

# Predators attract prey through ecosystem engineering in the Arctic

TAZARVE GHARAJEHDAGHIPOUR AND JAMES D. ROTH†

*Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2 Canada*

**Citation:** Gharajehdaghypour, T., and J. D. Roth. 2018. Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere* 9(1):e02077. 10.1002/ecs2.2077

**Abstract.** Predators can affect prey through mechanisms other than predation; for example, redistributing resources could modify habitats favorably for other organisms. We examined Arctic fox (*Vulpes lagopus*) den use by lemmings, their primary prey, in winter during a year of low lemming densities. We found winter nests, which are built by lemmings under snow, on 69% of fox dens, whereas no control sites had nests. In August, dens had twice the vegetation cover and 50% greater nitrogen content in grass than controls, suggesting soil enrichment by foxes increased food quantity and quality for herbivores. Snow was ~4 times thicker in April on dens than controls, and 1.4 times thicker on dens with lemming nests than dens without, suggesting lemmings choose thicker snow for thermal insulation. Snow cover thickness was positively related to vegetation cover on dens, but not on control sites. Thus, Arctic foxes not only prey on lemmings but also engineer productive habitat that attracts lemmings. During winters with low lemming densities, when foxes often leave the denning area and predation risk is lower, fox dens may provide a refuge that could buffer the effects of deteriorating snow conditions with Arctic warming. This additional mechanism of predators interacting with their prey illustrates how ecosystem engineers potentially alter food web interactions and highlights the importance of integrating these bodies of theory in attempts to understand community dynamics.

**Key words:** *Dicrostonyx richardsoni*; food web; indirect interactions; nitrogen concentration; non-consumptive effects; snow depth; vegetation cover; vegetation quality; *Vulpes lagopus*.

**Received** 6 October 2017; accepted 12 October 2017. Corresponding Editor: Debra P. C. Peters.

**Copyright:** © 2018 Gharajehdaghypour and Roth. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** jim.roth@umanitoba.ca

## INTRODUCTION

Predators often have strong impacts on ecological communities by regulating the abundance and changing the dynamics of species in lower trophic levels through predation (Soulé et al. 2005). However, investigation of the role of predators has evolved from focusing solely on prey–predator relationships to trying to understand the impact of predators on both the whole community of species and the abiotic constituents within their system (Ray 2005). For example, predators can enhance ecosystem nutrient cycling strongly enough to increase vegetation productivity (Schmitz et al. 2010). Thus, considering the simultaneous negative

and positive effects of predators through both trophic and non-trophic interactions is essential for understanding the broader role of predators in an ecosystem.

One of the most prominent generalist predators of the Arctic is the Arctic fox (*Vulpes lagopus*). Arctic fox population dynamics often follow the multiannual, high-amplitude cyclic population dynamics of lemmings (*Dicrostonyx* and *Lemmus* spp.), particularly in regions such as Canadian Arctic, northern Alaska, and Fennoscandia where lemmings are their primary terrestrial prey (Chesmore 1969, Angerbjörn et al. 1995, Elmhagen et al. 2000, McDonald et al. 2017). Arctic foxes rely on well-established dens to shelter pups from the

harsh Arctic climate and predators (Tannerfeldt et al. 2003). Climate, soil type, and permafrost can hinder developments of new dens spatially and temporarily (Smits et al. 1988, Tannerfeldt et al. 2003). Arctic fox dens are mostly dug on raised topographical features (e.g., ridges, banks, mounds, moraines). Specific sites are chosen because of their greater depth to permafrost and well-draining coarse sediment composition, which assist in less energetically costly excavations (Smits et al. 1988, Szor et al. 2008). Dens can persist for years, with some dens estimated to be hundreds of years old (Macpherson 1969). These dens can support lush green vegetation due to nutrient addition by Arctic foxes (Smits et al. 1988, Bruun et al. 2005, Gharajehdaghhipour et al. 2016), and the greater vegetation productivity on dens compared to surrounding areas could attract herbivores to these dens (Gharajehdaghhipour et al. 2016). Lemming latrines can occur in vicinity of Arctic fox dens on alpine tundra (Bruun et al. 2005), and lemming winter nests have been observed on Arctic fox dens in the Hudson Bay region of Canada (J. D. Roth, *unpublished data*). The presence of lemming winter nests and latrines suggests that lemmings make use of Arctic fox dens during winter despite the presumably higher predation risk and that predators (Arctic foxes) could positively influence their main prey (lemmings) through their engineering activities.

