \pm 6.3 \text{ cm}$), followed by uncompacted linear features ($15.6 \pm 12.0 \text{ cm}$), frozen rivers ($15.8 \pm 9.4 \text{ cm}$), game trails ($19.3 \pm 9.1 \text{ cm}$), and uncompacted natural substrates ($24.0 \pm 10.2 \text{ cm}$). In our dataset, human use was largely the result of snowmobile activity (84.2%); the rest was the result of

ploughing or automobiles. Snowmobiling was especially prevalent on seismic lines, with 63% of paths on seismic lines showing signs of snowmobile use.

Comparing on-path to off-path snow conditions. — Of the three sampling distances we considered, snow depths and estimated sinking depths were lowest on wolf paths, and highest 10 m away (Table 2). Differences in snow depth between off-path and on-path measurements ranged from -37.0 to +78.5 cm (at the 1 m scale). Differences were heavily influenced by substrate type. For paths on compacted human linear features, the difference in snow depth at the 1 m scale was 18.3 ± 20.0 cm. In contrast, the difference on uncompacted natural substrates was 2.8 ± 8.3 cm. Trends for sinking depth were similar. Sinking depth for paths on compacted human linear features was 4.5 ± 6.0 cm less than sinking depth 1 m away. The difference in sinking depth for paths on uncompacted natural substrates was 1.1 ± 4.6 cm.

Snow depth analysis. — Our snow depth analysis included 2432 on-path/off-path pairs along 115 sampled paths. We excluded river and game trail substrates because they were rarely sampled and only occurred in one habitat type (Table 2). Cover type, distance from path, and an interaction between substrate type and off-path snow depth were included in all top-ranking models ($\Delta AIC < 4$; Table S4). Difference in snow depth between off-path and on-path measurements was most pronounced when paths were in closed cover, and when wolves travelled on compacted human linear features (Table 3). However, when off-path snow depth was low, the difference in depth used by wolves was similar across all substrate types (Fig. 3). As off-path depth increased, the difference in depth between the wolf path and off-path became highly dependent on substrate type (Fig. 3).

Sinking depth analysis. — Our sinking depth analysis was performed on 454 on-path/off-path pairs (~18% of our original dataset), and successfully reduced the correlation between on-

path snow depth and estimated sinking depth ($r=0.30$). All top models ($\Delta AIC < 4$) included month, substrate, and an interaction between substrate and off-path depth as important explanatory variables (Table S5). Cover type was also important in all but one of the top models. Wolf paths sampled in February were relatively more supportive (compared to off-path conditions) than paths sampled earlier in the season. Wolves achieved the greatest difference in sinking depth when traveling on compacted human linear features; however, in this model, uncompacted linear features did not offer a significant advantage when compared to natural substrates (Table 4). In this analysis, the magnitude of difference between on-path and off-path measurements did not depend upon distance from the wolf path (Table 4).

DISCUSSION

This study sought to answer whether grey wolves expressed path-level selection for shallow, compact snow conditions. We also wanted to understand how snow conditions changed across different habitats and substrates, and consequently affect the snow conditions experienced by wolves. In our study, wolves consistently travelled in areas with less snow depth and less sinking depth when compared to snow measurements 1 and 10 metres away, but the difference they achieved depended on the habitat and substrate they were travelling on. Under natural conditions, wolves appear to be highly limited by their environment. When wolves travelled on natural substrates, average snow depth was only 3.2 cm shallower than depth 1 m away; in contrast, wolf paths on linear features were 17.5 cm shallower (in open cover habitat; Table 2). Trends for sinking depth were similar, but the magnitude of difference was much smaller (Table 2). With respect to habitat type, absolute differences were greater in open habitats than in closed ones, but snow was also deeper and less compact in open habitats (Table 2). Instead, our models suggest that wolves achieved higher relative differences in snow depth and sinking depth when

travelling in closed canopy (Table 3; Table 4). Closed cover habitat may offer more heterogeneous snow conditions than open habitats, as the presence of a forest canopy causes small-scale differences in snow depth and snowmelt (Storck et al. 2002).

