Foxes facilitate other wildlife through ecosystem engineering activities on the Arctic tundra

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Abstract

Top predators largely affect ecosystems through trophic interactions, but they also can have indirect effects by altering nutrient dynamics and acting as ecosystem engineers. Arctic foxes (*Vulpes lagopus*) are ecosystem engineers that concentrate nutrients around their dens, creating biogeochemical hotspots with lush vegetation on the nutrient-limited tundra. Red foxes (*V. vulpes*) similarly engineer subarctic environments through their denning behavior, and have recently expanded onto the tundra where they now often occupy historically Arctic fox dens. We evaluated the impact of Arctic and red fox denning behavior on other tundra wildlife by comparing predator and herbivore visits to dens and adjacent control areas using camera traps in northeastern Manitoba, where both fox species are sympatric. Both the capture rates and species richness of wildlife were significantly greater at fox dens relative to control sites. Predators were detected almost exclusively on dens occupied by foxes, suggesting carcass or fox presence attracts predators to den sites. This is supported by observations of predators investigating and scavenging prey remains (carrion, feathers) from the dens. Caribou (*Rangifer tarandus*) visited dens more often than control areas, and we hypothesize they are attracted to the enhanced vegetation typically found on dens. Our results suggest Arctic fox ecosystem engineering has a prolonged, indirect effect on caribou by enriching vegetation at dens, whereas both Arctic and red foxes directly facilitate predators by provisioning resources. Understanding how predators affect other organisms via non-trophic interactions provides an enriched view of their functional roles within ecosystems.

Key words: Arctic fox, carrion, ecosystem functioning, nutrient cycling, red fox, scavenging

1. Introduction

Predators largely impact other organisms via trophic interactions, but their influence often extends beyond mechanisms such as predation and competition. Top predators can affect ecosystem nutrient dynamics by killing prey and redistributing the nutrients and energy across the landscape (Wilmers et al. 2003b, Bump et al. 2009, Schmitz et al. 2010). For example, brown bears *(Ursus arctos*) consume salmon (*Oncorhynchus* spp.) and transfer marine-derived nutrients to terrestrial habitats, increasing nitrogen concentrations in forest soils (Holtgrieve et al. 2009, Levi et al. 2020). Predators may also facilitate scavengers by providing carrion and other prey remains (e.g., feathers for nest-building material; DeVault et al. 2003, Pereira et al. 2013, Moleón and Sánchez-Zapata 2016, Prugh and Sivy 2020), an often-overlooked trophic interaction that can influence the spatial distribution and diversity of scavenger guilds (Wilmers et al. 2003a, Wilson and Wolkovich 2011, Barton et al. 2013, Moleón et al. 2014).

Organisms that influence the flow of energy and resources by physically modifying their environment are known as ecosystem engineers (Jones et al. 1994). Ecosystem engineers are

recognized as important facilitators of community assemblages by generally increasing species richness and diversity in their environments (Jones et al. 1997, Romero et al. 2014, Yeakel et al. 2020). Engineering via soil enrichment and nutrient cycling is particularly important in physically stressful ecosystems where nutrients are often limited, although it is less widely recognized as an engineering mechanism than structural modifications to the environment (Crain and Bertness 2006).

Arctic foxes (*Vulpes lagopus*) are top predators and prominent ecosystem engineers in tundra environments. They are important generalist predators on the tundra that can influence the reproductive success and population size of shorebirds (Robinson et al. 2014, McKinnon et al. 2014, Flemming et al. 2019), waterfowl (Bêty et al. 2001, Reiter and Andersen 2011, Nolet et al. 2013), and microtine rodents (Angerbjörn et al. 1999, Elmhagen et al. 2000, Ims and Fuglei 2005). Arctic foxes also influence tundra environments via non-trophic means through their denning behavior. Den sites are restricted in the tundra, leading Arctic foxes to use established dens for decades or longer (Macpherson 1969, Garrott et al. 1983). They also have the largest litters of any canid, likely a life history adaptation that evolved in response to fluctuating food resources (mainly microtine rodents) (Tannerfeldt and Angerbjörn 1996, 1998, Angerbjörn et al. 2004). Nutrient concentrations and vegetative production are therefore greater at dens than other areas on the tundra due to the large amounts of urine and excrement produced on site, repeated site disturbance from digging burrows, and the accumulation of prey remains from adult foxes provisioning pups (Smith et al. 1992, Gharajehdaghipour et al. 2016, Gharajehdaghipour and Roth 2018). By enriching den sites Arctic foxes indirectly alter the biomass and community composition of vegetation at dens (Bruun et al. 2005, Fafard et al. 2020). Ultimately, Arctic fox dens act as ecological hotspots in the nutrient-limited tundra that may influence other wildlife (Gharajehdaghipour and Roth 2018).

The combined effects of climate change and human-derived resource subsidies have facilitated the range expansion of red foxes (*V. vulpes*) onto the tundra (Sokolov et al. 2016, Elmhagen et al. 2017, Gallant et al. 2020). Red foxes are larger than Arctic foxes and can outcompete the latter species for food resources and denning sites (Tannerfeldt et al. 2002, Rodnikova et al. 2011, Gallant et al. 2014, Ims et al. 2017), although the degree to which the two ecologically similar predators compete seems to vary (Gallant et al. 2012). If red foxes do supplant Arctic foxes on the tundra, it is unclear whether they can replicate the functional role of Arctic foxes. But recent research from the subarctic has shown that, similar to Arctic foxes, red foxes can also act as ecosystem engineers by concentrating nutrients at frequently used den sites (Kucheravy et al. 2021, Lang et al. 2021). Thus, it seems plausible that tundra dens occupied by red foxes may have similar ecological impacts as those occupied by Arctic foxes.

