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# Evidence for a survival-driven traveling wave in a keystone boreal predator population

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**Cyclical population dynamics are a common phenomenon in populations worldwide, yet the spatial organization of these cycles remains poorly understood. In this study, we investigated the spatial form and timing of a population collapse from 2018 to 2022 in Canada lynx (*Lynx canadensis*) across the northwest boreal forest. We analyzed survival, reproduction, and dispersal data from 143 individual global positioning system (GPS) collared lynx from populations across five study sites spanning interior Alaska to determine whether lynx displayed characteristics of a population wave following a concurrent wave in snowshoe hare (*Lepus americanus*) abundance. Reproductive rates declined across the study sites; however, site-level reproduction declined first in our easternmost study sites, supporting the idea of a population wave. Despite a clear increase in percent of dispersing lynx, there was no evidence of directional bias in dispersal following a hare population wave. Analysis did show increasingly poor survival for lynx dispersing to the east compared to combined resident and westward dispersal. This pattern is consistent with a survival-mediated population wave in lynx as the driver of the theorized population wave. The combination of these factors supports the idea of a hierarchical response to snowshoe hare population declines with a drop in lynx reproduction followed by increased dispersal, and finally reduced survival. All of this evidence is consistent with the expected characteristics of a population undergoing a traveling wave and supports the hypothesis that lynx presence may facilitate and mirror the underlying wave patterns in snowshoe hare.**

cyclic population | population wave | Canada lynx | snowshoe hare | dispersal

Traveling population waves are a commonly documented phenomenon across the world, arising as consumers take advantage of some abundant resource (1, 2). In the most general sense, these waves take a fairly intuitive shape, with a steep transition to high population density at the front of the wave, supported by an abundance of resources and lack of intraspecific competition. This peak is followed by a lower, more stable equilibrium population near carrying capacity dictated by lower resource abundance and increased competition (3). Such waves commonly form in the context of biological invasions, as a new species arrives in a region, sweeps through it, and eventually becomes a part of a stable ecological community (4). Although the specific mechanisms are more complicated, invasive waves are usually singular (the wave does not recur), as an ecosystem transitions from a species' absence to its presence in the community (4). By contrast, population waves can occur as a regular part of a stable cyclic population. Cyclical population dynamics are well documented throughout the world existing as limit cycles in a dynamic but stable ecosystem state (5–7). Cyclic populations can range from broadly synchronized to wave-like pulses across the landscape commonly referred to as a traveling waves (2, 8, 9). Relative to invasion waves, the dynamics of population waves as a part of cyclic population dynamics are less well understood, in that consumers already exist across the entire spatial domain through which the wave travels. Despite their commonality, much less is known about the spatial organization of such cycles. There are several hypotheses as to what governs synchrony in population dynamics including physical connectivity, consumer mobility, and large-scale weather patterns (10–13). Among these factors, weather tends to be locally correlated and influential regionally, whereas physical connectivity and predator mobility can affect the movement scale of the animals in question (14). Highly connected populations tend to be more synchronous, while highly mobile predators also facilitate synchrony even where populations are fragmented. In advection–diffusion analyses, traveling waves have been recreated in predator–prey

## Significance

Cyclic population dynamics are a common feature of ecological systems, but the spatial organization of these cycles is not well understood. Using an large scale dataset of Canada lynx populations in Alaska, this study provides empirical evidence of a westbound traveling population wave, with reproduction declining first in eastern regions and subsequent survival declines biased toward lynx dispersing against the direction of the wave. These findings align with theoretical models predicting that intermediate dispersal of mobile predators can facilitate the emergence and propagation of traveling waves in prey populations. This work significantly advances our fundamental theoretical understanding of how mobile consumers can influence and shape the complex spatial patterns observed in cyclic ecological systems.

The authors declare no competing interest.

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models with the inclusion of mobile specialist predators (15, 16). Predators capable of increasing synchrony among populations typically display long-distance dispersal, high reproductive capacity, and specialization in prey species. Specialized predators allow the boom and bust dynamics seen in traveling waves, as generalists tend to maintain more stable populations through prey switching, preventing peaks in any specific prey species (8, 15, 17). High reproductive capacity allows predators to rapidly take advantage of increases in prey density with subsequent population booms of their own (8). Critically, mathematical simulations of cyclically synchronous systems, indicate that predators must be able to disperse from the high population wave to areas of cyclic low, thereby extending the duration of the cyclic low (15).

As the iconic example of a cyclical predator–prey system, research on Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) harvest led to the discovery of a continent-wide population cycle (6). Recent research on broad-scale hare populations suggested that cycles in Northwestern North America take the form of a population wave emerging from central Canada and expanding outward to Western Alaska (17). One possible driver of this type of a wave-like pulse is the presence of lynx as a synchronizing force, with dispersal allowing lynx to track the wave as it progresses across the continent. Lynx populations could track a snowshoe hare population wave in one of two ways: Dispersing individuals may move to area of increased prey density through biased dispersal toward population peaks, or differential survival and reproduction locally could form a functional wave of population increase without a bias in dispersal direction. In this second instance, we would expect to see differential survival for lynx either following the direction of the wave or those traveling against the direction of the wave.