Lemmings remain active during winter and reproduce under the snow (Millar 2001). Therefore, conditions that promote reproduction in winter (which can last up to 9 months in Arctic regions) could be critical for the occurrence of regular peaks in these species' population dynamics (Reid and Krebs 1996, Kausrud et al. 2008). In winter, lemmings inhabit a layer of lightly packed snow crystals close to the soil surface called the subnivean space (Korslund and Steen 2006), and use of this space provides thermal insulation against the harsh arctic ambient air temperatures, protection against predators, and access to food (Scott 1993). In the subnivean space, lemmings make winter nests from vegetation, which they use for further thermal insulation (Chappell 1980, Casey 1981), breeding, and raising litters (Krebs et al. 1995, Sittler 1995, Duchesne et al. 2011). Winter nests are typically found in locations forming a thick snow cover, providing lemmings with better thermal insulation (Reid and Krebs 1996, Reid

et al. 2012, Bilodeau et al. 2013*b*). At snow thickness above the hiemal threshold (20–30 cm), air and ground temperatures are no longer coupled, and the environment at the soil surface becomes more stable and suitable for lemmings compared to the highly fluctuating air temperatures (Pruitt 1970, Huryrn and Hobbie 2012). If Arctic fox dens offer better thermal insulation to lemmings during winter, we predicted that Arctic fox dens would have a greater snow cover thickness than surrounding areas and that dens with lemming winter nests on them would have greater maximum snow cover thickness than dens without lemming nests. However, to reduce predation, risk lemmings may avoid dens currently occupied by Arctic foxes, so dens with signs of recent fox use may be less likely to have lemming winter nests.

On the tundra, areas with thick snow accumulation usually occur on the lee side of topographical features such as slopes, banks, and ridges where wind-blown snow drifts deposit (Reid and Krebs 1996, Duchesne et al. 2011). Vegetation stands can also increase snow cover thickness by decreasing wind speed (Benson and Sturm 1993). Shrub presence, for example, can increase snow cover thickness up to about 30% independent of local topographic heterogeneity (McFadden et al. 2001). Arctic foxes concentrate nutrients on their dens, leading to nearly three times greater vegetation biomass than surrounding tundra (Gharajehdaghhipour et al. 2016). Thus, we predicted greater vegetation cover on dens would trap blowing snow, leading to greater snow cover thickness that would be positively related to vegetation cover.

Higher quality vegetation could also attract lemmings to Arctic fox dens. Herbivores, including lemmings, typically prefer to consume plants with higher nitrogen content [N] (Mattson 1980, Rodgers and Lewis 1985). Fertilization experiments on heath tundra have shown that lemmings and voles prefer fertilized areas during winter and consume graminoids and vascular plants considerably (Grellmann 2002). Similarly, nutrient addition by Arctic foxes leads to much higher nutrient levels in soils on fox dens than surrounding tundra (Gharajehdaghhipour et al. 2016). These nutrient additions could also translate to higher quality vegetation on dens that make them attractive nesting and feeding sites for lemmings in winter. Therefore, we predicted

that vegetation on dens would have higher N content than vegetation on surrounding areas.

## METHODS

Our study was conducted on the tundra adjacent to western Hudson Bay, in and around Wapusk National Park in Manitoba, Canada, in conjunction with our long-term monitoring of Arctic fox and lemming populations in this area (Berteaux et al. 2017, McDonald et al. 2017). The region is an extensive flat coastal plain that is part of the Hudson Bay lowlands (Brook and Kenkel 2002). Arctic fox dens in this area are almost exclusively found on north–south oriented beach ridges, one of the main landform features in this region that are made by post-glacial rebound of the land, separated by peat lowlands with many shallow lakes and ponds (Ritchie 1957, Roth 2003). Low moisture levels due to the sandy soils and greater depth to permafrost make these beach ridges suitable denning habitats for Arctic foxes (Chesemore 1969, Smits et al. 1988, Dalerum et al. 2002). Vegetation on beach ridges is characteristic of low-growing heath communities (Johnson 1987), specifically *Dryas* heath (Brook and Kenkel 2002), due to the dominance of *Dryas integrifolia*. However, Arctic fox dens are usually covered with lush green vegetation, dominated by fast-growing species such as *Leymus mollis* and *Salix planifolia* (Gharajehdaghypour et al. 2016). Based on trapping efforts (Roth 2002, McDonald et al. 2017), the only lemming species inhabiting this area is the collared lemming (*Dicrostonyx richardsoni*).

In April 2014, we measured snow thickness on 60 dens and paired control sites. Using an avalanche steel probe, we measured snow thickness at the point on the den with highest elevation and at four additional points 5 m from the center, approximately in the four cardinal directions (two parallel to the beach ridge and two perpendicular to the beach ridge). For each den, a paired control area was chosen 50 m from the center of the den at a similar elevation, slope, and aspect, and five snow thickness measurements were taken following the same protocol as den measurements. We also assessed the activity status of each den based on the presence of burrows (i.e., active dens had tunnels dug by foxes through the snow to the den).

In June 2014, we surveyed a subset of dens for the presence of lemming winter nests. Similar to April, for each den site, we also surveyed a paired control site with a similar area, elevation, slope, and aspect. The center of the control site was designated 50 m away from the center of the den (the midpoint of a straight line connecting the two farthest open burrows) to ensure that control area was not overlapping with the fox denning area. We also examined nests for evidence of predation by weasels, which leave a dense carpet of hair or lemming body fragments and partly consumed carcasses in the middle of the nest (MacLean et al. 1974, Sittler 1995). Additionally, presence of willow scars made by lemmings during winter (Predavec et al. 2001) and lemming latrines were recorded haphazardly. We also counted lemming nests in two strip transects (10 × 2 km) along a large beach ridge (~3 m high) in the middle of our study area, one on the top of the ridge in habitat similar to our control sites and the other in the middle of the slope on the lee (east) side of the ridge, where snow accumulates in winter and lemming nests are commonly observed (J. D. Roth, *unpublished data*). We also estimated lemming density using mark–recapture estimates on two trapping grids (8 × 8; 15 m between stakes) and two transects (300 m; 15 m between stakes) following previously published protocols (McDonald et al. 2017).