To fully understand the functional role of foxes in tundra environments, their non-trophic effects on other organisms must be evaluated. Here, we used camera traps to evaluate how Arctic fox dens influence other wildlife (predators and herbivores) by comparing the frequency animals visited dens versus control areas on the tundra along the western coast of Hudson Bay, in

northeast Manitoba, Canada. We hypothesized that fox dens attract wildlife, and predicted other wildlife would be captured by camera traps at dens more often than adjacent control areas. We expected predators would be attracted to prey remains around dens actively occupied by foxes, while herbivores would be attracted to the lush vegetation on dens regardless of fox activity. Fox dens in this area were presumably first created and occupied only by Arctic foxes, and the ecosystem engineering influence on dens here have been previously attributed to Arctic foxes (Gharajehdaghipour et al. 2016, Gharajehdaghipour and Roth 2018, Fafard et al. 2020). However, red foxes have been observed using these Arctic fox dens in recent years (J.D. Roth, unpublished data, and this study), and may therefore also be responsible for some of the influence on other wildlife.

2. Materials and methods

2.1 Study area and study design

Our study occurred in Wapusk National Park, Manitoba, Canada, along the western Hudson Bay coastline, between June 1 and August 10 in 2015 and 2016. These dates correspond with the denning period for foxes in our study area. Fox dens in Wapusk are situated on elevated, well-drained beach ridges running parallel to the coast, separated by peat lowlands (Roth 2003).

Fox dens in our study area are long-lasting, prominent landscape features, and previous work has demonstrated that these dens have enriched vegetation relative to other areas along the beach ridges (Gharajehdaghipour et al. 2016, Fafard et al. 2020; Fig. 1, supplementary material Fig. S4). While both Arctic and red foxes have occupied tundra dens in recent years (including in this study), during the mid-1990s none of these dens were occupied by red foxes (Roth 2003). Due to the longevity of fox dens here (11/12 dens from this study were present in the 1990s), we attribute most of the enhanced vegetation at den sites to Arctic fox ecosystem engineering (Gharajehdaghipour et al. 2016, Gharajehdaghipour and Roth 2018, Fafard et al. 2020).

We used a paired study design to compare the frequency that animals were captured on camera traps between dens and control areas. We installed cameras onto the same 12 dens each summer (i.e., 2 deployments per den). A cased camera was secured on a steel post 1 m above the ground and placed 15 m from the den edge, allowing for maximum visual coverage of the den. We installed control camera traps 200 m away from each of the 12 dens on the same beach ridge that each den was located on, at a similar elevation, slope, and aspect as the den cameras. We considered 200 m a sufficient distance such that control cameras would not capture animals on their way to dens. Similar paired study designs were used in the previous studies of these fox dens that evaluated the ecological impacts of Arctic fox ecosystem engineering (Gharajehdaghipour et al. 2016, Gharajehdaghipour and Roth 2018, Fafard et al. 2020).

Three different camera trap models were used in this study (Table S1), but the same camera model was used at each paired site. Cameras were set in motion-detect mode with high

sensitivity, and captured a series of three pictures with 10 s interval. If a camera failed mid-deployment or was knocked over by a polar bear (*Ursus maritimus*), we truncated data from each site to the smaller coverage duration of the den or control camera. We retained sites that collected data from both cameras for >25 trap nights.

2.2 Image evaluation and cataloging behaviors

Animals captured by camera traps were identified to species. We considered events independent if >10 min elapsed between captures (Palmer et al. 2017), unless a different species was captured on camera. With the exception of caribou (*Rangifer tarandus*) herds foraging on den sites, almost all other capture events lasted <10 min. To evaluate whether animals were attracted to dens specifically, we excluded any events where the animal was present <1 min, unless the animal(s) was observed directly interacting with the den or control area (e.g., sniffing the ground, foraging; Fig. 2). The 1 min threshold was used to exclude animals captured on camera that were solely traveling through the camera's viewshed. We excluded any events if the animal(s) only interacted with the camera (see supplementary material, table S2).

For each event, we counted the maximum number of individuals observed within a single image. We counted all animals observed within the image, unless *all* animal(s) photographed were clearly not within the main focal area of the camera (e.g., caribou foraging in the background and not on a den). Several dens had tall vegetation that affected the visibility range of the camera (e.g., Fig. 2e), so we may not have detected all wildlife at den sites since the vegetation may have obstructed some animals. There is also considerable variation in the sizes of fox dens in Wapusk and some camera deployments were not able to capture the entire den within its viewshed. Consequently, our detection data across dens may be biased low compared to control areas that were unobstructed by vegetation.

We determined whether dens were 'active' or 'inactive' based on the frequency that foxes were captured on camera. Dens where foxes were photographed on the den at least once per ten trap nights were considered 'active'.

2.3 Statistical analysis

We evaluated our hypothesis that wildlife are attracted to fox dens by comparing capture rates at dens and control sites using generalized linear mixed-effects models implemented in the 'glmmTMB' package (Brooks et al. 2017) in R (R Core Team 2020). We compared (1) species richness, (2) number of all wildlife captures, (3) number of predator captures, and (4) number of herbivore captures between the paired den and control sites. To evaluate our hypothesis that predators are attracted to dens by fox activity while herbivores are unaffected, we compared (5) species richness, (6) number of predator captures, and (7) number of herbivore captures between active and inactive dens. We also evaluated whether capture rates differed for (8) avian and (9) mammalian predators between active/inactive dens. Each model was fit with either a negative binomial or Poisson distribution. We assessed model residuals using simulation diagnostic

methods from the 'DHARMa' package (Hartig 2020), and adjusted the distribution family only if model convergence or overdispersion issues occurred.