In Western North America, for example, lynx moving west would be moving in the direction of the population wave, and thus should experience relatively higher survival, while those moving east would be moving against the wave and into regions where prey population had already declined, and should experience lower survival. This pattern should be reversed as a new population wave begins in the east, likely inverting the survival differential. In this study, we examined the degree to which five collared lynx populations displayed characteristics of a traveling wave by analyzing survival, reproduction, and dispersal data across interior Alaska. Given the evidence of a traveling wave in snowshoe hare populations (17), we expected to see a similar traveling wave in lynx populations with a 1 to 2 y lag. Lynx possess a dispersal capacity of thousands of kilometers, so we predicted that the traveling wave of population increase will arise as a directionally biased dispersal toward areas of higher productivity (westward). Additionally, we expected that lynx reproductive output would follow a similar trend with decreasing reproduction as the hare wave passed through.

This research began during a population peak, occurring in ~2018, as evidenced by Alaskan statewide trapping records with peak harvest of 3,370 lynx in 2018 and declining to 817 lynx in 2022 (18). Additionally, hare abundance data from our study sites specifically are consistent with a westward population wave, as the southwestern study site (Tetlin) peaked 1 y earlier than the northernmost site (Wiseman) (Fig. 1). The following decline in snowshoe hare populations across the region, provided an opportunity to examine lynx population response in survival, reproduction, and dispersal to a rapid decline in prey abundance. Beyond this expected demographic response to declining prey, we can evaluate these data against the predicted characteristics of a predator–prey system exhibiting characteristics of a stable, cyclic population wave.

**Fig. 1.** Mean snowshoe hare pellets per plot (as an index for hare abundance) across Tetlin National Wildlife Refuge and Gates of the Arctic National Park (Wiseman). The bold black line represents average pellet count across all transects with lighter-colored lines as individuals transect at each site. Data collection stopped at many Tetlin NWR transect sites due to complications around the COVID-19 pandemic. Abundances peaked in 2017 at Tetlin and 2018 at Wiseman.

## Results

Between 2018 and 2022 we captured and collared 143 individual lynx (56 female and 87 males), providing 324 unique lynx/y with 64 total mortalities. These mortalities were not spread equally across years, with 7 mortalities in 107 individuals in the 2018 to 2019 y (survival of 0.94), 23 mortalities in 124 individuals in the 2019 to 2020 y (survival of 0.81), 29 mortalities in 70 individuals in the 2020 to 2021 y (survival of 0.59), and 5 mortalities in 25 individuals in the 2021 to 2022 y (survival of 0.8).

**Directional Dispersal.** The first objective of this analysis was to examine the degree to which dispersal movements were consistent with a traveling wave, with the expectation that dispersal would be biased west. We did see increasing dispersal rates as lynx populations declined with 28% dispersal in 2018 ($n = 106$), 35% in 2019 ($n = 124$), 41% in 2020 ($n = 69$), and 40% in 2021 ($n = 25$) (Table 1); however, our results do not show a clear bias in westward dispersal as movements appear to occur relatively equally in all directions (Fig. 3). There is some evidence for a bias toward longer distance movements toward the southeast, but this is explained by lack of westward land area constraining westward dispersal. One dispersal path leads to the northwestern coastline before doubling back and moving east. In this case, we believe that any bias in distance dispersed is an artifact of available space as opposed to behavioral choice (Fig. 2).

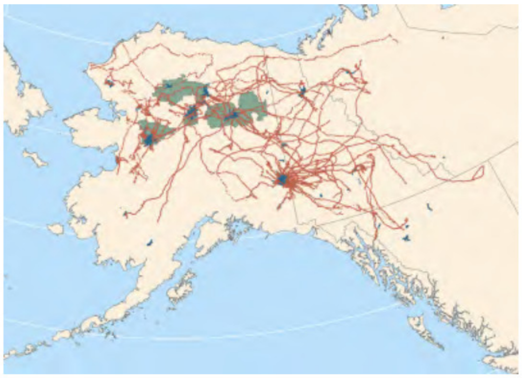

**Fig. 2.** GPS tracks of 141 collared lynx across the Northwest boreal region from 2018 to 2022. Data resulted in 325 individual lynx/y. Refuge boundaries are green regions on map.