Our sinking depth analysis underscored the importance of temporal factors in influencing snow cover characteristics. All top models included month of sampling as an explanatory variable (Table S5). Compared to off-path areas, travel paths sampled in February had the most supportive snow (Table 4). Because our natural substrate category only included paths that had not been used by animals or humans, path revisitation does not serve as an explanation for the temporal differences we found. If wolves improved in their ability to discern favourable snow areas over time, differences in sinking depth should have been even greater in March, but this was not observed (Table 4). Travel paths may have been most supportive in February because of a lack of fresh snow. Settled snow may provide more opportunities for wolves to exploit natural heterogeneity in snow conditions, as wind, sun, and forest cover continue to influence differences in snow cover at various spatial scales (Pruitt 2005). Our data does indicate that snowfall events were rare in February, compared to January and March, and that snow was more compact during that period (Droghini 2016). Although sinking depth is a more biologically relevant metric than snow depth (Parker et al. 1984), the method we used underestimated true sinking depth and performed poorly at low sinking depths values. Dropping a weighted object from a height into the snow is a commonly used method to measure sinking depth of canids (e.g. Murray and Boutin 1991; Crête and Larivière 2003; Kolbe et al. 2007). While this method may be appropriate for relative difference studies such as ours, data on animals' sinking depth should still be collected to see whether the use of an estimated sinking depth metric is appropriate.

Are wolves severely impeded by natural snow conditions? In ungulates, movement costs are predicted to double when sinking depth reaches ~50% chest (brisket) height (Fancy and White 1987). This physiological threshold may be similar in canids, as the energetic costs of both group increase exponentially with snow conditions (Parker et al. 1984; Crête and Larivière 2003). In wolves, then, we would expect energetic costs to double at sinking depths ≥ 25 cm (based on the chest height of adult males; Telfer and Kelsall 1984). In our study, wolves sank to these depths 24% of the time, with most (72%) of these instances occurring on natural substrates. Even though wolves were often travelling in areas below this estimated threshold, they still exhibited a strong preference for shallow, supportive snow. It is unknown whether small energetic savings, such as those acquired when sinking depth is below an individual's threshold, are important when summed over the entire winter.

Snow conditions in our study area were representative of boreal forest snow conditions (Sturm et al. 1995; Dawe and Boutin 2012), with moderate average monthly snow depths that from 30 to 50 cm (Droghini 2016). The boreal forest ecosystem currently experiences a unique combination of small, frequent snowfalls, cold temperatures, and low wind speeds that results in soft fluffy snow with little crusting (Sturm et al. 1995). However, climate change is expected to affected these characteristic snow conditions. Boreal forests in North America are already experiencing warming winter temperatures and shorter periods of snow cover, as well as a higher percentage of precipitation that is falling as rain rather than snow (Vincent et al. 2012; Price et al. 2013). Wet, heavy snow or freezing and crusting may therefore become more common (Price et al. 2013), with potential negative consequences on animals' energetic balances. In ungulates, locomotion in wet, high-density snow is costlier than in low-density snow, and energy expenditure increases drastically if crusting is not strong enough to fully support an animal's

weight (Parker et al. 1984). Predator-prey interactions may also shift in favour of either the hunter or the hunted, as animals are differentially affected by changes in snow conditions (Telfer and Kelsall 1984).