For each fitted model, the number of unique species or wildlife (i.e., total number of animals, not the number of events) captured during each deployment was the response variable, while year and treatment (den/control) or activity status (active/inactive) were fixed covariates. Year was included as a fixed, rather than random, effect because variance estimates of random effects can be imprecise with fewer than five levels (Harrison 2015, Harrison et al. 2018). Den ID was input as a random effect for all models. Paired den/control sites had the same camera model to account for detection biases. Although different camera trap models may be a confounding variable for the den activity analyses, we elected not to include camera model as a fixed effect due to the limited degrees of freedom within our models from our low sample sizes (generally recommended 5–10% of effective sample size; Burnham and Anderson 2002, Giudice et al. 2012, Fieberg and Johnson 2015). To control for variable sampling duration, we used the log of trap nights as an offset term in each model. We obtained coefficient estimates, standard errors, confidence intervals, Z-values, and *p*-values for each parameter using the 'summary' and 'confint' functions in R.

To understand whether herbivores were attracted to particular vegetation type(s) on fox dens, we conducted vegetation surveys on ten dens in 2015 and performed a correlational analysis on cover type and herbivore daily capture rates. Similarly, we evaluated whether a coarse index of carrion availability (number of prey items captured by cameras) could explain significant variation in predator capture rates at dens (details of these methods are in the supplementary material).

3. Results

3.1 Comparing wildlife visits between dens and control sites

We retained data from 16 paired den-control deployments (8 of 12 dens per year) to evaluate the influence of fox activity on wildlife capture rates. Among the 16 paired deployments, four dens collected sufficient data from both survey years (8 deployments), while the other eight dens collected sufficient data from both cameras for only one year (8 deployments). We detected four species (other than foxes) on control cameras, compared to 11 species detected on den cameras (Table 1).

Compared to control areas, dens were visited by more wildlife species (i.e., greater total species richness; $\beta_{den} = 0.647$, 95% confidence interval [CI]: [0.131, 1.162]), and a greater number of wildlife were likewise detected at dens ($\beta_{den} = 0.994$, 95% CI: [0.350, 1.638]) (Fig. 3a, b; supplementary material, Table S3). Dens were visited more often by both predators ($\beta_{den} = 3.638$, 95% CI: [1.652, 5.623]) and herbivores ($\beta_{den} = 0.83$, 95% CI: [0.146, 1.515]) than control areas (Fig. 3c, d). However, a post-hoc analysis revealed that the difference in herbivore visits

was driven by caribou (β_{den} = 0.850, 95% CI: [0.131, 1.569]), as goose visits did not differ between den and control sites (β_{den} = 0.743, 95% CI: [–1.861, 3.346]); supplementary material, table S3).

3.2 Comparing wildlife visits between active and inactive dens

We used data from 18 den camera deployments (10 from 2015, 8 from 2016) to compare species richness and wildlife capture rates between active and inactive dens (the two additional dens from 2015 had control cameras that did not collect sufficient data). Based on the frequency that foxes were detected on cameras, 6/18 dens were determined to be 'active'. Three of the six active dens were occupied by red foxes, and only three of the active dens produced pups (two Arctic fox dens, one red fox den); the other three active dens had adult foxes using the dens regularly but failed to produce pups. Despite no pups at these other three active dens, adult foxes were captured on camera bringing back prey remains to the dens. Only one den (E81) was active both years – by an adult red fox(es) in 2015, and Arctic fox adults and pups in 2016.

Active dens were visited by more wildlife species (i.e., greater species richness) than inactive dens ($\beta_{inactive}$ = –0.718, 95% CI: [–1.139, –0.296]). The total number of predators observed was greater at active dens, ($\beta_{inactive}$ = –2.556, 95% CI: [–3.584, –1.527]) (Fig. 4a, b), while herbivore visits did not differ between active and inactive dens ($\beta_{inactive}$ = –0.474, 95% CI: [–1.762, 0.815]). More avian ($\beta_{inactive}$ = –3.643, 95% CI: [–5.744, –1.543]) and mammalian ($\beta_{inactive}$ = –2.040, 95% CI: [–3.031, –1.342]) predators were detected at active dens compared to inactive dens (Fig. 4c, d; supplementary material, table S4). The random effect of 'den ID' was not influential (i.e., the variance and standard deviation of the random effect term was essentially 0) for all den activity models except for the model comparing the total number of predators between active and inactive dens.

Herbivore visits were unrelated to vegetation cover type at dens (supplementary material, table S5). Predator visits to dens were unrelated to the number of prey items captured on camera (supplementary material, table S6).

4. Discussion

Our paired camera trap study design demonstrated that the species richness and capture rates of wildlife were significantly greater at fox dens than adjacent control areas on the tundra (Fig. 3a, b). Despite our relatively low sampling effort, results from our study nonetheless clearly distinguish fox dens as hotspots of wildlife activity (e.g., 38 predators detected on dens vs. 1 on control cameras over the same sampling period; Table 1). The ecosystem engineering effects of Arctic, and likely red, foxes appear to not be limited to physical modifications of the environment, but also extend to facilitating and influencing the spatial distribution of other tundra wildlife by attracting them to dens. These other wildlife likely excrete waste during their

visits to dens as well, creating a positive feedback that may further enhance nutrient enrichment at den sites.

Predators were captured almost exclusively on dens actively occupied by foxes (Fig. 3d, 4b-d, Table 1), which appears to drive the difference in species richness between den/control areas, and active/inactive dens (Fig. 3a, 4a). Prey remains are often littered around active fox dens during the breeding season (Garrott et al. 1983, Roth 2003), and numerous predators were captured on camera scavenging or otherwise investigating prey remains (Fig. 2b-d). An alternative interpretation of these observations may be that the avian predators were removing feathers from these carcasses for nest building materials, as has been observed in other areas (Moleón and Sánchez-Zapata 2016). Given the observations from this study and elsewhere in the Arctic (Mallory 1987) of predators scavenging and removing prey remains from fox dens, we suggest foxes facilitate predators by provisioning carrion and other prey remains (e.g., feathers) to scavengers at a concentrated location. The lack of relationship between our coarse metric of carcass abundance and predator visits (supplementary material, table S6) was likely due to low sample size and the inability to capture the entire den within the camera's viewshed. Since fox dens are such long-lasting, prominent features on the landscape, predators may learn to associate dens with carcass availability and routinely check them for supplemental resources during summer.

