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Original article

Footload influences wildlife use of compacted trails in the snow

John P. Whiteman & Steven W. Buskirk

Animals moving across snow surfaces sink to varying depths, increasing the energetic cost of travel. For ease of movement, animals may follow compacted trails created by sports such as snowmobiling and snowshoeing. We tested the assumption that animals less-adapted to snow travel (i.e. animals with a high footload (body mass/foot surface area)) are more likely to use compacted trails and follow them for greater distances than animals well-adapted to moving on snow. We sampled animal movements on compacted and non-compacted transects in northwestern Wyoming and southeastern Idaho, USA, during two winters. Consistent with our prediction, footload positively influenced the probability of animals following compacted transects, and positively influenced their following distance, although the latter relationship was weaker. Additionally, we found that different snow sports cause similar increases in snow density. We suggest that future researchers experimentally test whether the use of compacted trails by animals with high footloads alters their habitat selection and dispersal, and whether it affects their competitive and predatory success.

Key words: footload, movement, snow, snow compaction, snowmobiling, winter sports

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Animals traveling on top of the snow surface sink into the snow, with greater sink depths incurring greater energetic costs of travel (Parker et al. 1984, Crête & Larivière 2003). The increased cost of travel due to sinking into snow drives morphological and behavioural adaptations (Telfer & Kelsall 1984), influences habitat selection (Halpin & Bissonette 1988), and restricts the dispersal and distribution of some species to areas of shallow snow (Krohn et al. 1997, Carr et al. 2007). This cost increases the vulnerability of some species to predation (Huggard 1993), and likely confers a competitive advantage to species that are well-adapted to moving in snow (Buskirk et al. 2000).

Animals reduce their sink depth and therefore also their cost of travel by selecting for harder snow surfaces (Murray & Boutin 1991). Such behaviour can include traveling on trails of high-density snow compacted by winter sports such as snowmobiling (Murray & Boutin 1991, Crête & Larivière 2003), which is growing in popularity. In the U.S., participation in snowmobiling increased by 67% from 1982 to 2009 (Cordell et al. 2009). Growth is robust in Europe and Russia as well, where 25% of worldwide sales of new snowmobiles occurred in 2011 (ISMA 2012). There are > 360,000 km of designated snowmobile trails in North America (ISMA 2012) and an unknown length of trails created by dispersed activity (snowmobiling off designated trails).

Discussions of animal use of compacted trails have assumed that animals utilize trails according to their degree of adaptation to travel on the snow surface (Buskirk et al. 2000). However, this assumption has not been verified, and it is possible that animal use of compacted trails varies with other factors. To establish a basis for predicting animal use of compacted trails, we tested the prediction that species with higher footloads (i.e. less adapted to snow) would follow compacted trails more often and for longer distances than species with lower footloads (i.e. more adapted to snow). Additionally, animal use of compacted trails is likely influenced by trail surface hardness and snow density, which may vary among snow sports. For example, animal use of trails compacted by snowmobiling has been considered different from the use of trails compacted by snowshoeing (Crête & Larivière 2003). However, it is not clear whether compaction differs among snow sports. Thus, we compared trails compacted by three common winter sports: snowmobiling, snowshoeing and cross-country skiing.

Material and methods

Study area

Our field work was conducted in northwestern Wyoming and southeastern Idaho (43°N, 110°W) in Grand Teton National Park, John D. Rockefeller Memorial Parkway and Caribou-Targhee National Forest. We performed sampling in areas with slopes of 2-12°, dominated by lodgepole pine *Pinus contorta* and subalpine fir *Abies lasiocarpa*, between 1,900-2,300 m a.s.l. and with mean mid-winter snow depths of 40-160 cm. Animals commonly active on the snow surface include red squirrels *Tamiasciurus hudsonicus*, northern flying squirrels *Glaucomys sabrinus*, ermines *Mustela erminea*, long-tailed weasels *M. frenata*, American martens *Martes americana*, snowshoe hares *Lepus americanus*, red foxes *Vulpes vulpes*, coyotes *Canis latrans*, ruffed grouse *Bonasa umbellus* and dusky grouse *Dendragapus obscurus*.

