The dynamic interaction between predator and prey drives mesopredator movement and foraging ecology

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Abstract
Prey availability is a fundamental driver of animal distribution, movement, and foraging ecology. The perceived risk of predation also influences these aspects of animal ecology. Our paper explores how animals balance these tradeoffs, which are seldom analyzed together. Such understanding becomes increasingly important as species that face anthropogenic-caused ecosystem change. In the Arctic, there has been substantial research on consequences of sea ice loss, however our understanding of top-down and bottom-up processes is limited. Ringed seals (*Pusa hispida*) and polar bears (*Ursus maritimus*), form a strong predator-prey relationship but limited information is available explaining how fear of polar bears affects ringed seal ecology. Using a large tracking dataset from 26 ringed seals with >70,000 dives and >10,000 locations, we explored the influence of top-down (polar bear space use based on >18,000 locations) and bottom-up (modeled fish distribution) processes on the movement, habitat selection, and foraging behavior of this mesopredator. Our results suggest that polar bears spatially restrict seal movements and reduce the amount of time they spend in area-restricted search and at depth, which likely decreases the seals' foraging success. However, we found tradeoffs between

predation risk and foraging, where ringed seals were more likely to be present and dive for a long duration in high-risk areas when prey diversity was high. Prey habitat use models that excluded predators overestimated core space use. These findings illustrate the dynamic tradeoffs that mesopredators are forced to make when balancing the risk of predation and need to forage.

Significance Statement

Our paper explores how animals balance finding food and avoiding predators. This balancing act is often poorly understood, particularly in Arctic ecosystems, but is necessary for understanding and conserving species. Our results show that interactions between polar bear presence and prey diversity explain the foraging behavior, habitat selection, and activity budgets of ringed seals. Seals constrained their movements to areas with low predation risk, but entered high-risk areas if prey diversity was high. Additionally, our inference on the relationship between ringed seals and their prey would be overlooked if the potential risk of polar bear predation was not included. Our study advances our understanding of the complex dynamics in predator-prey ecology, which is essential to incorporate when identifying critical habitat.

Introduction

Balancing demands to forage and avoid predators shapes the spatial distribution, behavior, and habitat use of animals (e.g., (1–3). Optimal foraging theory posits that prey will select areas with plentiful resources (4) and avoid regions where predation risk is high (e.g., the landscape of fear, (5)). In some cases, individuals will avoid areas of abundant resources due to the risk of predation, producing non-consumptive effects from foregone foraging opportunities (6). In addition to these spatial tradeoffs between predation risk and foraging resources, prey will also allocate time and energy to antipredator behaviors (e.g., vigilance) during – or in lieu of – foraging (2, 7). The influence of predation risk on foraging behaviors can have significant consequences for energetic gain and expenditure (6). Thus, it is critical to incorporate information on both predation risk and prey distribution when aiming to understand animal ecology and the space use and behavioral tradeoffs animals make between food and risk. Given the rapidly changing environmental conditions and increasing anthropogenic pressures on natural ecosystems (e.g., (8)), it is critical to understand predator-prey dynamics and their role in influencing habitat use and movement decisions of vulnerable species (9, 10).

Animal tracking is an essential and increasingly accessible tool to assess movement and behaviour, especially for wide-ranging or cryptic species (11–13) and the resulting data can be used to understand habitat selection, movement, and space use (14, 15). Further, as multi-species tracking studies become more common, these data provide an unprecedented opportunity for simultaneous assessment of top-down and bottom-up influences on species. Such studies have the potential to resolve longstanding uncertainties in animal ecology, where studies often focus on bottom-up processes only, which can cloud inference and may misrepresent space use patterns and metrics used to inform conservation efforts (e.g., identification of critical habitat).

Polar bears (*Ursus maritimus*) and ringed seals (*Pusa hispida*) form a strong predator-prey relationship (16) where polar bears are the main predator of ringed seals and ringed seals are the main prey of polar bears (e.g., (17)). Polar bears are likely to create a strong landscape of fear for seals according to the criteria of (18): 1) both species share a heterogeneous physical landscape associated with the sea ice, 2) polar bears use an ambush-style of hunting (i.e., “sit and wait”, (19)), and 3) ringed seals do not have morphological defenses (20). At the end of a dive, seals must return to the water’s surface to breathe through one of the multiple holes they

maintain in the sea ice. This surfacing provides opportunities for seals to breathe and provides polar bears the opportunity to capture seals from the sea ice (21). The sea ice is an important substrate for both ringed seals and polar bears; ringed seals also maintain haul-out lairs between the sea ice and snow which are accessible from the water and provide an opportunity for ringed seals to breathe and shelter from harsh weather conditions; but polar bears commonly capture seals in these lairs (21). Predators have previously been found to affect the diving patterns of sea ice-associated prey. For example, bowhead whale (*Balaena mysticetus*) dives were deeper and shorter when predation risk from killer whales was high (22). Similarly, we expect ringed seals to modify their diving behavior to mitigate the risk of polar bear predation.

Ringed seals and polar bears are both threatened by climate change due to their reliance on snow and sea ice, particularly for building birth lairs and foraging, respectively (23–25). Further, climate change has influenced lower trophic levels, where the prey (fish) regime for seals has undergone a shift in species composition, quality, and distribution across the Arctic that is projected to continue and accelerate (26–29). Simultaneously studying ringed seals, polar bear predation risk, and food resources is critical to understanding trophic relationships and subsequently for enabling effective conservation (9).