In August 2014, we estimated vegetation cover and den area by taking aerial photographs from den and control pairs (with a DJI Phantom 2 Vision<sup>+</sup> drone). Centers of dens and paired control sites were designated following the same protocol as in June. To ensure the visibility of den and control centers in aerial photographs, a stake and a 1-m<sup>2</sup> quadrat were placed at the center of each den and control site. To compare the vegetation quality on and off dens, *L. mollis* samples were collected from den and surrounding areas when available.

To compare snow depth between den and control pairs, we used linear mixed effect analysis in R (R Core Team 2015), applying the *lmer* function of the *lme4* package (Bates et al. 2015). Site (den vs. control) was entered as a fixed effect into the model. As a random effect, we let intercepts vary for individual sites. The measurements for each site were averaged and log<sub>10</sub>-transformed to meet the normality and homoscedasticity assumptions. Likelihood ratio test of the full model against a

null model was used to obtain a  $P$ -value for the fixed effect. Marginal  $R^2$  (proportion of variance explained by the fixed factor) and conditional  $R^2$  (proportion of variance explained by both the fixed and random factors) values were calculated based on Nakagawa and Schielzeth (2013). To compare the maximum snow cover thickness measurements (taken in April) between dens with and without lemming winter nests, we used Welch's  $t$ -test. To test whether fox activity affects lemming winter nest presence on dens, we used Fisher's exact test.

Den areas were calculated from aerial drone photographs using Photoshop CS6 (Adobe Systems Inc., San Jose, California, USA). For each den, a circular selection that encompassed the farthest *S. planifolia* and/or *L. mollis* stands was made using the Marquee tool. Area of this selection was measured in pixels (D). The area of the 1-m<sup>2</sup> quadrat (placed on the center of each den) was also measured in pixels (Q). Area of each den in m<sup>2</sup> was then calculated by dividing D by Q. Lemming nest density at each den was calculated by dividing nest counts by den area. To calculate nest densities along transects, we assumed all nests within 5 m of the transect line were detected and divided nest counts by 10 × transect length.

Vegetation dominated by *S. planifolia*, *L. mollis*, and *D. integrifolia* and total vegetation cover estimates were calculated from aerial photographs using Photoshop CS6. For each photograph, the length of one side of the 1-m<sup>2</sup> quadrat visible in the photograph was measured in pixels (L), and the photograph was then cropped into a circle with a diameter of 10 × L centered on the stake (placed on the center of the den or control site). The total area of the circle was measured in pixels. The number of pixels belonging to *S. planifolia*, *L. mollis*, and *D. integrifolia* was measured using the lasso and color range tools. We chose the same level of sensitivity (fuzziness) of the color range tool for all species. The cover for each species was then measured by dividing the number of pixels of each species by the total area of the circle. For photographs with only one plant species, the area of barren ground (including dead vegetation) was determined and subtracted from the total area. Measurements were then compared between den and control sites using paired  $t$ -tests. To test whether *S. planifolia*, *L. mollis*, and *D. integrifolia* trap snow and result in thicker snow cover, we ran a multiple linear regression analysis for den and

control sites separately. Snow cover measurements were log<sub>10</sub>-transformed to meet the normality and homoscedasticity assumptions. Multicollinearity between predictor variables was not an issue (all variance inflation factor values were <2.5).

Samples of *L. mollis* were dried to constant weight, and a portion of each was homogenized with a ball mill. Nitrogen content (%N based on mass) in 3-mg sub-samples was measured using an elemental analyzer at University of Windsor. N content of plants was compared between dens and controls using a paired  $t$ -test.

## RESULTS

Lemming density was 0.60 ha<sup>-1</sup> (±0.32 SE), similar to the low-density years measured previously (Roth 2002, McDonald et al. 2017). We found lemming winter nests on 69% of the dens surveyed (25 out of 36, mean = 1.39, SE = 0.23), but no nests on control areas (i.e., 0 ha<sup>-1</sup>). Predation by weasels occurred on only one den (two of 50 nests). The area covered by dens averaged 563.2 m<sup>2</sup> (±112.0 SE). Nest density on dens averaged 33.9 ha<sup>-1</sup> ( $n = 19$ , SE = 12.0), compared to 36.1 ha<sup>-1</sup> on the ridge slope and 5.4 ha<sup>-1</sup> on the ridge top. Fox activity was present on 28% of our surveyed dens ( $n = 60$ ) and did not affect the presence of lemming nests on dens (Fisher's exact test,  $n = 36$ ,  $P = 0.353$ ). We found willow scars on 36% (five out of 14) of the dens that had willows growing on them, and latrines on 19% of the surveyed dens (seven out of 36). Latrines were only present on dens that had lemming nests.

Total vegetation cover differed between den and control areas ( $t_{17} = 4.363$ ,  $P = 0.0002$ ), with dens having nearly twice as much vegetation cover as control sites (Fig. 1). *Salix planifolia* and *L. mollis* were not found on control sites. *Dryas integrifolia* cover was about three times greater on control sites than on den sites ( $t_{17} = -3.535$ ,  $P = 0.001$ ). N content in vegetation was significantly greater on dens than on control sites ( $t_{13} = 8.185$ ,  $P < 0.0001$ ; Fig. 2).