Animal use of compacted snow: field methods

We recorded animal trails that encountered strip transects (60 cm wide) spaced $\geq$ 3 km apart. We sampled 10 transects during January-March 2007, and eight of the same transects plus five new transects during December 2007-January 2008. On each transect, we first recorded animal trails existing in the area prior to snow compaction; these data reflected animal movement in the absence of a compacted trail. During this first sampling, we compacted the transect itself by snowshoeing. We waited 1-8 nights after the first sampling; then, in a second sampling, we recorded animal trails on the transect again; these data reflected animal movement in the presence of a compacted trail.

During our first sampling, we snowshoed 250-450 m from existing roads or sport trails. We then used a compass to snowshoe a straight transect (500 m or 1,000 m) through an area free from human compaction (Fig. 1A), and we recorded where animal trails encountered the transect using global positioning system receivers (GPS60; Garmin International, Olathe, Kansas, USA). We did not record animal trails on the existing road (or trail), nor on the access trail (see Fig. 1A). We noted whether animals crossed the transect or entered and followed it for $\geq$ 2 m (see Fig. 1B). The distance between where an animal trail

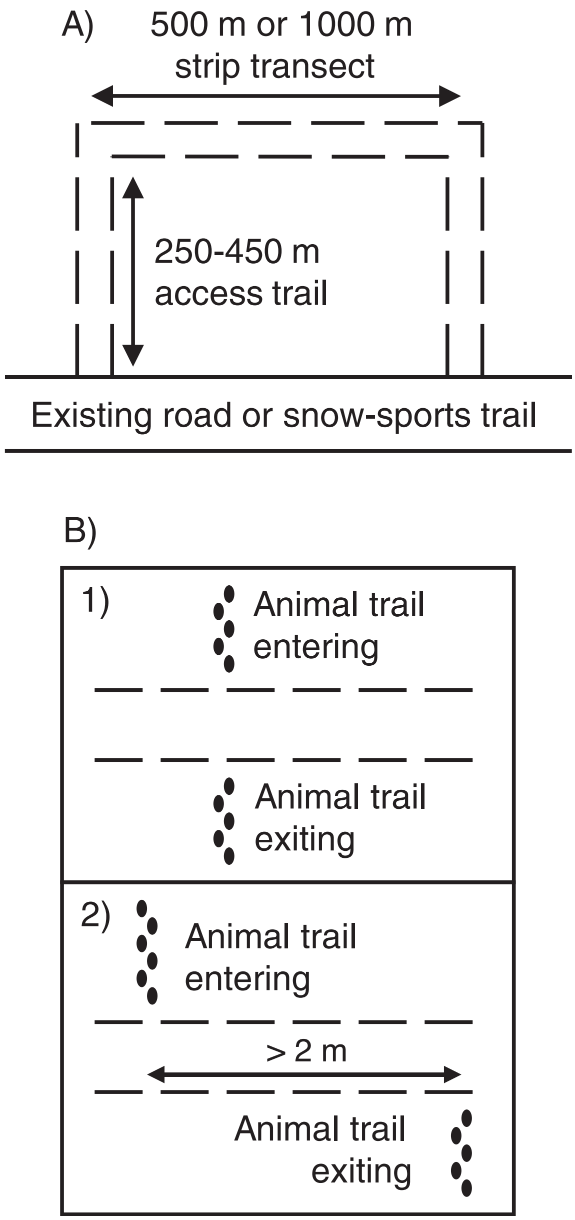

Figure 1. Strip transect for sampling animal tracks in the snow, connected to an existing road or snow-sports trail by access trails (A). The figure is not to scale. Access trails and strip transect were 60 cm wide. Footprints in the snow (B) showing an animal trail (1) crossing a strip transect, and (2) following it.

entered and exited the transect we defined as the 'following distance'. We defined the 'following proportion' as the number of animal trails which entered and followed the transect, divided by the total number of animal trails which encountered the transect (see Fig. 1A). We walked over the transect three times to thoroughly compact the snow and then laid a thin layer of undisturbed snow on both transect ends so animals entering transects by traveling on our access trails would leave visible footprints.