Influence of human linear features on snow conditions. — In our study area, compacted linear features – most of which were seismic lines used by snowmobilers – radically transformed natural snow conditions. Snow conditions on linear features can be highly advantageous for predators because they decrease energetic costs and allow for faster travel, and facilitate access into deep snow areas (Crête and Larivière 2003; Bunnell et al. 2006). Our results suggest that these features are increasingly advantageous in deep snow conditions because they remain relatively snow-free, both when compared to the local environment and to other substrate types (Fig. 3). These results may explain why canids' use of linear features increases with increasing snow depth (Crête and Larivière 2003; Gese et al. 2013). The relationship between linear features and deep snow has potential consequences for predator-prey interactions. Ungulates are vulnerable to predation by wolves in deep snow, even in natural habitats (Nelson and Mech 1986; Fuller 1991; Huggard 1993). The benefits conferred by linear features may further increase prey's vulnerability, and there is some evidence to support this idea (James and Stuart-Smith 2000; Paquet et al. 2010). Industrial development in boreal forests is of particular concern for caribou conservation efforts. development. Some boreal landscapes have been dramatically transformed by industrial development (Lee and Boutin 2006), leading to a vast network of linear features across wide tracts of land that may function as travel corridors for wolves and increase search rates and kill rates (James and Stuart-Smith 2000; Paquet et al. 2010; Latham et al. 2011). While several other factors might influence winter use of linear features (e.g. lack of obstacles, further line-of-sight; Latham et al. 2011), we found clear differences in snow depth

even compared to areas only 1 m away. As most linear features in our study were between 5 to 8 m wide, our findings suggest that snow conditions play an important role in wolves' travel path choices and that wolves choose the most favourable snow conditions even within the same substrate and habitat.

The importance of behavioural adaptations in generalist species. — The fine-scale use of favourable snow conditions is likely a winter coping strategy employed by many year-round residents that live on the surface of the snow, and one that complements a suite of other behavioural and morphological adaptations (Telfer and Kelsall 1984; Murray and Larivière 2002). Pruitt (1978) suggested that behavioral adaptations may be more pronounced in species that lack specific morphological adaptations to winter climate. There is some support for this idea. At the territory scale, Pozzanghera et al. (2016) found that coyotes, which had the highest foot-load, preferred areas of shallow, compact snow, while martens, the species with the lightest foot-load, preferred deep, fluffy snow. At the scale of the travel path, Whiteman and Buskirk (2003) found that species with high footloads used compacted trails more often than species that were light on their feet. Lastly, Murray and Larivière (2002) found that snow conditions do not exert strong selection pressures on morphology; thus, we expect northern populations of generalist species to employ other strategies to reduce the high costs of locomotion in snow. Of the three species that have been studied at the path level (Canada lynx, coyotes, and grey wolves), selection (as measured by the difference in snow conditions) was most pronounced in grey wolves (this study), and least pronounced in Canada lynx (Murray and Boutin 1991). This ranking is the one we would expect given these species' morphological characteristics. However, comparing snow selection behaviours under natural conditions is difficult because differences in habitat selection, hunting behaviours, and biological requirements introduce confounding

variables (Murray and Boutin 1991; Pozzanghera et al. 2016). Field experiments under standardized snow conditions would allow us to control for these factors and further explore the plasticity of snow selection behaviours both within and across species. Quantifying this behaviour for both predator and prey while measuring energy expenditure would provide valuable insight into different energetic strategies and predator-prey interactions. These data are becoming particularly important in understanding the impacts of human disturbance and predicted changes in snow conditions.

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TABLES

Table 1. — Variables used in our models to explain the difference in snow depth or sinking depth between off-path measurements and the travel paths of grey wolves (*Canis lupus* L., 1758). Variables were collected in the field from January to March 2013 and 2014 by snow tracking grey wolves. Continuous variables were standardized prior to analysis.