Snow cover was about four times thicker on den sites than on control sites (Fig. 3a;  $\chi^2_{(1)} = 115.616$ ,  $P < 0.0001$ ,  $\beta = 0.657$ ). The full model had a marginal  $R^2 = 0.599$  and conditional  $R^2 = 0.728$ . Furthermore, dens with lemming winter nests had about 1.4 times greater maximum snow thickness than dens without lemming winter nests ( $t_{22.1} = 2.259$ ,  $P = 0.034$ ; Fig. 3b).

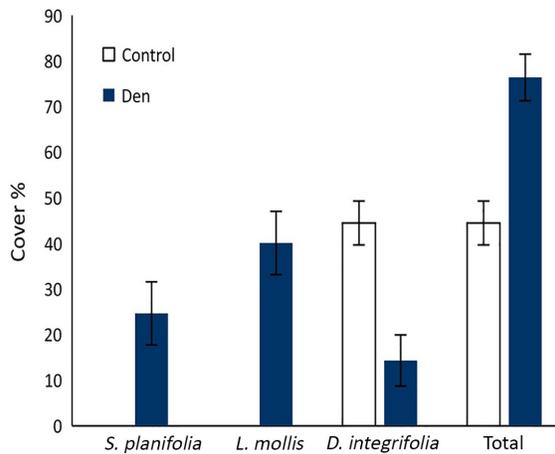


Fig. 1. Vegetation cover percentage (mean  $\pm$  SE) on 18 fox dens and paired control sites in Wapusk National Park, Canada, in August 2014.

Snow thickness on den sites (T) was affected by vegetation cover ( $F_{3,14} = 41.632$ ,  $P < 0.0001$ ,  $R^2_{Adjusted} = 0.877$ ;  $\log_{10}T = 0.006C_S + 0.003C_L - 0.0002C_D + 1.301$ ), increasing with cover of *S. planifolia* ( $C_S$ ,  $t_{17} = 8.89$ ,  $P < 0.0001$ ) and *L. mollis* ( $C_L$ ,  $t_{17} = 4.30$ ,  $P = 0.0007$ ), but *D. integrifolia* ( $C_D$ ) had no effect ( $t_{17} = -0.17$ ,  $P = 0.869$ ; Fig. 4a). Likewise, *D. integrifolia* cover did not

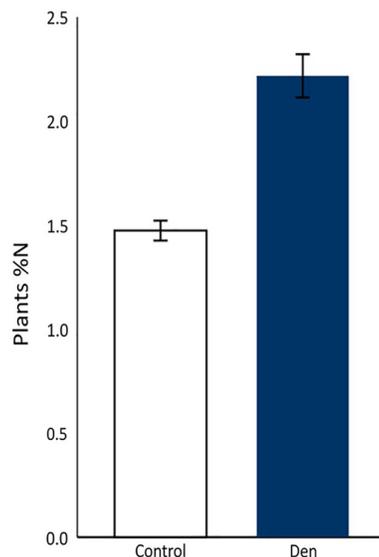


Fig. 2. Percent nitrogen (mean  $\pm$  SE) in *Leymus mollis* leaf samples collected from 14 fox dens and control areas in Wapusk National Park, Canada, in August 2014.

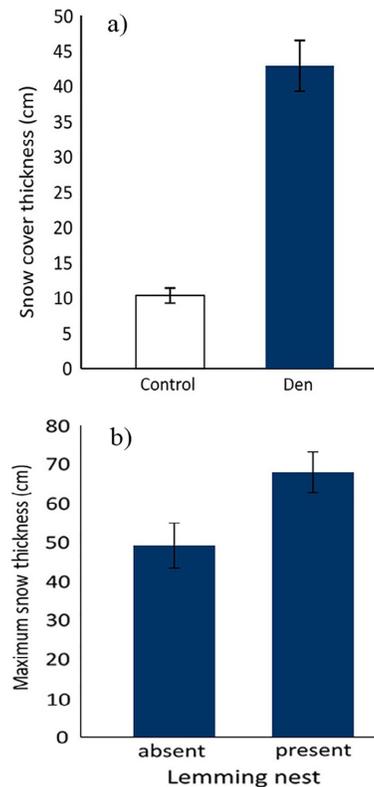


Fig. 3. Snow thickness (mean  $\pm$  SE) on (a) 60 fox dens and paired control sites and (b) fox dens with ( $n = 24$ ) or without ( $n = 11$ ) lemming winter nests, in the greater Wapusk ecosystem in April 2014.

affect snow thickness on control sites ( $n = 18$ ,  $F_{1,17} = 0.005$ ,  $P = 0.947$ ; Fig. 4b).