Most of the predators we detected in this study have been documented to kill fox pups (e.g., Garrott and Eberhardt 1982, Chevallier et al. 2015), so it is also possible that predators may frequent fox dens for hunting opportunities. For instance, predation by eagles (*Aquila chrysaetos* and *Haliaeetus eucocephalus*) may be a substantial source of pup mortality (Garrott and Eberhardt 1982, Meijer et al. 2011). With only three dens producing pups in this study, we did not have a large enough sample size to evaluate whether predator captures were greater at dens with pups. Regardless, our results clearly demonstrate that predators consistently visit fox dens more often than adjacent tundra areas, and that fox denning activity serves as an attractant. Future studies evaluating the relative influence of the possible drivers of predator visits (carrion, feathers/non-food prey remains, hunting foxes) will be beneficial for understanding their attraction to fox dens.

Consistent with our prediction, herbivores visited fox dens more often than paired control areas (Fig. 3c). While caribou may frequent the elevated beach ridges where most dens are located to enhance predator detection or intercept the relatively strong winds that may reduce insect harassment (Hagemoen and Reimers 2002), caribou are more likely to visit fox dens than other areas on the beach ridges. Caribou are likely attracted to the greater biomass and nutrient content of vegetation typically found on dens (Fig. 1, supplementary material, Fig. S5; Gharajehdaghipour et al. 2016), with no clear interest in particular vegetation type(s). Thus, caribou visits to dens are likely driven by a combination of vigilance behavior and enhanced foraging opportunities. For geese, the risk of predation near dens may offset the nutritional benefits of the lush den vegetation. Due to the size disparity between foxes and caribou,

predation risk for caribou is presumably very low at dens, and is likely why we found no difference in herbivore visits between active and inactive dens.

Fox denning behavior appears to facilitate other wildlife by attracting them to dens through both immediate, direct, and prolonged, indirect pathways. The concentration of prey remains at dens, and perhaps the presence of foxes themselves, appears to have an immediate and direct effect on the spatial distribution and resource provisioning of tundra predators. Predators visited occupied dens of both Arctic and red foxes, suggesting den activity by both species may facilitate predators in a similar manner (although our small sample size precluded effective evaluation of this idea). While these behaviors attract predators in the short-term, they are also the ultimate mechanisms by which fox ecosystem engineering transforms den sites into ecological hotspots. The lush vegetation that grows on Arctic fox dens (Bruun et al. 2005, Gharajehdaghipour et al. 2016, Fafard et al. 2020) continues to indirectly affect the spatial distribution of caribou even if no foxes are present at the dens, demonstrating the long-term effects that fox ecosystem engineering has on other wildlife.

Arctic foxes in the southern Arctic are threatened with range contraction in response to the northward expansion of red foxes (Elmhagen et al. 2017, Gallant et al. 2020) and anthropogenic climate change (Verstege 2016). Our results suggest that the potential disappearance of Arctic foxes could affect other wildlife via reduced ecosystem engineering and resource provisioning. Although red foxes occupying tundra dens may influence predators similarly, we still do not know whether they can transform den sites via ecosystem engineering to the same degree. With fewer prey remains concentrated on dens (J.D. Roth, personal observation) and fewer foxes present (red foxes have smaller average litter sizes), nutrient deposition rates around red fox dens may be lower, which may ultimately impact the magnitude of their ecosystem engineering effects. Continued long-term monitoring of wildlife visits to fox dens may provide more comprehensive evaluations of the non-trophic effects of foxes on other wildlife, and information on how these relationships may vary alongside changes to Arctic and red fox presence on the tundra.

Although most research on predators focuses on trophic interactions (both consumptive and non-consumptive), there is growing recognition that predators impact ecosystem dynamics through important non-trophic pathways. For instance, similar to tundra fox dens, eagle nests are relatively large, long-lasting structures that act as localized biodiversity hotspots in forest environments (Maciorowski et al. 2020). As top predator populations continue to decline throughout many parts of the world (Estes et al. 2011), understanding the complex pathways they impact ecosystems is crucial for advancing the research, conservation, and management of their populations worldwide (Gable et al. 2020). Broadening research on predators to include thorough evaluations of their non-trophic effects provides us with a more holistic knowledge of their ecological role(s) that are integral to functional ecosystems.

Ethics

This study was conducted under Parks Canada research permit WAP-2013-13539.

Data accessibility

Data and R code available from the Dryad Digital Repository [39].

Authors' contributions

S.T.Z. and J.D.R. conceived, designed, and carried out the study. S.M.J-B. prepared and analyzed the data. S.T.Z. and S.M.J-B. wrote the manuscript, with input and revision from J.D.R. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests

The authors declare no competing interests.

Funding

Funding was provided by the Natural Sciences and Engineering Research Council of Canada, University of Manitoba Faculty of Science Fieldwork Support Program, Parks Canada, and the Churchill Northern Studies Centre (CNSC) Northern Research Fund.

Acknowledgements

The CNSC, Wapusk National Park, and Manitoba Conservation provided logistical support. We thank J. Verstege, C. Warret Rodrigues, and students in the University of Manitoba Arctic Field Ecology course in 2015 and 2016 for assistance. J. Verstege, J. Markham, and J. Detwiler provided comments and suggestions on previous drafts.