If animal trail entries and exits on a transect could not be clearly associated, we paired them sequentially. We did not distinguish between trails made by red squirrels and flying squirrels, ermine and long-tailed weasels, and ruffed grouse and dusky grouse. We defined coyote trails as those with footprints $\geq$ 7.6 cm long or with straddle measurements of $\geq$ 12.7 cm; otherwise we assumed them to be red fox trails (Fuhrmann 1998).

We waited 1-8 nights after the first sampling, then returned to the transect and recorded animal trails for the second sampling. If $\geq$ 8 cm of snow accumulated on the transects, we compacted the transects again and waited 1-8 nights before performing the second sampling.

During the second sampling, we measured additional variables every 100 m. First, we quantified compaction caused by snowshoeing during the first sampling by measuring snow depth (increments of 5 cm) and sink depth of a penetrometer (150-g cylinder with a basal surface area of 34 cm^2, dropped from 50 cm above the snow) in the middle of the transect and 10 m away on alternating sides. We then calculated differences between on-transect and off-transect measurements, and bootstrapped (1,000 repetitions) mean differences (and 95% CIs). Second, we collected data for predictor variables (used in modeling, as described below) 10 m away from the transect on alternating sides. We measured percent canopy cover (increments of 4%) using a spherical densiometer (Forestry Suppliers, Jackson, Mississippi, USA) and calculated a bootstrapped mean. We measured distance to the nearest live, woody stem with a 1-7 cm diameter (distances > 340 cm were truncated to 340 cm). We calculated stem density as stems/ha = 10,000/(2(bootstrapped mean distance)^2) (Barbour et al. 1999:233).

Animal use of compacted snow: modeling following proportion

We created logistic regression models to predict following proportion. A response variable with a value of 0 indicated that an animal crossed the transect without following, and a value of 1 indicated that an animal entered and followed the transect. Each response could occur multiple times on a transect, so for each species on each transect we weighted responses by the number of occurrences. For example, a transect could have 19 snowshoe hare trails which crossed it and three snowshoe hare trails which entered and followed it. The response of 0, indicating that the hare crossed the transect, would be weighted by 19; and the response of 1, indicating that the hare entered and followed the transect, would be weighted by 3.

A priori, we identified six predictor variables and two interaction terms as potentially influencing factors on following proportion on a transect (Table 1). We limited modeling to species for which published footloads have been measured using similar methods (see Table 1). We then listed biologically plausible combinations of these terms, creating 56 candidate

Table 1. Predictors included in regression models to predict whether animals will turn and follow transects in the snow, and for how long a distance.

Predictor	Description
Canopy	Mean % canopy cover on the transect
Comp	Whether the transect was compacted (0 = no, 1 = yes)
Ftld	Footload = body mass (g)/foot surface area (cm^2; American marten 11[a], red fox 45[b], snowshoe hare 18[c] and coyote 121[c])
Species	Category for each species because species-specific behaviour may not be related to footload
Species/transect	Category for each species on each transect as one animal may create all tracks of that species on a transect
Stems	Estimated number of live, woody stems (with a diameter of 1-7 cm)/ha
Ftld*Comp	Interaction term because footload may only influence animal use of a transect if the transect is compacted
Species*Comp	Interaction term because animal use of a compacted transect may be influenced by species characteristics other than footload

[a] Krohn et al. 2004
[b] Nasimovich 1955
[c] Murray & Boutin 1991

models (Appendix I). The correlation coefficients were < 0.6 for pairs of continuous predictors. Visual inspection of a scatterplot matrix suggested potential collinearity between species and ftld, species and ftld*comp, and ftld and ftld*comp. However, species was not included in the best supported models (see the Results section), and collinearity between an interaction term and its constituents is difficult to resolve (Echambadi & Hess 2007). We evaluated our results for consequences of collinearity (parameter estimate instability and standard error inflation).