Variable	Definition
DIST	Distance from wolf travel path Categorical variable with two levels: 1 m or 10 m
DEPTH	Off-path depth
MONTH	Month of sampling Categorical variable with three levels: January, February, March
YEAR	Year of sampling Categorical variable with two levels: 2013, 2014
SUBST	On-path substrate type Categorical variable with three levels: Uncompacted natural, compacted human linear feature, uncompacted human linear feature
COVER	On-path cover type Categorical variable with two levels: Open, closed
PACK	Name of wolf pack
ID	Transect ID (<i>snow depth analysis only</i>) Random intercept with 115 unique IDs. Every 1 km wolf path, comprised of 11 on-path measurements and its off-path pairs, was given a unique transect ID

Table 2. — Averages and standard deviations for snow depth, sinking depth of grey wolf (*Canis lupus* L., 1758) tracks, and estimated sinking depth across two habitats (open and closed cover) and a range of substrates. Absolute values for on-path measurements are shown, and measurements 1 m and 10 m away are expressed relative to on-path measurements. Positive differences indicate that off-path measurements were greater than on-path. Measurements on rivers and game trails are presented here, but were excluded from analyses. *N* is the number of on-path measurements. Each on-path measurement has associated measurements 1 m and 10 m away.

Substrate types: *NAT* = uncompacted natural, *GTR* = game trail, *RIV* = river, *CLF* = compacted human linear feature, *ULF* = uncompacted human linear feature.

<i>Open</i>	<i>Snow depth</i>	<i>1 m diff.</i>	<i>10 m diff.</i>	<i>Wolf sink. depth</i>	<i>Est. sink. depth¹</i>	<i>1 m diff.</i>	<i>10 m diff.</i>	<i>N</i>
<i>NAT</i>	48.2 (15.3)	+3.2 (10.3)	+3.4 (11.8)	24.3 (10.7)	21.1 (9.1)	+2.1 (4.3)	+2.3 (4.6)	122
<i>CLF</i>	13.6 (13.1)	+17.5 (19.7)	+34.5 (21.5)	4.5 (5.3)	6.8 (5.9)	+4.2 (5.9)	+6.9 (6.5)	384
<i>ULF</i>	28.7 (23.7)	+13.7 (17.7)	+27.4 (24.6)	15.6 (12.5)	15.3 (8.9)	+2.3 (5.3)	+4.1 (7.5)	104
<i>RIV</i>	30.0 (10.2)	+6.8 (11.2)	+15.7 (12.9)	15.8 (9.4)	21.6 (9.9)	+1.4 (4.9)	+2.6 (6.5)	22
<i>Closed</i>								
<i>NAT</i>	40.3 (12.8)	+2.6 (7.2)	+5.1 (10.5)	23.8 (10.0)	19.9 (8.9)	+0.7 (4.6)	+1.9 (4.9)	331
<i>CLF</i>	13.0 (14.5)	+20.6 (20.9)	+34.8 (16.8)	6.9 (7.8)	9.8 (8.2)	+5.2 (6.2)	+9.1 (7.1)	181
<i>ULF</i>	26.3 (17.4)	+10.1 (17.3)	+18.5 (22.9)	15.7 (11.5)	17.1 (10.2)	+3.2 (6.3)	+5.0 (7.1)	94
<i>GTR</i>	36.8 (12.0)	+5.7 (10.1)	+7.1 (10.7)	19.9 (8.7)	20.6 (8.3)	+1.5 (4.3)	+2.9 (6.7)	26

¹ Although we performed our analyses using a subset of sinking depth measurements, the values shown here are meant to be representative of the overall snow conditions encountered, and were therefore calculated using the full dataset. To better approximate wolf sinking depth, a linear transformation was applied to estimated sinking depth values (see Materials & Methods for more details).

Table 3. — Model estimates (β), standard errors (SE), z values, and p values (P) for our snow depth model, which analysed the difference in snow depth between travel paths of grey wolves (*Canis lupus* L., 1758) and off-path measurements 1 m and 10 m away. Values were obtained by averaging top-ranking models ($\Delta\text{AIC} < 4$).