References

Angerbjörn, A., M. Tannerfeldt, and S. Erlinge. 1999. Predator-prey relationships: arctic foxes and lemmings. Journal of Animal Ecology 68:34–49.

Angerbjörn, A., P. Hersteinsson, and M. Tannerfeldt. 2004. Arctic foxes: Consequences of resource predictability in the Arctic fox—two life history strategies. Pages 163–172 *in* D. W.

Macdonald and C. Sillero-Zubiri, editors. The Biology and Conservation of Wild Canids. Oxford University Press, Oxford, UK.

Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–772.

Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388–400.

Brooks, M. E., K. Kristensen, K. J. V. Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Bruun, H., S. Österdahl, J. Moen, and A. Angerbjörn. 2005. Distinct patterns in alpine vegetation around dens of the Arctic fox. Ecography 28:81–87.

Bump, J. K., R. O. Peterson, and J. A. Vucetich. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159–3167.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag New York.

Chevallier, C., S. Lai, and D. Berteaux. 2015. Predation of arctic fox (*Vulpes lagopus*) pups by common ravens (*Corvus corax*). Polar Biology 39:1335–1341.

Crain, C. M., and M. D. Bertness. 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. BioScience 56:211–218.

DeVault, T. L., O. E. Rhodes Jr, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Elmhagen, B., D. Berteaux, R. M. Burgess, D. Ehrich, D. Gallant, H. Henttonen, R. A. Ims, S. T. Killengreen, J. Niemimaa, K. Norén, T. Ollila, A. Rodnikova, A. A. Sokolov, N. A. Sokolova, A. A. Stickney, and A. Angerbjörn. 2017. Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. Polar Research 36:sup1:3.

Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjörn. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. Journal of Zoology 251:139–149.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin,

A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic Downgrading of Planet Earth. Science 333:301–306.

Fafard, P. M., J. D. Roth, and J. H. Markham. 2020. Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. Journal of Vegetation Science 31:173–179.

Fieberg, J. R., and D. H. Johnson. 2015. MMI: Multimodel inference or models with management implications? The Journal of Wildlife Management 79:708–718.

Flemming, S. A., E. Nol, L. V. Kennedy, A. Bédard, M.-A. Giroux, and P. A. Smith. 2019. Spatio-temporal responses of predators to hyperabundant geese affect risk of predation for sympatric-nesting species. PLoS ONE 14:e0221727.

Gable, T. D., S. M. Johnson-Bice, A. T. Homkes, S. K. Windels, and J. K. Bump. 2020. Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. Science Advances 6:eabc5439.

Gallant, D., B. G. Slough, D. G. Reid, and D. Berteaux. 2012. Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. Polar Biology 35:1421–1431.

Gallant, D., D. G. Reid, B. G. Slough, and D. Berteaux. 2014. Natal den selection by sympatric arctic and red foxes on Herschel Island, Yukon, Canada. Polar Biology 37:333–345.

Gallant, D., N. Lecomte, and D. Berteaux. 2020. Disentangling the relative influences of global drivers of change in biodiversity: A study of the twentieth-century red fox expansion into the Canadian Arctic. Journal of Animal Ecology 89:565–576.

Garrott, R. A., and L. E. Eberhardt. 1982. Mortality of Arctic fox pups in northern Alaska. Journal of Mammalogy 63:173–174.

Garrott, R. A., L. E. Eberhardt, and W. C. Hanson. 1983. Arctic fox den identification and characteristics in northern Alaska. Canadian Journal of Zoology 61:423–426.

Gharajehdaghipour, T., and J. D. Roth. 2018. Predators attract prey through ecosystem engineering in the Arctic. Ecosphere 9:e02077.

Gharajehdaghipour, 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.

Giudice, J. H., J. R. Fieberg, and M. S. Lenarz. 2012. Spending degrees of freedom in a poor economy: A case study of building a sightability model for moose in northeastern Minnesota. The Journal of Wildlife Management 76:75–87.

Hagemoen, R. I. M., and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71:883–892.

Harrison, X. A. 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. PeerJ 3:e1114.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794.

Hartig, F. 2020. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models [R package version 0.3.2.0]. Comprehensive R Archive Network (CRAN).

Holtgrieve, G. W., D. E. Schindler, and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 24:1125–1135.

Ims, R. A., and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. BioScience 55:311–323.

Ims, R. A., S. T. Killengreen, D. Ehrich, Ø. Flagstad, S. Hamel, J.-A. Henden, I. Jensvoll, and N. G. Yoccoz. 2017. Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. Polar Research 36:sup1:8.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Kucheravy, C. E., J. D. Roth, and J. H. Markham. 2021. Red foxes increase reproductive output of white spruce in a non-mast year. Basic and Applied Ecology.

Lang, J. A., J. D. Roth, and J. H. Markham. 2021. Foxes fertilize the subarctic forest and modify vegetation through denning. Scientific Reports 11:3031.

Levi, T., G. V. Hilderbrand, M. D. Hocking, T. P. Quinn, K. S. White, M. S. Adams, J. B. Armstrong, A. P. Crupi, C. T. Darimont, W. Deacy, S. L. Gilbert, W. J. Ripple, Y. N. Shakeri, R. E. Wheat, and C. C. Wilmers. 2020. Community ecology and conservation of bear-salmon ecosystems. Frontiers in Ecology and Evolution 8:513304.

Maciorowski, G., Ł. Jankowiak, T. H. Sparks, M. Polakowski, and P. Tryjanowski. 2020. Biodiversity hotspots at a small scale: the importance of eagles' nests to many other animals. Ecology n/a:e03220.

Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series No. 8. Ottawa, CA. 52 pp.

Mallory, F. F. 1987. Foraging behavior and diet of lesser sandhill cranes in low arctic tundra near Eskimo Point, Northwest Territories, Canada. The Wilson Bulletin 99:495–496.