We rejected models with $P \leq 0.05$ in the Hosmer-Lemeshow goodness-of-fit test (Hosmer & Lemeshow 1989). We ranked the remaining models using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002:66) and assumed that top models separated by ≤ 2 units had equivalent support (Burnham & Anderson 2002:70, Symonds & Moussalli 2011). We described models with Nagelkerke's R^2 (Nagelkerke 1991) and area under the receiver operating characteristic curve (AUC). AUC values ≤ 0.5 indicate models which provide more incorrect than correct predictions, whereas a value of 1.0 indicates no error in the predictions (Marcot 2012).

Animal use of compacted snow: modeling following distance

We created linear regression models to predict following distance. Each species could enter and follow a transect multiple times. Thus, for each species on each transect, we calculated a bootstrapped mean following distance, then log-transformed that value to meet assumptions of normality of residuals. We used the same predictors and candidate models as the logistic regression models of following proportion (see Table 1 and Appendix I). We rejected models with $P \leq 0.05$ in the Shapiro-Wilk test of normality of residuals and ranked remaining models using AIC_c (Burnham & Anderson 2002:66, Symonds & Moussalli 2011). We identified outlying data by large studentized residuals and described models using adjusted R^2 (Kutner et al. 2004:226).

Compaction by different sports: field methods

Separate from investigating animal use of compacted trails, we examined whether compaction differed among three snow sports. We made four passes of each sport: a person on a Ski-Doo Summit snowmobile (Bombardier Recreational Products, Quebec, Canada; 300 kg on a surface area of 7,025 cm^2), a person on Tubbs Altitude snowshoes (K2 Sports, Carlsbad, California, USA; 80 kg on a surface area of 1,375 cm^2) and a person on Alpina Cross-Terrain skis (Alpina Sports, Lebanon, New Hampshire, USA; 80 kg on a surface area of 1,300 cm^2). Between 1.0 and 4.5 hours after creating the trails, we measured the width and depth of each trail, as well as snow depth and penetrometer sink depth on the trail and in undisturbed snow 5 m away. We also measured snow density at the snow surface and every 10 cm