To explore how top-down and bottom-up processes may affect the habitat selection, activity budgets, foraging behavior, and predicted core-use areas of a mesopredator, we used satellite telemetry data from 26 ringed seals (over 70,000 dives and over 10,000 estimated locations) collected over three years (2010-2012) in eastern Hudson Bay, and combined this with modeled yearly prey (fish) biomass and diversity, daily estimates of predator space use derived from the movement data of 39 polar bears (over 18,000 locations) in the same study area, and daily sea ice concentration (Fig. 1). We assumed that polar bear use was proportional to perceived predation risk for ringed seals (18). We expected that because of the costs and benefits, ringed seals would avoid selecting and foraging in riskier areas, and instead use areas with low predation risk and high prey biomass and diversity. Further, we expected that there may be thresholds where abundant prey availability may outweigh high predation risk, or likewise, where high predation risk outweighs abundant prey availability. Additionally, we hypothesized that when predation risk was high, ringed seals would dive less frequently to reduce the number of ascents to the surface, ascend slower to allow for a cautious return to the surface, and shorten their dives to allow for time to return to an alternative breathing hole or haul-out lair if they detect a polar bear. Alternatively, we hypothesized that ringed seals would lengthen their dives when risk is high to reduce the required number of dives (and their surfacings) to reach stomach capacity (Fig. 2). Our study design and results advance our understanding of predator-mediated effects on foraging ecology using an understudied ecosystem and demonstrate how omitting predator effects when studying the space use and behavior of a mesopredator can distort ecological inference. Understanding the complex dynamics between trophic levels is fundamental for understanding animal ecology and of utmost importance for applied conservation efforts, such as identifying core habitat, especially for species facing rapid ecosystem changes.

Results

Ringed seal habitat selection, prediction maps, and movement. Our best-supported model describing ringed seal habitat selection included an interaction between polar bear relative use (hereafter referred to as polar bear use) and prey diversity (SI Appendix). As polar bear use

increased, the relative probability of ringed seal selection decreased, and for areas with high polar bear use, the relative probability of ringed seal selection was more likely if prey diversity was high (Fig. 3A, SI Appendix). We also found that ringed seal movement appeared to be constrained by high polar bear use (Movie S1). Additionally, this model indicated a positive relationship between ringed seal relative probability of selection and bathymetry and sea-ice concentration, where shallow areas and areas of high sea-ice concentration were associated with higher probability of selection by ringed seals (SI Appendix). Importantly, our best-supported model, which included top-down (polar bear), bottom-up (prey diversity), structural (bathymetry), and environmental (sea ice concentration) covariates, yields a prediction map that differs from the one predicted when top-down or bottom-up pressures are excluded from the best model (Fig. 4).

Polar bear use was a significant predictor of ringed seal move persistence (SI Appendix). We found that ringed seals spent more time in area-restricted search (low move-persistence) when in areas with low polar bear use, and more time traveling when in areas of high polar bear use (Fig. 3C,D). Additionally, area-restricted search behaviors were virtually absent when in areas with high polar bear use (Fig. 3C).

Ringed seal diving behavior. Our best-supported model for ringed seal dive duration included an interaction between polar bear use and prey diversity (SI Appendix). This model suggested that, as polar bear use increased, the duration of dives was more positively related to prey diversity (Fig. 3B). That is, when polar bear use was low, dive duration decreased with increasing prey diversity. However, under conditions of moderate polar bear use, dive duration increased with prey diversity. There was an even more drastic increase in dive duration with prey diversity when polar bear use was high (Fig. 3B). This model also included sea ice concentration and dive depth as significant covariates, where dives were shorter in areas of high sea ice concentration and longer when dives were deeper (SI Appendix).

We did not find the expected negative relationships between polar bear use and dive frequency or ascent speed; rather the best-supported models for these dive metrics did not include polar bear use as a covariate (SI Appendix). The best-supported model for dive frequency included positive estimates for prey diversity and dive depth and a negative estimate for sea ice concentration, and the best-supported model for dive ascent speed included a positive estimate for dive depth (SI Appendix).

Discussion

Our study explores the complex interactions between top-down and bottom-up processes that shape animal behavior and highlights the tradeoffs made by mesopredators under intense pressure from a specialized predator. Polar bears appear to create a landscape of fear for their primary prey, ringed seals, which affects their habitat selection, movement ecology, and diving behavior. These results show that polar bears affect ringed seals beyond their significant consumptive effects. Further, accounting for predators is a necessary consideration when examining the spatial ecology and behaviour of prey. Our results exemplify the consequences of overlooking top-down pressures in analyses of animal movement and behavior, where certain areas deemed as important may be overestimated due to the negative effects of predators.

As we predicted, and supported by theory (1, 30), the interaction between polar bear use and prey diversity suggests a higher probability of selection by seals in areas with low-risk and

high-prey diversity. We also found that ringed seals appear to select riskier areas when prey diversity was high, conforming with the hazardous duty pay hypothesis which suggests that prey balance fear and food and that areas that have plentiful resources afford sufficient fitness benefits or energetic returns to offset increased predation risk (6). In areas of low predation risk, we found dive duration was negatively related to prey diversity, but in areas of high risk, dive duration was positively related to prey diversity (Fig. 3). More generally, we found that ringed seals dove for a shorter duration when in high-risk areas, perhaps to allow for time to return to an alternative breathing hole or haul-out lair if they detected a polar bear. If we consider dive duration as a proxy for time spent foraging (e.g., (31)), our results may suggest implications for energetic gain imposed by perceived predation risk (e.g., (32)). Taken together, our results suggest that ringed seals maximize foraging opportunities when in high-risk areas if prey diversity is high (i.e., beyond a threshold of ~0.68, Fig. 3B).