McKinnon, L., D. Berteaux, and J. Bêty. 2014. Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. The Auk 131:619–628.

Meijer, T., K. Norén, and A. Angerbjörn. 2011. The impact of maternal experience on post-weaning survival in an endangered arctic fox population. European Journal of Wildlife Research 57:549–553.

Moleón, M., and J. A. Sánchez-Zapata. 2016. Non-trophic functions of carcasses: from death to the nest. Frontiers in Ecology and the Environment 14:340–341.

Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donázar, and N. Owen Smith. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89:1042–1054.

Nolet, B. A., S. Bauer, N. Feige, Y. I. Kokorev, I. Y. Popov, and B. S. Ebbinge. 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. Journal of Animal Ecology 82:804–813.

Palmer, M. S., J. R. Fieberg, A. Swanson, M. Kosmala, and C. Packer. 2017. A “dynamic” landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecology Letters 20:1364–1373.

Pereira, L. M., N. Owen Smith, and M. Moleón. 2013. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review 44:44–55.

Prugh, L. R., and K. J. Sivy. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecology Letters 23:902–918.

R Core Team. 2020. R: a language and environment for statistical computing [Version 3.6.3]. R Foundation for Statistical Computing, Vienna, Austria.

Reiter, M. E., and D. E. Andersen. 2011. Arctic foxes, lemmings, and Canada Goose nest survival at Cape Churchill, Manitoba. The Wilson Journal of Ornithology 123:266–277.

Robinson, B. G., A. Franke, and A. E. Derocher. 2014. The Influence of Weather and Lemmings on Spatiotemporal Variation in the Abundance of Multiple Avian Guilds in the Arctic. PLoS ONE 9:e101495.

Rodnikova, A., R. A. Ims, A. Sokolov, G. Skogstad, V. Sokolov, V. Shtro, and E. Fuglei. 2011. Red fox takeover of arctic fox breeding den: an observation from Yamal Peninsula, Russia. Polar Biology 34:1609.

Romero, G. Q., T. Gonçalves-Souza, C. Vieira, and J. Koricheva. 2014. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. Biological Reviews 90:877–890.

Roth, J. D. 2003. Variability in marine resources affects arctic fox population dynamics. Journal of Animal Ecology 72:668–676.

Schmitz, O. J., D. Hawlena, and G. C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. Ecology Letters 13:1199–1209.

Smith, C. A. S., C. M. M. Smits, and B. G. Slough. 1992. Landform selection and soil modifications associated with Arctic fox (*Alopex lagopus*) den sites in Yukon Territory, Canada. Arctic and Alpine Research 24:324–328.

Sokolov, A. A., N. A. Sokolova, R. A. Ims, L. Brucker, and D. Ehrich. 2016. Emergent rainy winter warm spells may promote boreal predator expansion into the Arctic. Arctic 69:121–129.

Tannerfeldt, M., and A. Angerbjörn. 1996. Life history strategies in a fluctuating environment: establishment and reproductive success in the arctic fox. Ecography 19:209–220.

Tannerfeldt, M., and A. Angerbjörn. 1998. Fluctuating resources and the evolution of litter size in the Arctic fox. Oikos 83:545–559.

Tannerfeldt, M., B. Elmhagen, and A. Angerbjörn. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. Oecologia 132:213–220.

Verstege, J. S. 2016. Fox and lemming responses to climate and snow conditions at the Arctic's edge. M.Sc. Thesis. University of Manitoba, Winnipeg, MB.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003a. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996–1003.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003b. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909–916.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. Trends in Ecology & Evolution 26:129–135.

Yeakel, J. D., M. M. Pires, M. A. M. de Aguiar, J. L. O'Donnell, P. R. Guimarães Jr., D. Gravel, and T. Gross. 2020. Diverse interactions and ecosystem engineering can stabilize community assembly. Nature Communications 11:3307.

Figure 1. Aerial view of a fox den on the tundra in Wapusk National Park during summer. Note the comparably lush, tall vegetation at the den site relative to the surrounding landscape. The elevated beach ridge is also evident in the photo, running from the bottom left of the den up past the top right of it in the photo. We assume that fox dens on the tundra in Wapusk were initially created and occupied by only Arctic foxes, and thus attribute most of the distinct vegetative characteristics of dens to Arctic fox ecosystem engineering.