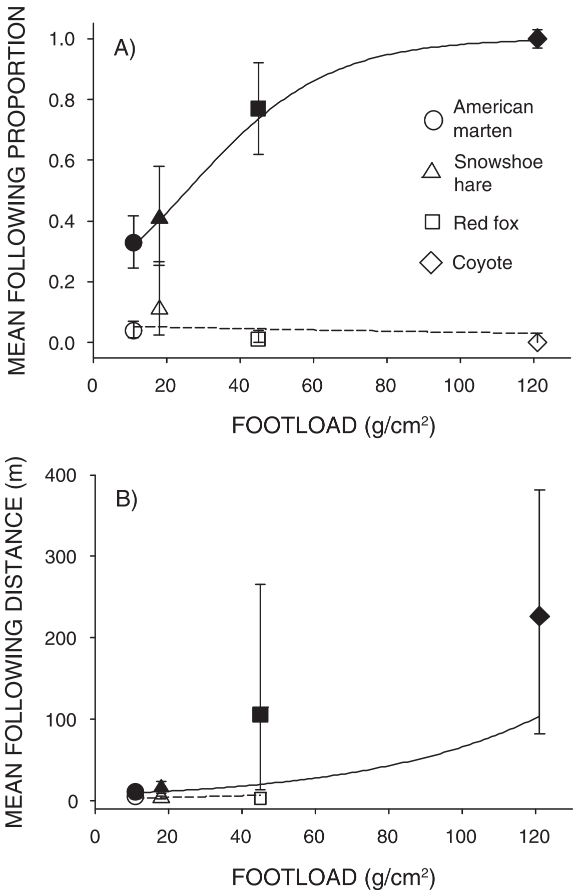

Figure 2. Mean (± 95% CI) proportion of animal trails (A) that encountered and followed non-compacted (open symbols) and compacted (filled symbols) transects in the snow. The x-axis represents footload (g body mass/cm^2 foot surface area). Data collected in northwestern Wyoming and southeastern Idaho, USA, 2007/08. The lines indicate predictions of the best logistic regression model, assuming that the transect is non-compacted (---) or compacted (—). Mean (± 95% CI) following distance on transects (B). The lines indicate predictions of the best linear regression model (using log-transformed following distances), assuming that the transect is non-compacted (---) or compacted (—). No coyote trails followed non-compacted transects, thus the subfigure does not contain an open diamond symbol and the dashed line is truncated.

Table 2. Ranking of regression models that use footload (g body mass/cm^2 foot surface area), compaction of snow and other variables (defined in the body text) to predict whether animals will turn and follow transects in the snow, and for how long a distance. The columns include sample size (N), change in Akaike's Information Criterion corrected for small sample size (ΔAIC_c), AIC_c weights (w_i), R^2 (Nagelkerke's[a] and adjusted[b]) and area under the receiver operating characteristic curve (AUC).

Predictors	N	ΔAIC_c	w_i	R^{2a}	AUC
Logistic models to predict frequency of following					
Ftld, Comp, Ftld*Comp	135	0	0.50	0.76	0.81
Ftld, Comp, Ftld*Comp, Canopy	135	1.85	0.20	0.76	0.82
Ftld, Comp, Ftld*Comp, Stems	135	1.89	0.20	0.76	0.81
Other models	135	≥ 3.97	≤ 0.07		
Predictors	**N**	**ΔAIC_c**	**w_i**	**R^{2b}**	
Linear models to predict log-transformed following distance					
Ftld, Comp	54	0	0.34	0.46	
Ftld, Comp, Ftld*Comp	54	1.46	0.16	0.46	
Ftld, Comp, Canopy	54	1.72	0.14	0.46	
Other models	54	≥ 2.42	≤ 0.10		

down to 50 cm, on each trail and in the undisturbed snow. We created and measured compacted trails at nine sites (separate from transects used to record animal trails).

Compaction by different sports: data analyses

Compaction is greatest at the snow surface and diminishes with depth; thus, we compared snow densities on trails created by sports to those of undisturbed snow at the same height above the ground. We used bootstrapping to calculate mean ratios of snow densities (on trail/in undisturbed snow). The 95% CIs that included 1 indicated no significant difference between sports trails and undisturbed snow.

Results

Animal use of compacted snow

Compacted transects were shallower and harder than nearby undisturbed snow. On compacted transects, mean snow depth was 10 cm less (95% CI = 10-15) and the mean penetrometer sink depth was 7.0 cm less (95% CI = 6.0-8.0) than 10 m off to the side.

Mean canopy cover on transects ranged from 64 to 98%, and mean density of live, woody stems (1-7 cm diameter) ranged from 595 to 6,920 stems/ha. Of 127 animal trails that followed compacted transects, eight had an unknown following distance because we were unable to pair an entry and exit.

For American martens, red foxes and coyotes, following proportion was higher on compacted

Table 3. Parameter estimates and descriptive statistics for the predictor variables (as defined in the body text) included in logistic regression models to predict whether animals will turn and follow transects in the snow.