## DISCUSSION

The much greater snow thickness on Arctic fox dens compared to control sites suggests den sites offer enhanced thermal insulation against the harsh Arctic climate, making them attractive sites for lemmings during winter. Furthermore, 90% of the den sites (compared to only 10% of the control sites) had average snow thickness greater than the hiemal threshold. Thus, dens sites not only provide better thermal insulation, but they also offer maximal dampening of the diurnal temperature fluctuations at ground level compared to ambient air (Pruitt 1970, Reid et al. 2012). The influence of snow on lemmings' choice of winter habitat is further supported when snow thickness on dens with and without

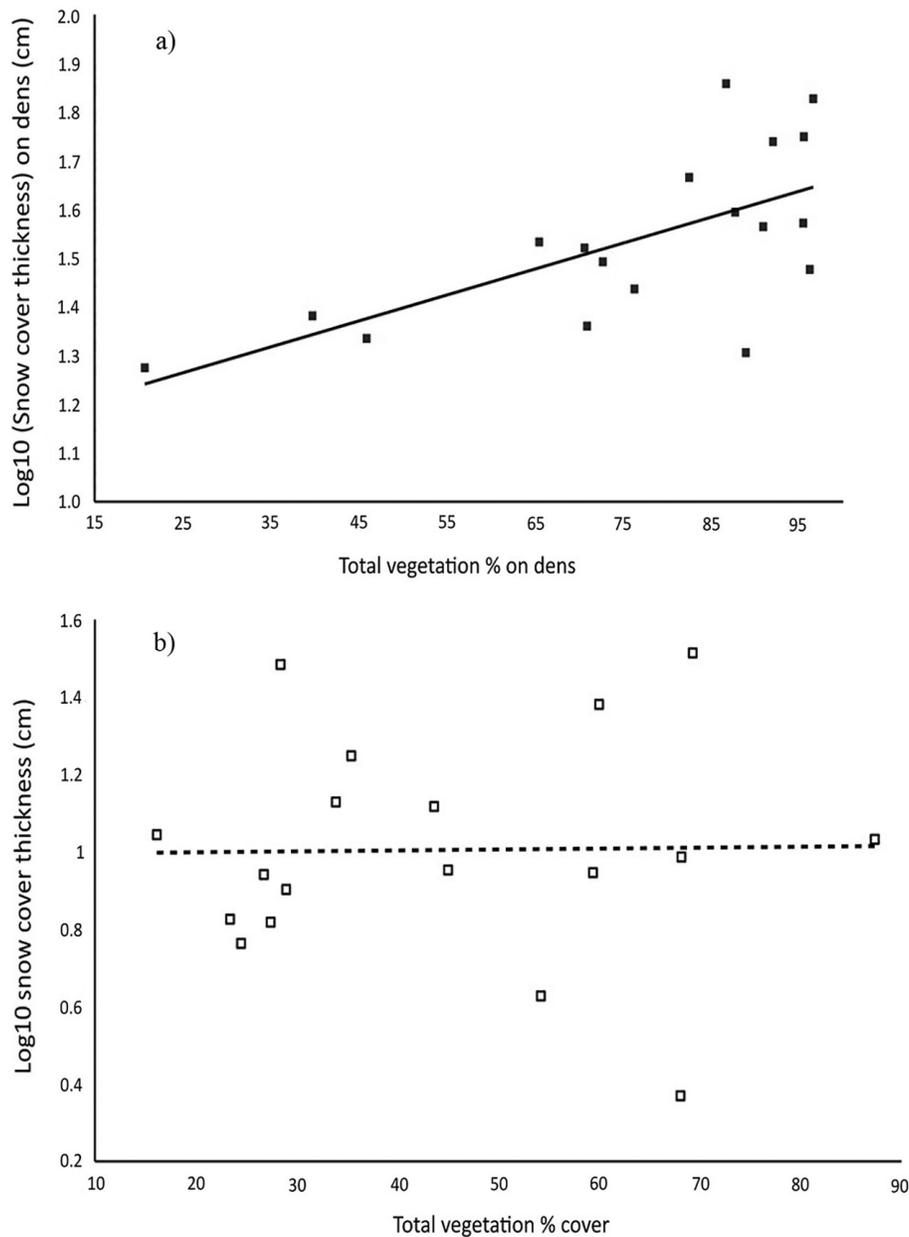


Fig. 4. Relationship between snow cover thickness (log-transformed) and vegetation cover on (a) fox dens and (b) on control sites ( $n = 18$  sites in each category).

dens are compared; dens with winter nests had greater snow cover thickness, thereby providing lemmings with better thermal protection than dens without nests. Even though lemming densities were low, with presumably little competition for winter nesting sites, lemming nest densities on Arctic fox dens were comparable to nest densities in preferred habitats on the lee side of

ridges where snow drifts accumulate, suggesting that Arctic fox dens are comparable in quality to preferred nesting sites.