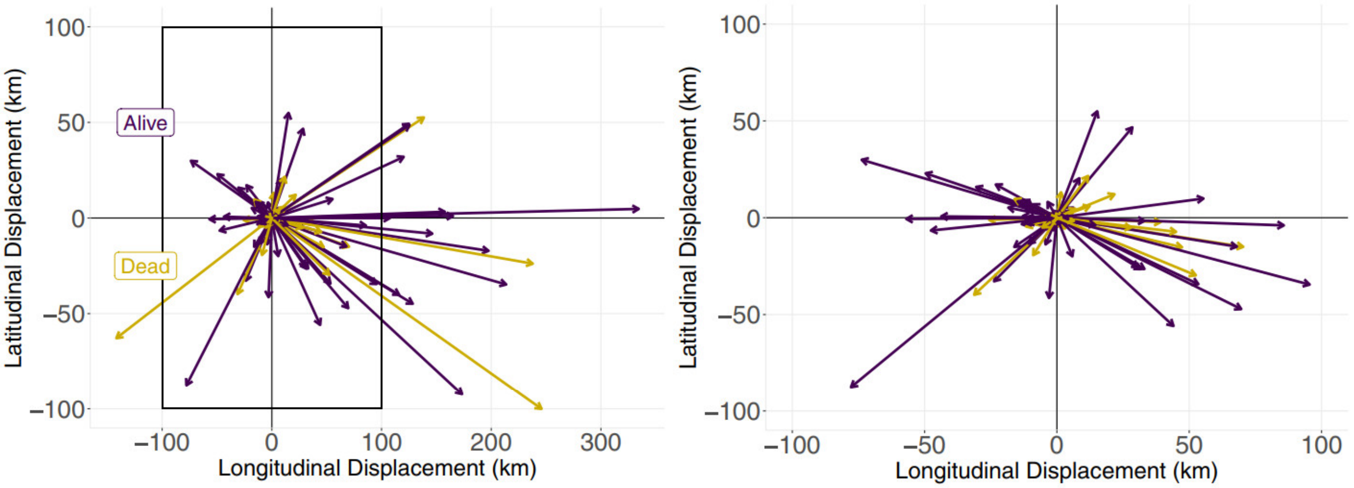

**Fig. 3.** Annual dispersal as a function of latitudinal and longitudinal displacement. Mortality status as yellow for dead and purple for alive. Zoomed-in panel (on the *Right*) displays fine-scale displacement in box indicated on the main (*Left*) panel. Tracks are colored by behavioral state.

**Reproduction.** Reproductive rates showed a clear decline over the course of the study from 2018 to 2022, declining from 89% (n = 19) in the summer of 2018 to 27% (n = 37) in 2019 to 0% in both 2020 (n = 28) and 2021 (n = 10) (Table 1). Despite the clear trend toward decreasing reproduction as populations declined, we detected a more nuanced picture of the decline when we examined reproduction on a site-specific level. During the 2018 breeding season, there was 75% reproduction at the easternmost and central study sites with full (100%) reproduction at the northern and western study sites. The following year there was no reproduction at the two easternmost sites, but ≥50% reproductive rate in the northern and westernmost study sites. Over the following two years (2020 and 2021), no collared females produced litters. These data are consistent with a westward traveling wave, with decreases in reproduction in response to declining hare densities (Fig. 4).

**Survival.** Model selection showed the highest support for two different baseline hazard functions; one for eastward dispersal and another for combined westward dispersal and resident lynx (Table 2), with parameter estimates in Table 3.

Overall lynx survival declined every year as the population decline progressed (Fig. 4). The decline in survival was, however, spread unequally across dispersal status, with eastward dispersing lynx faring increasingly poorly as the population decline progressed. The combined state of resident lynx and westward dispersing lynx had consistent survival patterns for the duration of this study after an initial survival decline. In addition to the differential survival patterns, we saw a delay in the effect of population declines between the reproductive and survival data. In the 2019 to 2020 reproductive data, we saw reproductive declines, at which point survival is similar for both of the dispersal behaviors. The following year was when we detected differences in survival across dispersal status.

**Table 1. Alaska-wide reproductive and dispersal rates by season**

| Year | Reproduction rate | Dispersal rate |
|---|---|---|
| 2018 to 2019 | 0.89 | 0.28 |
| 2019 to 2020 | 0.27 | 0.34 |
| 2020 to 2021 | 0 | 0.41 |
| 2021 to 2022 | 0 | 0.40 |

Reproduction ceased entirely in 2020 and onward, while dispersal rates increased from 2018 to 2021 and then leveled off near at 40%.

## Discussion

Given their complex and spatially broad nature, the majority of advancements in our understanding of traveling population waves have come from mathematical simulation (2, 3, 14, 16, 19, 20), with comparatively little field research on large spatial scales (21–23). At their inception, these mathematical simulations were one dimensional, partial differential equations that greatly simplified natural systems in order to infer the drivers of population waves (1). Building on these models, mathematicians have been able to extend these theories to include multispecies systems, two-dimensional spatial domains, and leptokurtic distributions which more appropriately align these theoretical models with biological systems (19, 24, 25). Multispecies models of predator–prey systems specifically have advanced our understanding of predator's role in mediating periodic traveling waves through dispersal capacity and reproductive rates (8, 15, 26). In this analysis, we aimed to examine the degree to which our empirical analyses supported the predictions of such multispecies predator–prey models.