Our movement models and activity budgets suggest that low move-persistent behaviors conclude or are avoided when risk is high. Low move-persistence may reflect area-restricted search and is often associated with foraging; however, it may also represent a composite of resident movement patterns including resting, sleeping, intraspecific interactions, or predator avoidance (e.g., (33–35)). Regardless of the specific behavior, low move-persistence is associated with residency, and our results show it to be explained by polar bear use. The reduction of area-restricted search and increase of directed movements (i.e., traveling) associated with increasing polar bear use suggests that animals reduce these residency behaviors and instead travel through areas of high risk. Thus, the top-down control appears to affect the activity budgets of ringed seals. These results further concur with our findings of tradeoffs in diving where polar bears are associated with reduced time spent foraging (i.e., dive duration). Taken together, such trait-mediated effects of polar bears on ringed seal movement and foraging behavior likely have demographic consequences for ringed seals. Specifically, these results suggest that ringed seals are likely traveling further to reach low risk or high reward sites and/or are foregoing foraging in areas that may have good, but not great, foraging payoff but have high risk. Any of these possibilities would reduce the average energy intake and increase the average energy expense of seals, leading to potential downstream effects on survival and reproduction (6). In extreme situations, ringed seals may become sufficiently undernourished to make riskier decisions, thus increasing mortality due to predation (36, 37).

Our study included both prey and predator modeled data in our ringed seal habitat selection, movement, and diving models, and the inclusion – or omission – of polar bear use in our models resulted in different ecological inference on the relationship between ringed seals and their prey. For example, if polar bear use was not included as an interacting term with prey diversity in our habitat selection or dive duration models against prey diversity, prey diversity would not be interpreted as an important variable (grey dashed line in Fig. 3A, B, and see (35)). This simpler model not only performed worse than the models that included polar bear use, but also overlooked the complex relationship between ringed seals, prey diversity, and polar bear use, which could lead to misleading inference (35). Once polar bear use was included as a covariate, the model revealed a possible predator-mediated relationship between ringed seals and their prey, demonstrating the importance of including top-down pressures when studying the ecological response of species to their prey and environment.

Prediction maps can serve as an invaluable resource for managers to protect species, especially in helping identify areas of conservation priority (e.g., protected areas, (12, 38). Here we show that if models do not adequately represent species' ecology, and the complex

interactions between top-down and bottom-up processes, the subsequent maps can be less effective. Excluding polar bear use from the model covariates resulted in prediction maps that overestimated the use of areas characterized as most important for ringed seals and delineated different locations of the study region (Fig. 4). Specifically, the prediction maps without polar bear use overestimated the probability of selection in the north-central regions of the study area, and instead delineated areas in the southern region (James Bay, Fig. 4). Given the extensive socio-economic challenges associated with creating protected areas and applying management policies (39), it is critical to provide the most accurate information (13) and thus incorporate these important complex dynamics.

Under widespread climate change and habitat alteration, insight into complex – and likely changing – trophic interactions is important for understanding how species' ecology may shift. For example, many species globally are suffering from reduced foraging success (40) and under the starvation-predation hypothesis, animals in poor body condition may forego anti-predator behaviors to focus on foraging (36, 37, 41). In other cases, the influx of new (or more common) predators may provide additional predation pressures (22, 42). The changing habitat and anthropogenic pressures may alter predator-prey relationships and movement(8); for example, the increase in roads and seismic lines have increased gray wolf (*Canis lupus*) predation on boreal caribou (*Rangifer tarandus caribou*, (43)). Further, large carnivores have undergone population declines globally (44), resulting in weakened landscapes of fear (45). In our system, both ringed seals and polar bears are vulnerable to climate-mediated reductions in sea-ice habitat (23, 24). The projected reductions in polar bear abundance may weaken the landscape of fear (e.g., as in the case of reduced Tasmanian Devils, *Sarcophilus harrisii*, (46)) and the expected increase in prey diversity (29) may increase foraging opportunities for seals. However, these benefits for ringed seal populations will likely be offset by the demographic consequences of reduced sea ice (25), and the predicted smaller body size and lower energetic value of prey (29). Polar bears have evolved as a specialized predator, and in response, ringed seals have evolved antipredator behaviors. Our observations of polar bear use explaining ringed seal habitat selection and dive duration may suggest that ringed seals have tactics of identifying high-risk areas. As reduced sea ice results in decreased polar bear population sizes, and increased access for other predators, such as killer whales (*Orcinus orca*, (47)), the usefulness of these antipredator tactics by seals is unknown. Further, reductions in the size of the foraging arena (i.e., sea ice extent) may inflate relative polar bear density in the interim, increasing top down pressures (48). Thus, our observations of reduced foraging behavior in high-risk areas may contribute to observed reductions in ringed seal body condition (25).

We expect ringed seals to avoid polar bears, but we also would expect polar bears to match ringed seal distribution (i.e., a positive relationship) through predator-prey evolution. We suggest that while ringed seals are an important food source for polar bears –especially females throughout the fall, winter, and spring– they are not the only source (e.g., (17)) and other seasonal prey distributions, as well as habitat requirements (e.g., adequate ice for travel and foraging) also likely drive the habitat use of polar bears (49). In other systems, low-risk areas are associated with areas that are not conducive to prey capture (e.g., (50, 51)). In our study, ringed seals may employ antipredator strategies in the early winter (mid-December thru mid-January) where they rely on open water (SI Appendix). Open water generally limits polar bear's movement and ability to successfully hunt seals (49, 52). Polar bears and ringed seals may play a dynamic game of cat and mouse where the "behavioral race" is dependent on the mobility and

response of both the predator and prey (53); future work should explore the lag effects between predation risk and mesopredator habitat selection.