Deeper snow also increases soil temperature, which in turn results in greater over-winter nitrogen mineralization rates and available nitrogen in tundra ecosystems by causing increased microbial activity (Schimel et al. 2004). Thus,

dens have greater inorganic nitrogen concentrations because of both deposition of nutrients by foxes (Gharajehdaghypour et al. 2016) and deeper snow. Higher amounts of nutrients in turn increase plant biomass (Gharajehdaghypour et al. 2016) and cover, as well as changing the plant community toward more nutrient-demanding species such as *Leymus mollis* and *Salix planifolia*. As our results demonstrate, snow cover thickness increases as the cover of *S. planifolia* and *L. mollis* increases, confirming that vegetation on dens can trap the blowing snow and increase snow cover thickness in a positive feedback mechanism. *Dryas integrifolia* did not affect snow thickness on dens or on control sites, possibly because it is a shrub species that is only found dwarfed in our study area (Johnson 1987) and therefore would not trap a significant amount of snow. Given that 2014 was a low lemming density year and that average snow thickness on 90% of control sites did not reach the hiemal threshold, it is not surprising that we did not find any lemming nests on control sites. Similarly, lack of thermal insulation is likely the reason nest densities on ridge tops were very low. Our results are consistent with studies on the effects of height of erect shrubs such as willows on the amount of snow accumulation in tundra areas (McFadden et al. 2001). However, based on our model, *L. mollis*, which is a perennial grass, also traps snow (even on dens where willows are absent). Due to its extensive rooting system, *L. mollis* acts as a stabilizer in sub-Arctic coastal dunes (Gagné and Houle 2002), and therefore, the dense *L. mollis* cover on Arctic fox den could resist the wind during winter and trap the blowing snow.

N content of vegetation was higher on dens than control sites, suggesting that the greater inorganic N in soil on den sites also increases vegetation quality. N content of plant species is positively correlated with the diet preference of *Dicrostonyx groenlandicus* (Rodgers and Lewis 1985). Moreover, collared lemmings have a preference for *Salix* species (Batzli and Pitelka 1983, Batzli 1993), which are commonly found on dens (Gharajehdaghypour et al. 2016). *Salix planifolia* and *L. mollis* are both perennial species, and their higher N content makes them valuable food sources during winter, and the presence of scars on *S. planifolia* plants growing on fox dens further suggests that

lemmings consume the vegetation on dens. Control areas, where *D. integrifolia* is the dominant vegetation, could be considerably less attractive lemming feeding sites than den areas because elevated catechin (a plant secondary metabolite) concentrations in *Dryas* spp. negatively affect their consumption rates by collared lemmings (Berg 2003). Thus, higher quality and quantity of food, in addition to better thermal insulation, could make Arctic fox dens attractive nesting sites for lemmings. As mammalian herbivores in Arctic tundra can elevate soil nitrogen and phosphorus concentrations through deposition of their waste products (McKendrick et al. 1980), lemming use of Arctic fox dens (and the lemming latrines we observed on dens) could further enhance local nutrient dynamics. Increased vegetation quality may attract other herbivores (geese, caribou, or hares) to these dens, adding additional nutrients that further enhance plant growth. This positive feedback between nutrient enhancement and herbivores attraction suggests improved vegetation quality and quantity would persist even if den use by foxes decreased, either due to a long-term population reduction or just a cyclic prey decline.

In years with low lemming densities, Arctic foxes in coastal areas often leave their dens and venture on to sea ice to feed on ringed seal (*Phoca hispida*) pups and seal carcasses killed by polar bears (*Ursus maritimus*; Roth 2002, Lai et al. 2017). In such years, predation risk on dens may be lower, allowing dens to become good winter refuges. Foxes produce a volatile rodent-carnivore kairomone (2-phenylethylamine) resulting in fear-like or aversive behavior in rodents (Ferrerio et al. 2011). Such compounds aerosolize and enable rodents to detect carnivores from a distance. Although not examined in lemmings specifically, receptors for these widely produced kairomones could allow lemmings to mitigate predation risk by selecting dens that are not currently occupied by foxes. However, fox activity on dens did not affect lemming nest presence, suggesting that either lemming could not detect the presence of foxes, or the perceived benefits associated with these dens outweighed the predation risk from foxes. Thick snow cover has been suggested to reduce predation rates on lemmings (Gill et al. 2006), but a recent study found that thick snow cover only weakly limited fox predation attempts made by jumping through

the snow, did not affect attempts made by digging, and did not provide lemming protection against ermine predation (Bilodeau et al. 2013a). These observations suggest in years with high lemming densities, when foxes continue to occupy dens consistently during winter (Lai et al. 2017), enhanced snow depth on dens may not protect lemmings from predators and predation risk on dens could be high. In such years, fox dens may act as ecological traps (reviewed in Hale and Swearer 2016), where net fitness is reduced by increased predation risk despite the benefits of enhanced thermal protection and improved quality and quantity of forage. Whether predation risk on dens is inversely related to lemming density certainly warrants further investigation.

This study provides additional evidence that Arctic foxes engineer arctic ecosystems on local scales: By enhancing the nutrient dynamics, foxes create a vegetation community with more erect species that trap snow during winter. Increased snow cover thickness can in turn increase the availability of nutrients to plants by increasing the mineralization rates. Higher concentration of nutrients in soil also increases vegetation biomass and cover on dens. Our results suggest thicker snow and increased quantity and quality of food are all features that could attract lemmings to Arctic fox den sites during winter, regardless of fox activity on dens. Although we were unable to isolate the benefit of den vegetation to lemmings from benefit of increased insulation, future investigations of lemming diets on fox dens may be able to disentangle these mechanisms of attracting lemmings to fox dens.