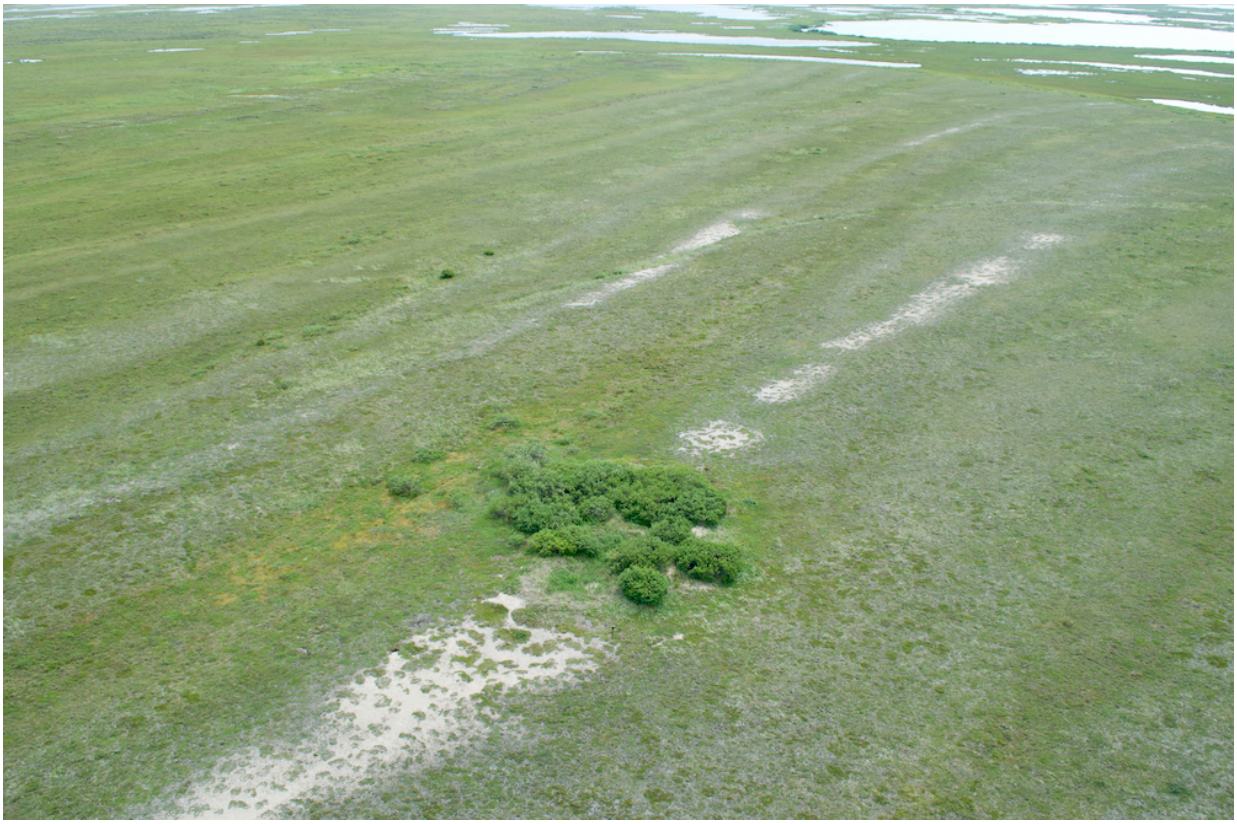


Figure 2. Images captured from cameras placed on dens. Panel (*a*) shows a polar bear (*Ursus maritimus*) leaving a den after interacting with an adult red fox (*Vulpes vulpes*) (tail and hind leg is visible behind the bear). Panel (*b*) shows a polar bear sniffing/investigating a goose carcass. Panels (*c,d*) shows a herring gull (*Larus argentatus*) and a raven (*Corvus corax*) removing prey remains/feathers from a den. Panels (*e,f*) show groups of caribou (*Rangifer tarandus*) foraging at fox dens.

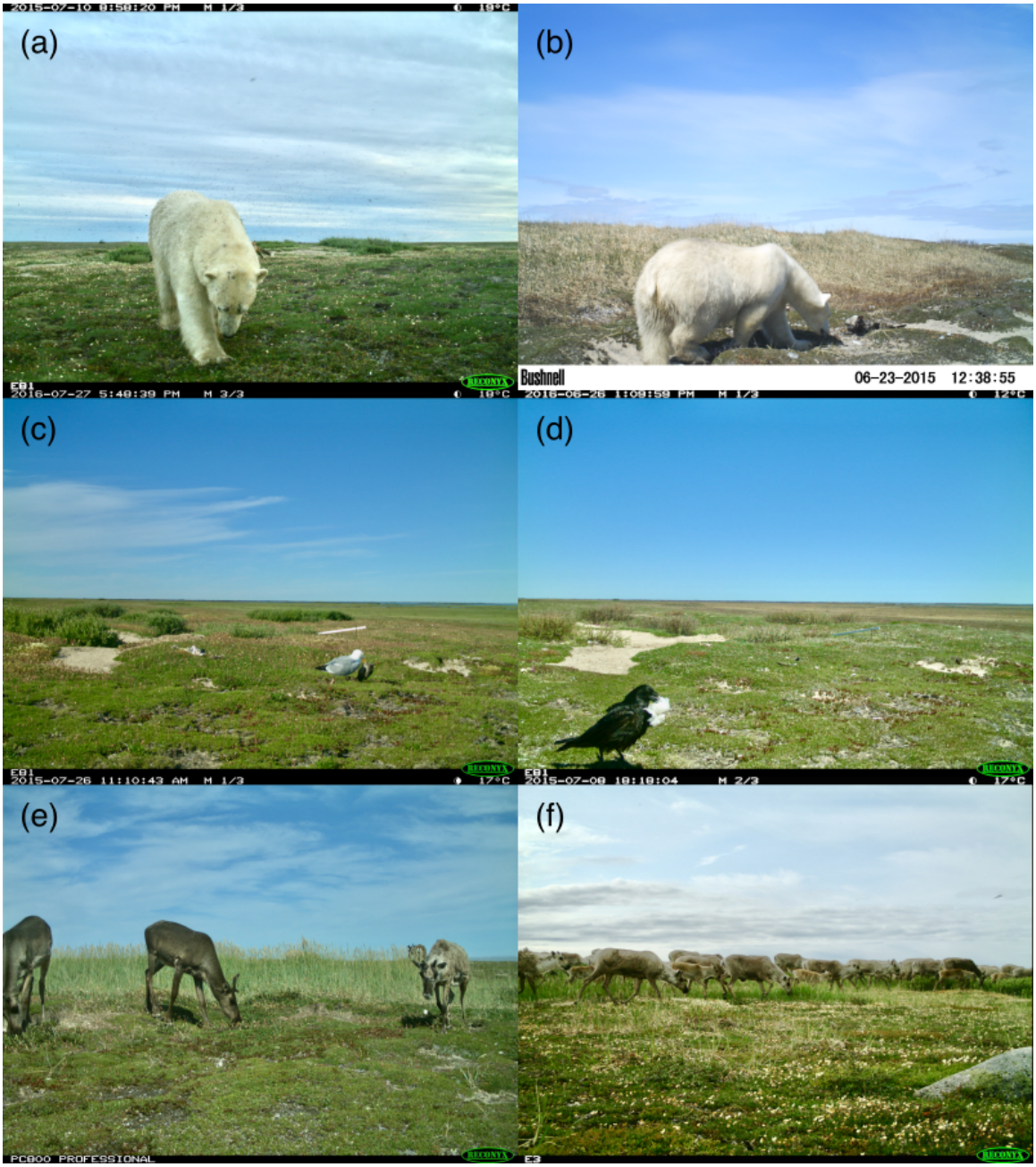


Figure 3. Species richness (*a*) and average daily capture rates (number of wildlife/trap night) of (*b*) all wildlife species, (*c*) herbivore species, and (*d*) predator species at fox dens and paired control sites (*p<0.05; **p<0.01).