	Model		
	Ftld, Comp, Ftld*Comp	Ftld, Comp, Ftld*Comp, Canopy	Ftld, Comp, Ftld*Comp, Stems
Variable	β (SE) Odds ratio (95% CI)		
Ftld	-0.01 (0.02)	-0.01 (0.02)	-0.01 (0.02)
	1.00 (0.96-1.03)	1.00 (0.96-1.03)	0.99 (0.96-1.03)
Comp	1.49 (0.42)	1.50 (0.42)	1.50 (0.42)
	4.41 (1.93-10.10)	4.48 (1.96-10.26)	4.45 (1.95-10.16)
Ftld*Comp	0.06 (0.02)	0.06 (0.02)	0.06 (0.02)
	1.06 (1.02-1.10)	1.06 (1.02-1.10)	1.06 (1.02-1.10)
Canopy	NA	0.01 (0.01)	NA
		1.01 (0.98-1.03)	
Stems	NA	NA	0.00 (0.00)
			1.00 (1.00-1.00)

Table 4. Parameter estimates and descriptive statistics for the predictor variables (as defined in the body text) included in linear regression models to predict how far animals will follow transects in the snow.

	Model		
	Ftld, Comp	Ftld, Comp, Ftld*Comp	Ftld, Comp, Canopy
Variable	β (SE)		
Ftld	0.02 (0.00)	-0.01 (0.03)	0.02 (0.00)
Comp	1.05 (0.32)	0.53 (0.64)	1.04 (0.32)
Ftld*Comp	NA	0.03 (0.03)	NA
Canopy	NA	NA	-0.01 (0.02)

transects than on non-compacted transects, but there was no clear difference for snowshoe hares (Fig. 2A). Following distance was greater on compacted transects than on non-compacted transects for snowshoe hares. There was no clear difference for American martens and a lack of samples of following distances on non-compacted transects precluded comparisons for red fox (N = 1) and coyote (N = 0; see Fig. 2B).

The probability of animals following transects was best predicted by three logistic regression models with similar support (AIC_c scores separated by ≤ 2 units; Table 2). The parameter estimates and odds ratios were consistent across these top three models (Table 3). The log-transformed following distance was best predicted by three linear regression models with similar support (separated by ≤ 2 AIC_c units; see Table 2). Parameter estimates were similar in two models and different in the third (Table 4). Two outlying data points on compacted transects included a coyote that followed for eight metres and a red fox that followed for 500 m; model selection results were not changed by removal of these data; therefore we retained them.

Of species without known footload values, grouse did not follow any transects. Squirrels and weasels had mean following proportions on non-compacted transects of < 0.01; on compacted transects, their respective means (95% CI) were 0.01 (0.00-0.03, N = 19) and 0.17 (0.04-0.33, N = 6). Grouse, squirrels and weasels all had 0-1 samples of following distances on non-compacted transects (data not shown).

Compaction by different snow sports

From the trail surface down to 50 cm below the surface, 95% CIs of snow density ratios (on trail/in undisturbed snow) for each sport overlapped (Fig. 3). Snowmobiling and snowshoeing increased snow density down to 20 cm, whereas cross-country skiing increased density down to 30 cm. For each snow sport, mean penetrometer sink depth was 15.1-15.4 cm less (CIs between 13.7 and 16.8 cm) on trails than in nearby undisturbed snow.

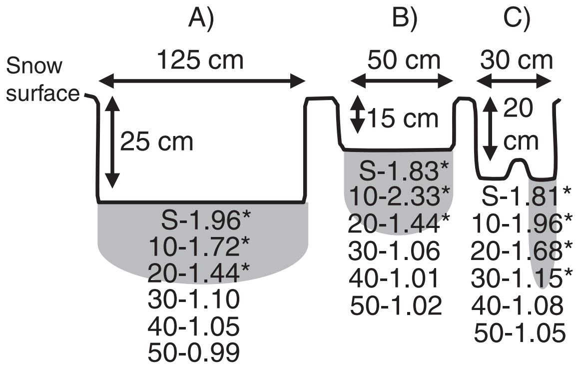

Figure 3. Cross section of snow cover showing mean dimensions of compaction of the snow surface, and mean increases in snow density, caused by four passes of snowmobiling (A), snowshoeing (B) and cross-country skiing (C), in northwestern Wyoming and southeastern Idaho, USA, during January 2008. The figure is not to scale. On the surface (indicated by S) and at 10-cm intervals beneath each trail, mean ratios of snow density (on trail/on undisturbed snow) ≥ 1 are indicated by asterisks and gray shading, indicating that compaction significantly increased snow density. Measurements were taken near the center of A) and B) and beneath a ski lane in C), thus the width of gray shading is not necessarily indicative of width of increased snow density.