Arctic foxes as predators can negatively affect lemming populations through predation, but our study illustrates that by enhancing winter habitats for lemmings, Arctic foxes could potentially influence lemming populations positively. Arctic fox den sites could be local refugia for collared lemmings at low densities or for populations whose cycles have dampened due to climate change effects, such as increasing temperatures affecting snow characteristics in a number of Arctic areas (Ims et al. 2008, Kausrud et al. 2008). Arvicoline rodents such as lemmings support a number of mammalian and avian predators in the Arctic (Korpimäki et al. 2005, Gilg et al. 2006, Gauthier et al. 2011). Thus, by helping sustain low-density

lemming populations, Arctic fox engineering activities could also indirectly affect other predators.

Non-trophic indirect interactions are not uncommon and often influence species biodiversity and the structural integrity of communities (Ohgushi 2008). Our study suggests that combining both trophic and ecosystem engineering impacts of predators into interaction webs would provide a better representation of their role in ecosystems than focusing solely on their impacts through predation.

## ACKNOWLEDGMENTS

This research was supported by the Natural Sciences and Engineering Research Council of Canada (Discovery grant 386704), the University of Manitoba Fieldwork Support Program, Parks Canada, and Churchill Northern Studies Centre (CNSC) Northern Research Fund. We are grateful to J. Markham, P. Fafard, I. Burrton, and the Wapusk National Park staff for field and laboratory assistance, to the CNSC staff for logistic support, and to J. Markham and R. Brook for feedback on earlier drafts of the manuscript.

## LITERATURE CITED

- Angerbjörn, A., M. Tannerfeldt, A. Bjärvall, M. Ericson, J. From, and E. Norén. 1995. Dynamics of the arctic fox population in Sweden. *Annales Zoologici Fennici* 32:55–68.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Batzli, G. O. 1993. Food selection by lemmings. Pages 281–301 in N. C. Stenseth and R. A. Ims, editors. *The biology of lemmings*. Academic Press, London, UK.
- Batzli, G. O., and F. A. Pitelka. 1983. Nutritional ecology of microtine rodents: food habits of lemmings near Barrow, Alaska. *Journal of Mammalogy* 64: 648–655.
- Benson, C. S., and M. Sturm. 1993. Structure and wind transport of seasonal snow on the Arctic slope of Alaska. *Annals of Glaciology* 18:261–267.
- Berg, T. 2003. Catechin content and consumption ratio of the collared lemming. *Oecologia* 135:242–249.
- Berteaux, D., et al. 2017. Harmonizing circumpolar monitoring of Arctic fox: benefits, opportunities, challenges and recommendations. *Polar Research* 36:2. <https://doi.org/10.1080/17518369.2017.1319602>
- Bilodeau, F., G. Gauthier, and D. Berteaux. 2013a. Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic. *Journal of Mammalogy* 94:813–819.

- Bilodeau, F., D. G. Reid, G. Gauthier, C. J. Krebs, D. Berteaux, and A. J. Kenney. 2013b. Demographic response of tundra small mammals to a snow fencing experiment. *Oikos* 122:1167–1176.
- Brook, R. K., and N. C. Kenkel. 2002. A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing* 23:4761–4776.
- Bruun, H. H., S. Osterdahl, J. Moen, and A. Angerbjörn. 2005. Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography* 28:81–87.
- Casey, T. 1981. Nest insulation: energy savings to brown lemmings using a winter nest. *Oecologia* 50:199–204.
- Chappell, M. A. 1980. Thermal energetics and thermoregulatory costs of small Arctic mammals. *Journal of Mammalogy* 61:278–291.
- Chesemore, D. L. 1969. Den ecology of the Arctic fox in northern Alaska. *Canadian Journal of Zoology* 47:121–129.
- Dalerum, F., M. Tannerfeldt, B. Elmhagen, D. Becker, and A. Angerbjörn. 2002. Distribution, morphology and use of Arctic fox *Alopex lagopus* dens in Sweden. *Wildlife Biology* 8:185–192.
- Duchesne, D., G. Gauthier, and D. Berteaux. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia* 167:967–980.
- Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjörn. 2000. The Arctic fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology* 251:139–149.
- Ferrero, D. M., J. K. Lemon, D. Fluegge, S. L. Pashkovski, W. J. Korzan, S. R. Datta, M. Spehr, M. Fendt, and S. D. Liberles. 2011. Detection and avoidance of a carnivore odor by prey. *Proceedings of the National Academy of Sciences* 108:11235–11240.
- Gagné, J.-M., and G. Houle. 2002. Factors responsible for *Honckenya peploides* (Caryophyllaceae) and *Leymus mollis* (Poaceae) spatial segregation on sub-arctic coastal dunes. *American Journal of Botany* 89:479–485.
- Gauthier, G., D. Berteaux, J. Bêty, A. Tarroux, J.-F. Therrien, L. McKinnon, P. Legagneux, and M.-C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. *Ecoscience* 18:223–235.
- Gharajehdaghypour, T., J. D. Roth, P. M. Fafard, and J. H. Markham. 2016. Arctic foxes as ecosystem engineers: Increased soil nutrients lead to increased plant productivity on fox dens. *Scientific Reports* 6:24020. <https://doi.org/10.1038/srep24020>
- Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. Functional and numerical responses of four lemming predators in high Arctic Greenland. *Oikos* 113:193–216.
- Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an Arctic tundra heath. *Oikos* 98:190–204.
- Hale, R., and S. E. Swearer. 2016. Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences* 283:20152647.
- Huryñ, A., and J. Hobbie. 2012. Land of extremes: a natural history of the Arctic North Slope of Alaska. University of Alaska Press, Fairbanks, Alaska, USA.
- Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. *Trends in Ecology and Evolution* 23:79–86.
- Johnson, K. L. 1987. Wildflowers of Churchill and the Hudson Bay region. Manitoba Museum of Man and Nature, Winnipeg, Manitoba, Canada.
- Kausrud, K. L., et al. 2008. Linking climate change to lemming cycles. *Nature* 456:93–97.
- Korpimäki, E., K. Norrdahl, O. Huitu, and T. Klemola. 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society of London B: Biological Sciences* 272:193–202.
- Korslund, L., and H. Steen. 2006. Small rodent winter survival: Snow conditions limit access to food resources. *Journal of Animal Ecology* 75:156–166.
- Krebs, C., R. Boonstra, and A. Kenney. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia* 103:481–489.
- Lai, S., J. Bêty, and D. Berteaux. 2017. Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic. *Oikos* 126:937–947.
- MacLean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. Population cycles in Arctic lemmings: winter reproduction and predation by weasels. *Arctic and Alpine Research* 6:1–12.
- Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. *Canadian Wildlife Service Report Series* 8:1–52.
- Mattson Jr., W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.
- McDonald, R. S., J. D. Roth, and F. B. Baldwin. 2017. Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the southern Arctic. *Polar Research* 36:5. <https://doi.org/10.1080/17518369.2017.1324652>
- McFadden, J. P., G. E. Liston, M. Sturm, R. A. Pielke, and F. S. Chapin. 2001. Interactions of shrubs and snow in arctic tundra: measurements and models. Pages 317–325 in A. J. Dolman, A. J. Hall, M. L. Kavvas, T. Oki, and J. W. Pomeroy, editors. *Soil-vegetation-atmosphere transfer schemes and*