Our models that included polar bear use performed well in our cross-validation exercise (SI Appendix) but are inherently subject to limitations that future work could further investigate. Further, ARGOS data are prone to error (54). We applied a state-space model (55), a class of model that has been shown to improve the location quality (56). However, newer tags (i.e., Fastloc-GPS, (56)) can provide finer-resolution and more accurate temporal and spatial data that could investigate smaller-scale patterns in movement and diving. Additionally, our prey and polar bear use data were modeled predictions and thus inherently represent a theoretical distribution of these species that may differ from empirical distributions. However, both approaches have performed well in validation exercises (29, 35, 57)(see SI Appendix). We acknowledge that our polar bear use variable was calculated using sea ice concentration and bathymetry as covariates, and that our models also included these covariates. We found no strong correlation between any of our covariates that were included in models together (SI Appendix). We did not find the hypothesized relationships between polar bear use and ringed seal dive frequency or ascent speed. Perhaps ringed seals can only detect cues of polar bear presence within the last few meters of ascent, and future work using more fine scale biologging tools (e.g., videologgers) could investigate dives at a resolution that would allow identification of such behavior. Finally, the polar bear use layers were generated using movement data from only female polar bears (SI Appendix) due to limitations in placing a collar on a male bear (their neck is wider than their head). However, male and female polar bears seem to have largely similar movement patterns (58) and sea ice habitat selection (59). Further, ringed seals generally contribute more to the diet composition of female than male polar bears (17) and thus female polar bears might impose more of a predation risk.

Predator avoidance is observed across many taxa (e.g., barnacle larvae *Semibalanus balanoides*: (60), northern elephant seals *Mirounga angustirostris:*(61), narwhal *Monodon monoceros;*(42)), however, combined top-down and bottom-up processes are seldom incorporated into the same models. Our findings fill knowledge gaps on the complex dynamics between predators and prey and advance our understanding of non-consumptive effects of predation. Simultaneously considering the influence of predator and prey is important for ecological inference and thus should be considered when modeling habitat use and selection, especially for critical habitat designation. In a time of rapid climate change, habitat degradation, and anthropogenic disturbance, properly directing conservation efforts by including top-down and bottom-up processes in habitat selection models for better understanding of animal ecology is of utmost importance.

Materials and Methods

Ringed seal transmitter deployment procedures. We captured, sampled, and tagged 26 ringed seals in August-October of 2010-2012 in eastern Hudson Bay near the coastline of the Belcher Islands, Nunavut, Canada (SI Appendix). We captured ringed seals using mesh monofilament nets set perpendicular to the shore in shallow water (<8 m depth). We equipped ringed seals with ARGOS satellite telemetry transmitters (9000x data loggers) from the Sea Mammal Research Unit (University of St. Andrews, UK) which recorded location and summary metrics for each dive.

Ringed seal location filtering and state-space modeling. ARGOS locations are prone to error (54, 55), thus we used a state-space model to predict locations that account for this error and used these predicted locations in all subsequent analyses. Specifically, we used the aniMotum R package (formerly foieGras; (55)) to fit a continuous-time correlated random walk state-space model that used irregularly sampled locations with error to produce predicted location data at a 2-hr interval. Before applying the model, we split tracks into multiple smaller segments when transmission halted for >12 hrs. The smaller segments were assigned a unique identification number. We removed tracks with <100 locations as these led to model convergence issues. The state-space model applied to this data (n = 16,719 raw locations) returned 10,022 predicted locations over a total of 877 seal days during the ice season (i.e., from autumn freeze-up [approx. early December] through spring break-up [approx. late June]).

Ringed seal dive data preparation. The tags also transmitted summarized metrics for each dive, including duration, maximum depth (herein "dive depth"), and five intermediate depth points for each dive along with the percentage of the duration elapsed since the beginning of the dive at each intermediate depth point. We calculated the ascent speed (meters per second) as the depth before the ascent divided by the duration from the last depth point to the end of the dive. We calculated dive frequency as the number of dives per seal per day. Each dive also had an associated date and time. We estimated the location of each dive by using the date and time of the dive and interpolating (in time and space) along the state space model-predicted movement track for each animal. There were 71,942 dives that were matched to the predicted movement locations for use in the dive analysis.

Polar bear collar deployment and relative use predictions. We captured and equipped 39 female polar bears with GPS collars in southern Hudson Bay between 2007 to 2013 (see SI Appendix for details). We estimated relative polar bear use by subsetting polar bear movement data within the defined study area (-82.0 to -76.0°W and 52.7 to 61.0°N) in the period between fall freeze-up and spring break-up for each year (n = 18,226 locations). We fitted resource selection functions using various combinations of daily sea ice, bathymetry, and distance to coast, where the final model was fitted using a Least Absolute Shrinkage and Selection Operator (LASSO) framework using the R package glmnet (57, 62). We predicted daily polar bear relative intensity of use (herein *polar bear use*) rasters for each day (63, 64), and used a spatial bilinear interpolation to match each ringed seal location and dive data with the corresponding value for polar bear use for the respective day (details in SI Appendix).

Prey base (fish) predictions. We used modeled ringed seal prey biomass data for three prey species that were shown to explain the movement ecology of Hudson Bay ringed seals (29, 35): Arctic cod (*Boreogadius saida*), capelin (*Mallotus villosus*), and northern sand lance (*Ammodytes dubius*). In addition, as ringed seal movement behavior was shown to be associated with prey diversity (35) we used a Simpson's Diversity Index (*D*, herein *"prey diversity"*) which included the eight most common ringed seal fish prey species: Arctic cod, capelin, northern sand lance, Pacific sand lance (*Ammodytes hexaoterus*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), shorthorn sculpin (*Myoxocephalus Scorpius*), mustache sculpin (*Triglops murrayi*), and rainbow smelt (*Osmerus mordax*). We calculated *D* as

$$D = 1 - \sum_{i=1} \left(\frac{B_{i,j}}{B_j}\right)^2 , \qquad \text{(eq. 1)}$$

where $n_{i,j}$ is the biomass of each species i in cell j, and N_j is the total biomass of all species in cell j, using the vegan package in R (65). (29) estimated prey biomass data using a dynamic bioclimate envelope model which used changes in ocean conditions to calculate changes in growth, population dynamics, habitat suitability, and movement for each species (separately) for each year from 1950 to 2100 on a 0.5 □ longitude by 0.5 □ latitude grid. We used the prey data that were modeled under a high-emission scenario (RCP 8.5) which aligns closely to emissions during our study period (similar to (35)). We matched each ringed seal location and dive with prey biomass and diversity using a spatial bilinear interpolation for the respective year.