Discussion

Influence of footload on animal use of compacted snow

Animals followed transects in the snow more often, and for longer distances, when transects were compacted. Consistent with our prediction, footload in the presence of compaction (represented by the interaction term ftld*comp) positively influenced whether an animal would turn and follow a transect. This interaction term had consistent parameter estimates across models, so it was unlikely that collinearity caused parameter instability. Adding the predictors of canopy cover and density of small, woody stems had almost no effect on the Nagelkerke's R^2, suggesting that these predictors had minimal influence on animal use of compacted snow. This lack of influence was also indicated by small parameter estimates and odds ratios near 1.

The best linear regression models to predict following distance included footload and compaction. These predictors had similar, positive parameter estimates in two models, but their estimates varied in the third model, which included their interaction term. We expected that footload would only be an important predictor on compacted transects, as indicated by the positive parameter estimates for the interaction term ftld*comp in models of following proportion. However, we speculate that models of following distance may reflect a sampling bias. The species with the highest footloads (i.e. red fox and coyote) had only one sample of following distance on a non-compacted transect but 12 samples of following distances on compacted transects. As a result, animals with high footloads essentially had following distances only on compacted transects, eliminating the influence of an interaction term.

The effect of compaction was greatest for the one species with the highest footload (i.e. the coyote), which never followed non-compacted transects, but followed every compacted transect encountered for a mean of 227 m. This distance is small compared to daily movements (which vary widely but can be up to 14 km in winter; Patterson et al. 1999), but it represents continuous travel only. That is, if a coyote left a transect for $\geq$ 2 m and then returned, a new following event began. The strong inclination of coyotes to follow compacted transects in our study, and the possibility of longer following distances that are not strictly continuous, suggest a potentially extensive use of compacted trails. A similar potential exists for red fox, which followed compacted transects in 0.77 of the encounters for a mean of 106 m.

Animals with high footloads can save substantial energy by using compacted trails. Our penetrometer sink depths were similar to coyote sink depths, and averaged 3.0 cm on-transect and 10.0 cm off-transect. Crête & Larivière (2003) modeled the heart rate of coyote-sized domestic dogs *Canis familiaris* traveling in snow. Their model, subsequently revised (M. Crête, pers. comm.), indicates that this increase in sink depth from 3.0 to 10.0 cm would increase the heart rate of a dog by 4%. Additionally, sinking to 16.0 cm, our deepest off-transect mean, would increase the heart rate of a dog by 13%.

Squirrels and weasels likely have low footloads and save little energy by using compacted trails. Even so, weasels followed transects more often if they were compacted, suggesting other benefits that may accrue from following trails, such as increased travel speed or increased rate of prey encounter. Sink depth may not be important for grouse, which travel on the snow surface for short distances. However, ruffed grouse grow specialized tarsal feathers in winter that increase their foot surface area (Trainer 1947) and reduce footload.

We sought to minimize confounding influences on animal use of compacted snow. Strip transects were straight and did not utilize natural travel corridors, obviating the possibility that use of compacted trails actually reflects use of cleared, linear corridors in which trails often occur (Kolbe et al. 2007). Habitat and cover did not differ between compacted and non-compacted transects because transects were sampled in both conditions.

We find it reasonable to assume that footload reflects adaptation to snow travel in our study. For example, North American red foxes in areas that receive $>$ 100 cm of annual snowfall have a foot surface area which is 18% greater than foxes in less snowy areas (Murray & Larivière 2002). Other characteristics, such as long legs, can reduce the difficulty of travel in snow (Telfer & Kelsall 1984). However, the data in our study come from species with chest heights less than the mean snow depths along transects (40-160 cm), indicating that snow was prohibitively deep for travel. Additional differences in morphology, gait and ecology also exist among species. It was not feasible to hold these variables constant and manipulate footload, and they likely provide unexplained variation in the models.