- large-scale hydrological models. International Association of Hydrological Sciences, Wallingford, UK.
- McKendrick, J. D., G. O. Batzli, K. R. Everett, and J. C. Swanson. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research* 12:565–578.
- Millar, J. S. 2001. On reproduction in lemmings. *Ecoscience* 8:145–150.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Ohgushi, T. 2008. Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facilitative interactions. *Entomologia Experimentalis et Applicata* 128:217–229.
- Predavec, M., C. J. Krebs, K. Danell, and R. Hyndman. 2001. Cycles and synchrony in the Collared Lemming (*Dicrostonyx groenlandicus*) in Arctic North America. *Oecologia* 126:216–224.
- Pruitt Jr., W. O. 1970. Some ecological aspects of snow. Pages 83–99 in *Ecology of the Subarctic Regions: Proceedings of the Helsinki Symposium*. UNESCO, Paris, France.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ray, J. C. 2005. Large carnivorous animals as tools for conserving biodiversity: assumptions and uncertainties. Pages 34–55 in J. Ray, K. H. Redford, R. Steneck, and J. Berger, editors. *Large carnivores and the conservation of biodiversity*. Island Press, Washington, D.C., USA.
- Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, B. S. Gilbert, M. C.-Y. Leung, D. Duchesne, and E. Hofer. 2012. Lemming winter habitat choice: a snow-fencing experiment. *Oecologia* 168:935–946.
- Reid, D. G., and C. J. Krebs. 1996. Limitations to collared lemming population growth in winter. *Canadian Journal of Zoology* 74:1284–1291.
- Ritchie, J. C. 1957. The vegetation of northern Manitoba. II. A prairie on the Hudson Bay lowlands. *Ecology* 38:429–435.
- Rodgers, A. R., and M. C. Lewis. 1985. Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): food preferences. *Canadian Journal of Zoology* 63:1161–1173.
- Roth, J. D. 2002. Temporal variability in Arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia* 133:70–77.
- Roth, J. D. 2003. Variability in marine resources affects Arctic fox population dynamics. *Journal of Animal Ecology* 72:668–676.
- Schimel, J. P., C. Bilbrough, and J. M. Welker. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36:217–227.
- Schmitz, O. J., D. Hawlena, and G. C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters* 13:1199–1209.
- Scott, P. A. 1993. Relationship between the onset of winter and collared lemming abundance at Churchill, Manitoba, Canada: 1932–90. *Arctic* 46:293–296.
- Sittler, B. 1995. Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North East Greenland: preliminary results from a long-term study. *Annales Zoologici Fennici* 32:79–92.
- Smits, C. M. M., C. A. S. Smith, and B. G. Slough. 1988. Physical characteristics of Arctic fox (*Alopex lagopus*) dens in northern Yukon Territory, Canada. *Arctic* 41:12–16.
- Soulé, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. *BioScience* 55:168–176.
- Szor, G., D. Berteaux, and G. Gauthier. 2008. Finding the right home: Distribution of food resources and terrain characteristics influence selection of denning sites and reproductive dens in arctic foxes. *Polar Biology* 31:351–362.
- Tannerfeldt, M., A. Moehrensclager, and A. Angerbjörn. 2003. Den ecology of swift, kit and arctic foxes: a review. Pages 167–181 in M. A. Sovada and L. N. Carbyn, editors. *The Swift fox: ecology and conservation of swift foxes in a changing world*. Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, Canada.