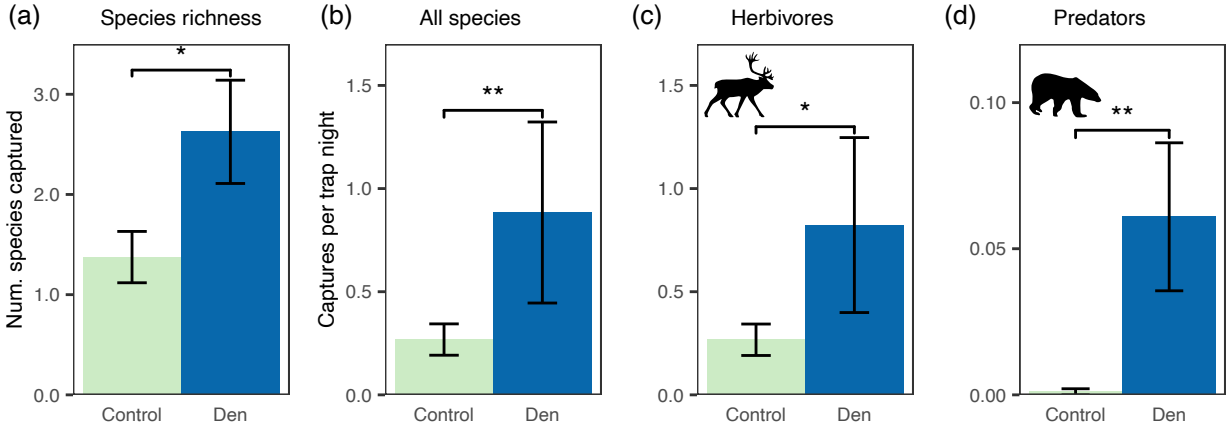
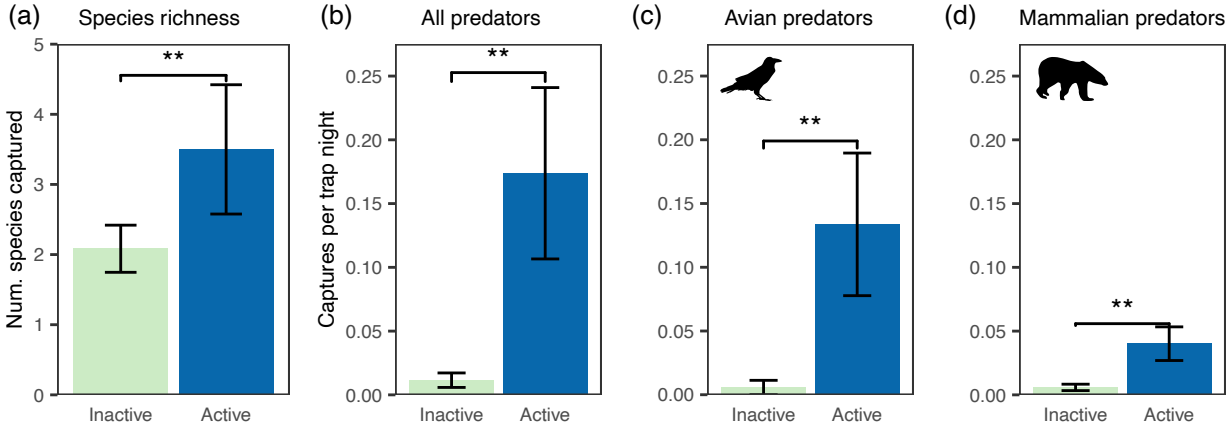


Figure 4. Total species richness (*a*) and average daily capture rates (number of wildlife/trap night) of (*b*) all predators, (*c*) avian predators, and (*d*) mammalian predators between active and inactive fox dens (**$p<0.01$).



531 Table 1. The number of captures by species on dens and paired control sites.

Species	**Category**	**Captures on control cameras**	**Captures on den cameras[1]**
Polar bear (*Ursus maritimus*)	Mammalian predator	0	7
Wolf (*Canis lupus*)	Mammalian predator	0	6
Grizzly bear (*Ursus arctos*)	Mammalian predator	0	1
Common raven (*Corvus corax*)	Avian predator	0	13
Sandhill crane (*Grus canadensis*)	Avian predator	0	7
[2]Eagle (*Aquila chrysaetos* or *Haliaeetus eucocephalus*)	Avian predator	1	2
Snowy owl (*Bubo scandiacus*)	Avian predator	0	1
Herring gull (*Larus argentatus*)	Avian predator	0	1
Caribou (*Rangiferus tarandus*)	Mammalian herbivore	109	269
Canada goose (*Branta canadensis*)	Avian herbivore	67	115
Snow goose (*Chen caerulescens*)	Avian herbivore	25	140

[1]Two Arctic hares (*Lepus arcticus*) were also detected on a den camera trap whose paired control camera failed.

[2]Observations of eagle species were lumped because it was difficult to distinguish juvenile golden eagles (*Aquila chrysaetos*) and bald eagles (*Haliaeetus eucocephalus*) from photographs.

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