Environmental data. We obtained daily sea ice concentration data (25 x 25 km resolution) from the National Snow and Ice Data Centre (NSIDC; www.nsidc.org) Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data satellites. We rasterized and extracted (using a bilinear interpolation in time and space) the sea ice concentration value associated with each ringed seal location and dive using the raster package in R (66). We obtained bathymetry data (0.01 □ resolution) for each ringed seal location and dive from the National Oceanic and Atmospheric Administration (NOAA) Environmental Research Division Data Access Program (ERDDAP) dataserver *etopo180* (67) using the rerddapXtracto package in R (68).

Modeling ringed seal habitat selection and move-persistence. We were interested in the potential effects of polar bears on ringed seal habitat selection within their home ranges and thus used a resource selection function (RSF, (69)). RSFs compare locations of an animal to locations deemed to be available for them (70, 71). We addressed the potential issue of pseudoreplication by thinning our dataset to one randomly selected predicted location per seal per day (71). While we focus on the results of this thinned data set, we show that an analysis on the full dataset of predicted ringed seal locations at a 2-hr time-step provides similar results in SI Appendix. The available locations consisted of a randomly generated set of locations (n = 25 per used location, (72)) within a minimum convex polygon developed using all locations with a 30-km buffer and clipped to exclude land. We determined the number of available points using a coefficient stabilization analysis, where we ran models with 1, 5, 10, 15, 20, and 25 available points per used location, and visually inspected at which number of available points the coefficient estimates stabilized (73). We then extracted sea ice concentration, polar bear use, and fish biomass and diversity for the corresponding date-times and locations. The RSF models the binary response (use/available) relative to the explanatory covariates (e.g., various combinations of sea ice concentration, polar bear use, and prey) using a logistic regression (a generalized linear model with a binomial distribution and logit link) that we fitted using the glmmTMB() function in the glmmTMB R package (74).

We ran RSFs with various combinations of polar bear use, sea ice concentration, and prey covariates to explore their ability to explain variation in ringed seal space use at the home-range scale. Our key objectives were to assess how polar bear use affects ringed seal habitat selection and behavior, thus, we used a model selection approach that considered only models that could help address this question and were ecologically relevant. First, since our prey metrics were correlated with each other, we determined which prey metric was most important at the home-range scale by fitting and ranking four models each with one single explanatory variable: biomass of Arctic cod, northern sand lance, capelin, or prey diversity. We used this “most important fish" metric to represent bottom-up influence in our subsequent analyses. Next, we fitted all combinations of sea ice concentration, best prey metric, and polar bear use, as well as

the interaction between best prey metric and polar bear use (n = 9 models). We also fitted a null model for comparison. All models (including the null) included bathymetry as a fixed effect to account for physical constraints in their diving behavior and thus access to prey.

We checked for correlation between covariates prior to modeling and found no signs of strong correlation (i.e., > 0.7, SI Appendix). We ranked models using Akaike's information criterion with small sample correction (AICc), where the model with the lowest AICc value was considered best. However, if another model was within two ΔAICc of the lowest AICc model and had fewer parameters, it was deemed more parsimonious and therefore "better".

We were also interested in the effects of polar bears and prey on ringed seal movement behavior. We fitted a move-persistence mixed-model on predicted ringed seal locations using the mpmm() function in the mpmm R package (75). The model provides an estimate of directional persistence along the movement tracks and is a continuous value between zero and one where lower values represent low directional persistence, likely associated with area-restricted search (e.g., residency behaviors including foraging and resting), and higher values represent high directional persistence, likely associated with traveling. We included polar bear use and prey diversity as covariates separately and together (n = 3 models). We also included bathymetry as a covariate in all models to account for structural constraints to their movement. We ranked these three models using AICc, as above. Our model formulations were limited to first-order terms as the mpmm package does not accommodate interactions.

Modeling ringed seal diving behavior. We investigated if ringed seal diving patterns were related to polar bear use, specifically focussing on three dive metrics: dive depth, duration, and ascent speed. We used linear mixed-effects models (LMM) to test the relationship between dive metrics and polar bear use using the glmmTMB() function in the glmmTMB R package. To reduce autocorrelation, we selected every 10th dive for each individual. Additionally, each model included a first order (AR1) autocorrelation structure to further account for the time-series nature of the dive observations. Similar to our RSF models, we fitted all combinations of sea ice concentration, best prey metric, and polar bear use, as well as the interaction between prey metric and polar bear use (n = 9 models per diving behavior). For consistency with the RSF methods, we used the same pre-selected prey metric. When modeling dive duration, ascent speed, and frequency, all of the above models also included dive depth to account for physiological limitations of diving (76). Finally, for each set of models, we fitted a null model for comparison with just a fixed effect for dive duration. All models included a random intercept term for ringed seal identification number to account for individual variation. We ranked models using AICc in the same approach outlined for the RSFs.

Data, Materials, and Code Availability. Fish data are available on Dryad at https://doi.org/10.5061/dryad.x69p8czjs. Ringed seal tracking data used in this study are available on MoveBank at https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study467037497.

Competing Interests. The authors declare that they have no competing interests.