Future research

Our results suggest that compaction may enable snow-limited species to use new areas. Compacted trails have been associated with wolves *Canis lupus* (Paquet et al. 2010) and coyotes (Bunnell et al. 2006) utilizing high-elevation areas of deep snow which were otherwise less accessible. Crête & Larivière (2003) speculated that compacted trails contributed to range expansion of coyotes in northeastern North America. However, Kolbe et al. (2007) found that coyote use of compacted trails did not influence the spatial distribution of their movements. We recommend experimentally introducing compacted trails $\geq$ 1 km to test whether species with high footloads alter their habitat use and distribution.

Our results also predict that greater differences in footload indicate greater disparities in use and benefit of compacted trails between competitors. Based on odds ratios in our following proportion models, if an animal encounters a compacted trail, an increase in footload of 1 g/cm^2 increases the odds that the animal will follow it by 6%. As a result, high-footload species (e.g. coyotes, 121 g/cm^2) should benefit more than low-footload species (e.g. Canada lynx *Lynx canadensis*, 29 g/cm^2; Murray & Boutin 1991). Predictions can also be made for the impact of compaction on predation, which may be substantial: wolf predation rates (kills/km) were 2-3 times higher on compacted trails than on natural trails (Paquet et al. 2010).

We found that medium-sized mammals with high footloads used compacted trails extensively, and we recommend that predicted effects of compaction be tested where snow sports are common and the wildlife species involved are of conservation concern. Importantly, different snow sports have similar effects on snow density, thus data collection regarding sports should include spatial distribution and frequency of activity.

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Appendix I. List of the 56 candidate models used in regression to predict whether animals will turn and follow transects in the snow, and for how long a distance.

Predictors used in model	
Ftld	Comp, Canopy, Stems
Comp	Comp, Canopy, Species/transect
Canopy	Comp, Stems, Species/transect
Stems	Comp, Species, Species/transect
Species	Comp, Species, Species*Comp
Species/transect	Canopy, Species, Stems
Ftld, Comp	Canopy, Species, Species/transect
Ftld, Stems	Canopy, Stems, Species/transect
Ftld, Species/transect	Ftld, Comp, Ftld*Comp, Canopy
Ftld, Canopy	Ftld, Comp, Ftld*Comp, Stems
Comp, Species	Ftld, Comp, Ftld*Comp, Species/transect
Comp, Stems	Ftld, Comp, Canopy, Stems
Comp, Canopy	Ftld, Comp, Stems, Species/transect
Comp, Species/transect	Ftld, Canopy, Stems, Species/transect
Species, Stems	Species, Comp, Canopy, Species*Comp
Species, Canopy	Species, Comp, Stems, Species*Comp
Canopy, Stems	Species, Comp, Canopy, Stems
Canopy, Species/transect	Species, Comp, Stems, Species/transect
Species/transect, Stems	Canopy, Stems, Species/transect, Comp
Species/transect, Species	Canopy, Stems, Species/transect, Species
Ftld, Comp, Ftld*Comp	Ftld, Comp, Ftld*Comp, Stems, Canopy
Ftld, Comp, Stems	Ftld, Comp, Ftld*Comp, Stems, Species/transect
Ftld, Comp, Canopy	Ftld, Comp, Canopy, Stems, Species/transect
Ftld, Comp, Species/transect	Species, Comp, Stems, Species*Comp, Canopy
Ftld, Stems, Canopy	Species, Comp, Stems, Species*Comp, Species/transect
Ftld, Stems, Species/transect	Species, Comp, Stems, Canopy, Species/transect
Species, Comp, Stems	Ftld, Comp, Ftld*Comp, Stems, Canopy, Species/transect
Species, Comp, Canopy	Comp, Stems, Canopy, Species/transect, Species, Species*Comp