Variable	β	SE	z value	P
Off-path Depth	0.449	0.029	15.564	<0.001
<i>Distance from path, reference = 10 m</i>				
1 m away	-0.084	0.018	4.617	<0.001
<i>Substrate type, reference = natural uncompacted</i>				
Human Compacted	1.067	0.037	28.711	<0.001
Human Uncompacted	0.462	0.038	12.073	<0.001
Human Compacted $\times$ Depth	0.356	0.031	11.499	<0.001
Human Uncompacted $\times$ Depth	0.219	0.035	6.335	<0.001
<i>Month, reference = January</i>				
February	-0.002	0.021	0.092	0.927
March	0.000	0.018	0.022	0.982
<i>Year, reference = Year 2013</i>				
Year 2014	-0.001	0.029	0.048	0.962
<i>Cover, reference = Open</i>				
Closed Cover	0.129	0.028	4.610	<0.001
Cover $\times$ Depth	0.000	0.003	0.024	0.981

Table 4. — Model estimates (β), standard errors (SE), z values, and p values (P) for our sinking depth model, which analysed the difference in sinking depth between travel paths of grey wolves (*Canis lupus* L., 1758) and off-path measurements 1 m and 10 m away. Values were obtained by averaging top-ranking models ($\Delta\text{AIC} < 4$).

Variable	β	SE	z value	P
Off-path Depth	0.678	0.054	12.616	<0.001
<i>Distance from path, reference = 10 m</i>				
1 m away	0	0.014	0.01	0.992
<i>Substrate type, reference = natural uncompacted</i>				
Human Compacted	0.315	0.123	2.553	0.011
Human Uncompacted	-0.025	0.106	0.238	0.812
Human Compacted $\times$ Depth	0.360	0.107	3.357	0.001
Human Uncompacted $\times$ Depth	0.094	0.116	0.811	0.418
<i>Month, reference = January</i>				
February	0.706	0.088	8.03	<0.001
March	-0.143	0.071	2.012	0.044
<i>Year, reference = Year 2013</i>				
Year 2014	0.083	0.117	0.715	0.475
<i>Cover, reference = Open</i>				
Closed Cover	0.136	0.105	1.293	0.196
Cover $\times$ Depth	-0.002	0.023	0.097	0.923

FIGURE LEGENDS

Fig. 1. — Map of our study area near the town of Fort McMurray in northeastern Alberta, Canada. From 2011 to 2013, we radio-collared 41 grey wolves (*Canis lupus* L., 1758) from ten packs, and one lone individual (“City”). The packs’ winter territories are represented using 95% kernel density estimates. We used telemetry data from collars with fix rates of ≤ 30 minutes to isolate wolf travel paths for snow tracking. We snow tracked 187 km of wolf paths from January to March 2013 and 2014; the centre of each path is shown here.

Fig. 2. — Study design used to compare snow conditions on travel paths of grey wolves (*Canis lupus* L., 1758) to the local environment. Each path was tracked for one km. At every 100 m along the path, we collected information on snow conditions, habitat, and substrate. Similar data were collected 1 m and 10 m perpendicularly away from path measurements. Off-path measurements alternated between the right and left side of the wolf path.

Fig. 3. — Interaction between off-path snow depth (1 m away) and substrate type on grey wolf (*Canis lupus* L., 1758) travel paths. Predictions are based on population-level averaged coefficients with open cover type and January 2013 as references. We considered three substrate types: compacted human linear features, uncompacted human linear features, and uncompacted natural substrates. Data points for these substrates are represented by solid black circles, dark grey crosses, and hollow light grey circles, respectively. 95% confidence intervals are shown for each predicted slope.

Fig. 1 Map of our study area near the town of Fort McMurray in northeastern Alberta, Canada. From 2011 to 2013, we radio-collared 41 grey wolves (*Canis lupus* L., 1758) from ten packs, and one lone individual ("City"). The packs' winter territories are represented using 95% kernel density estimates. We used telemetry data from collars with fix rates of ≤ 30 minutes to isolate wolf travel paths for snow tracking. We snow tracked 187 km of wolf paths from January to March 2013 and 2014; the centre of each path is shown here.

54x76mm (300 x 300 DPI)