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Figures

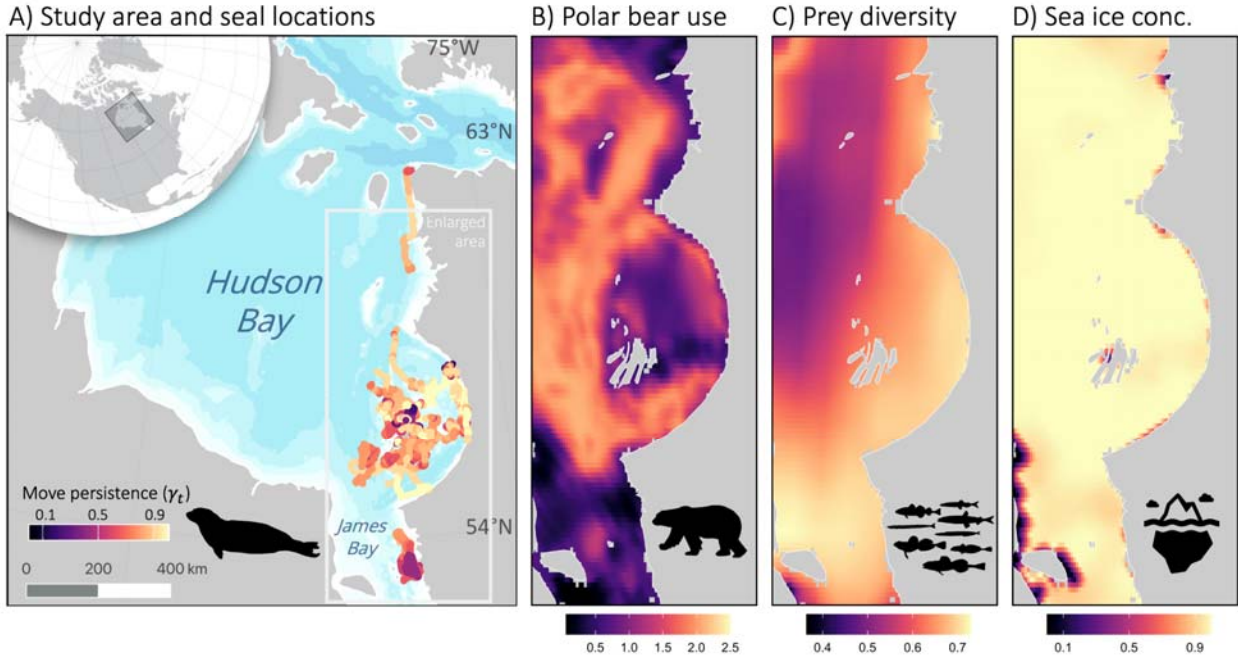


Figure 1. *Map of A) the study area with ringed seal predicted locations colored by estimated move persistence B), predicted polar bear use, C) estimated prey diversity (bilinearly interpolated at the scale of the polar bear use and sea ice resolution for visualization), and D) sea ice concentration in eastern Hudson Bay, Canada. Polar bear use and sea ice concentration are estimated daily; this is an example day, 15 February 2013. Prey data are estimated yearly; this is prey diversity in 2013. Presented ringed seal movement in (A) are for the full study period.*

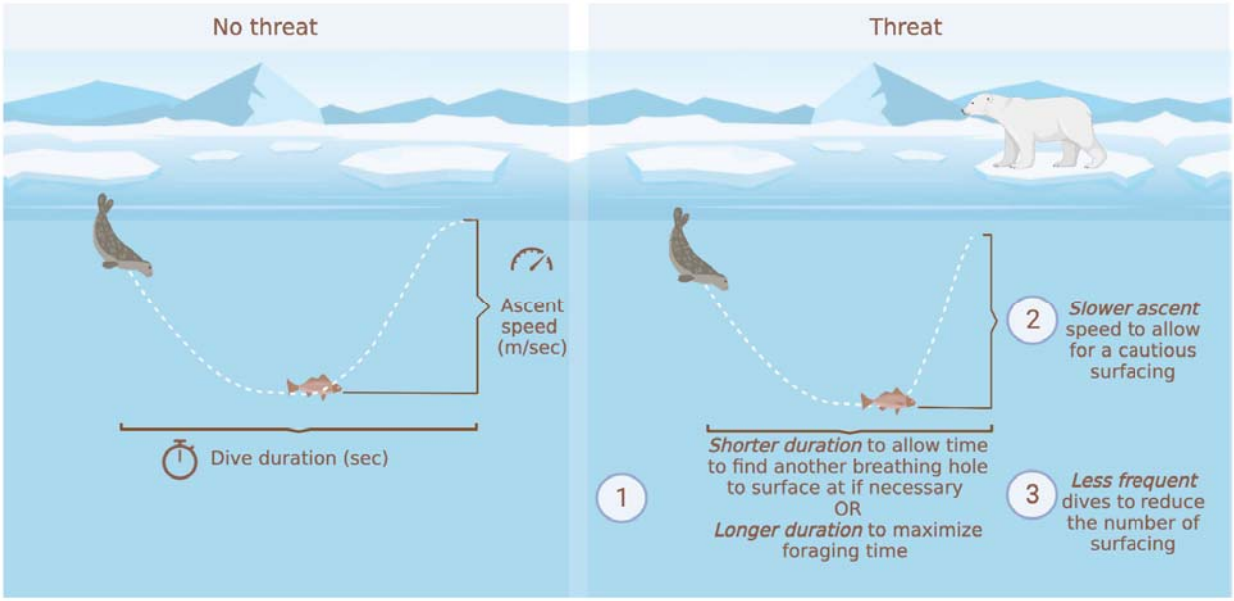


Figure 2. *Conceptual representation of three hypotheses for how perceived risk of polar bears at the surface may influence ringed seal diving behavior.*

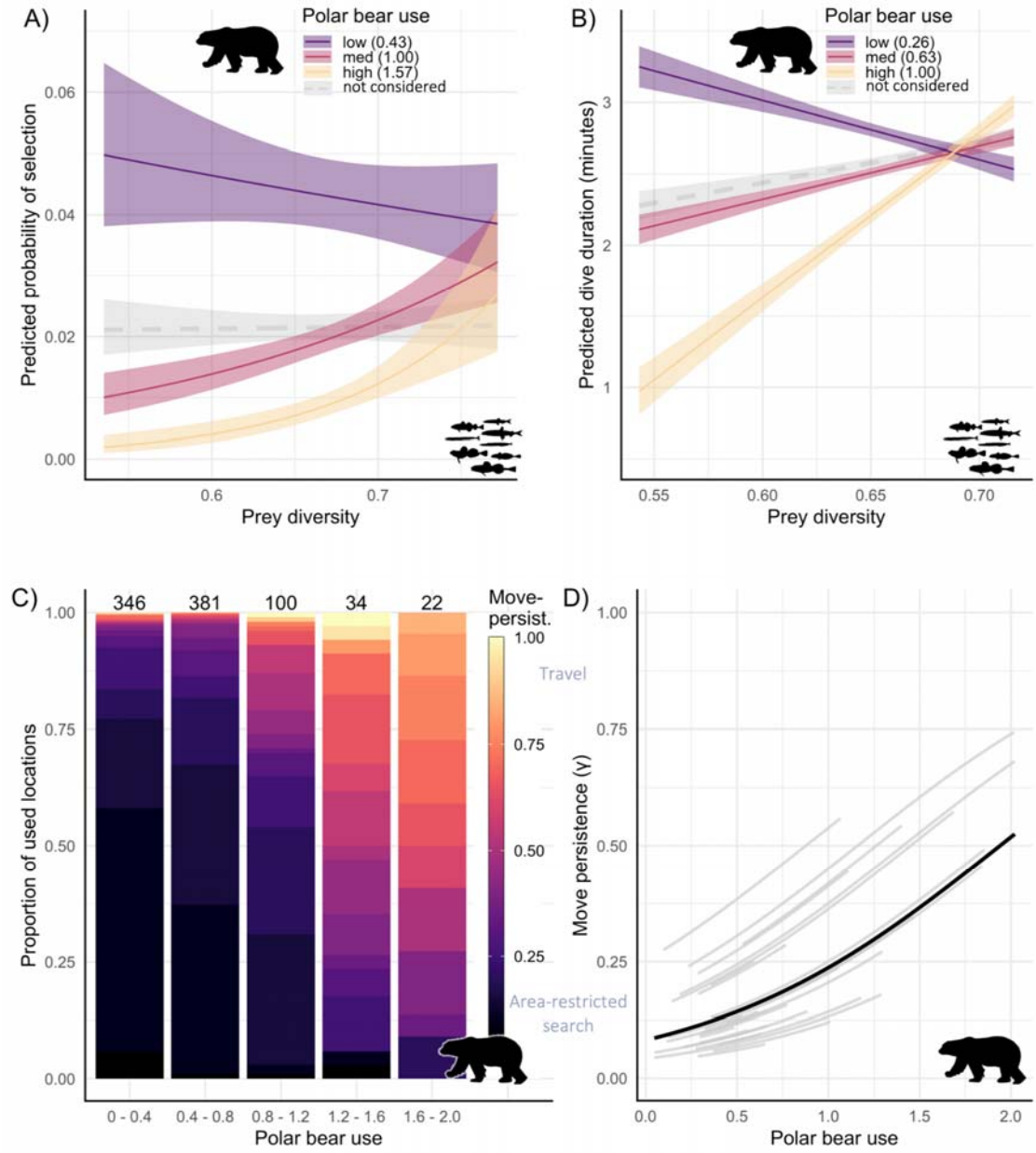


Figure 3. *Predicted ringed seal A) probability of habitat selection and B) dive duration as a function of the interaction between polar bear use and prey diversity; where the other covariates are held constant at their mean. Grey dashed line represents the model predictions where polar bear is excluded as a term in the model to highlight the insight that incorporating polar bear use provides. Shaded areas represent the 95% confidence intervals. C) Proportion of used locations of ringed seals (1 per seal per day) relative to polar bear use, grouped by predicted move persistence value. Move persistence values closer to zero are indicative of area-restricted search and values closer to one are indicative of travel. Polar bear use values are split into equal sized groups where the groups are delineated on the x-axis. Sample size is presented for each polar bear use group at the top of the bar. D) Results from the move persistence mixed model for fixed (black line) and random (individual seals, gray lines) effects.*

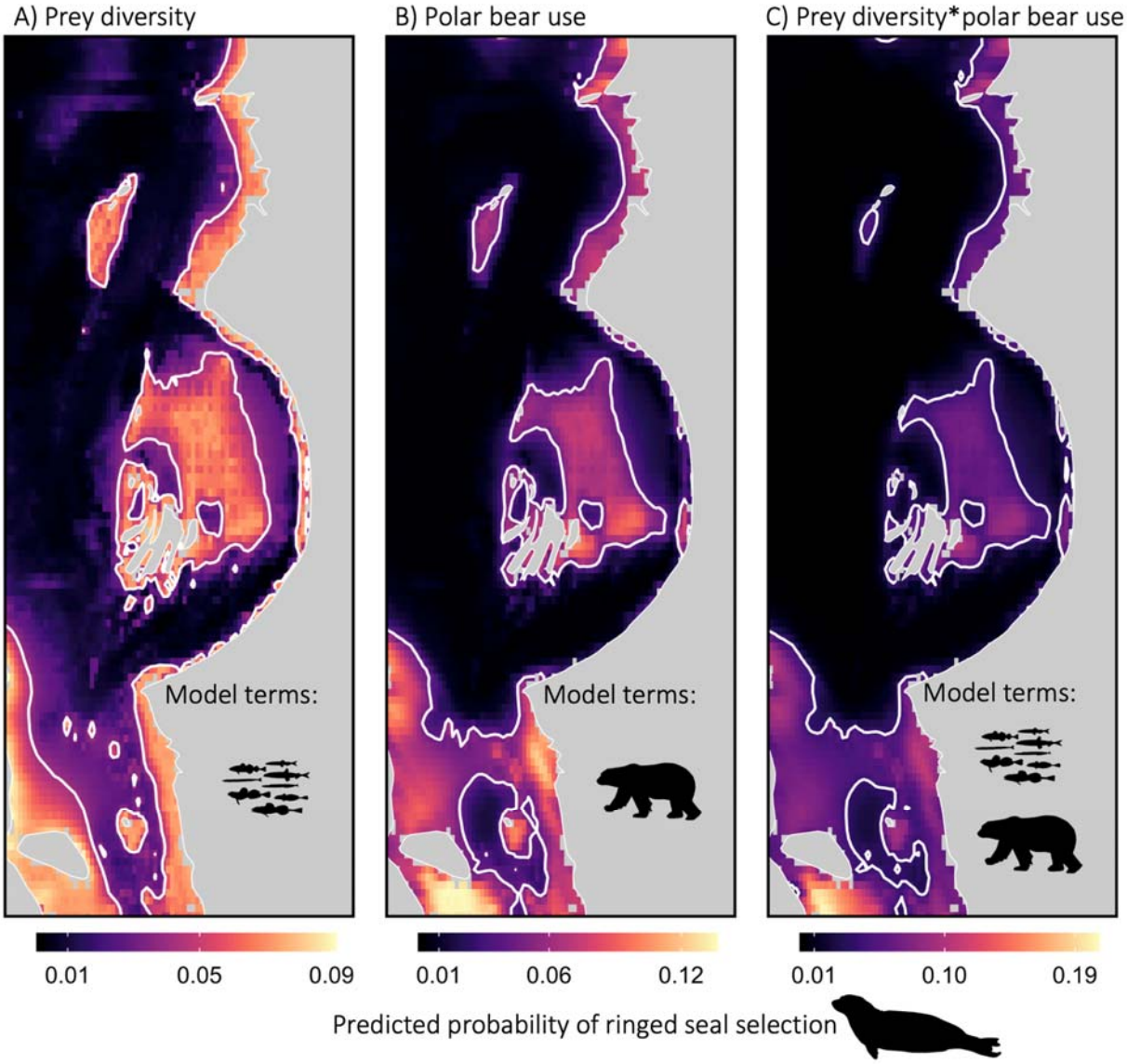
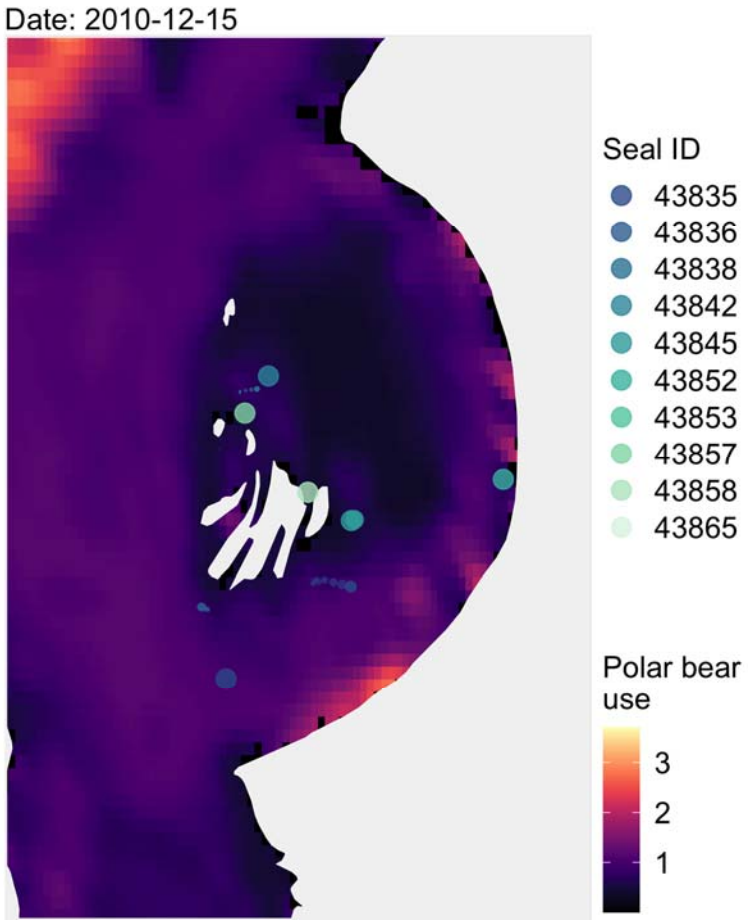


Fig 4. *Predicted ringed seal probability of selection from a model that included A) prey diversity, B) polar bear use, or C) the interaction between prey diversity and polar bear use (our best-supported model). Each model also included sea ice concentration and bathymetry as covariates. Covariates used to make predictions were taken for an example day, 15 February 2013. White contour lines delineate the 75% quantiles of predicted ringed seal selection probability for each panel.*



Movie S1. *State-space predicted movements of ten ringed seals (circles) relative to daily estimates of polar bear use from 15 December 2010 to 21 January 2011.*