These results provide support for the hypothesis that lynx populations move in wave-like pulses westward across Alaska following similar patterns in snowshoe hare abundance. Our survival and dispersal data are consistent with a traveling wave resulting from directionally biased survival as opposed to directionally biased dispersal. The lack of directional dispersal bias makes evolutionary sense as the location of the snowshoe hare peak will change over the course of a cycle (move from east to west), and this inconsistent difference in directional survival prevents evolution of a directional biased in dispersal. As snowshoe hare population waves begin in central North America, lynx in Alaska that disperse east would be able to take advantage of improving conditions by arriving at the wave before it had reached Alaska. Unfortunately, our data did not cover this period of the cycle, so we are not able to test these predictions. Given that any given location may be east, west, or coincident with the peak depending upon the phase of the wave, there could be no consistent selection for directional preference in dispersal.

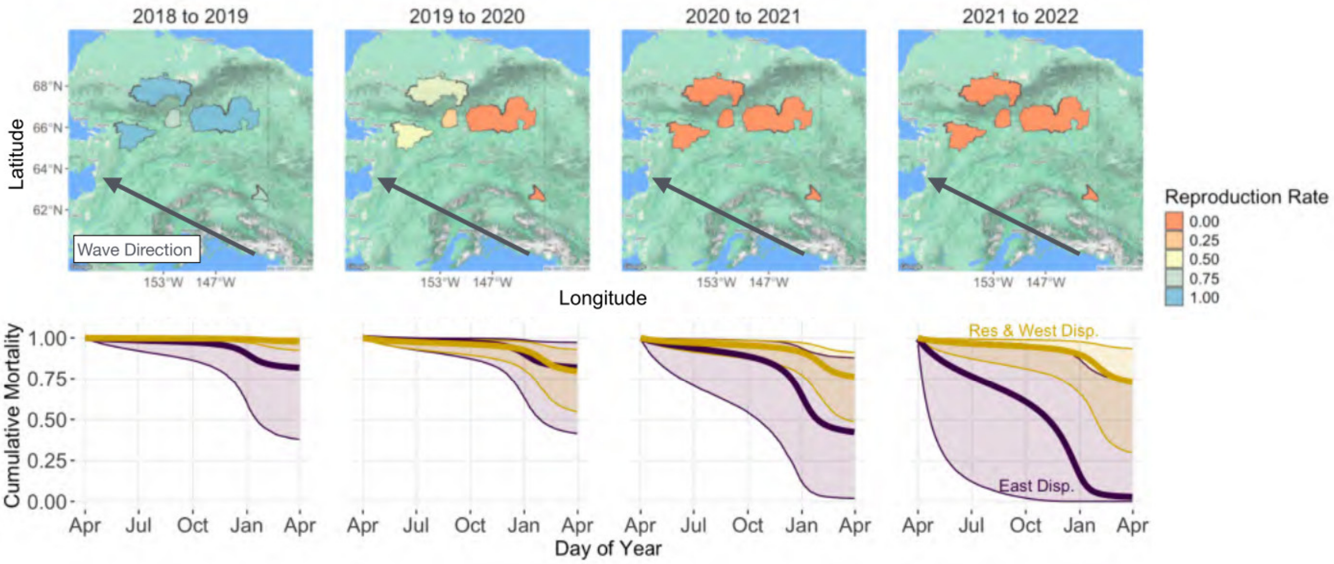

**Fig. 4.** Cumulative survival estimated for eastward dispersing individuals (yellow) and combined westward dispersing and resident lynx (purple). Daily survival decreases dramatically for eastward dispersing lynx specifically, with the trend resulting in complete mortality for eastward dispersal by the 2021 to 2022 y. Reproduction (colored scaled by site level reproductive rate) declined one year before survival indicating that cessation of reproduction is the first response to declining prey resources, followed by directionally biased declines in survival.

In addition to following the snowshoe hare wave, the dispersal and survival results are consistent with the hypothesis that the presence of lynx on the landscape may actually facilitate the development of the snowshoe hare population wave itself (17). In several diffusion-based mathematical models, researchers were able to simulate traveling waves of population growth only when predator dispersal was parameterized at certain intermediate levels (15). At low levels of dispersal, populations fluctuated independently, while at high levels, the population was completely in phase across the entirety of the domain. Intermediate levels of dispersal allowed predators to suppress populations in low areas, thereby extending cyclic lows (21). In our movement data, there were several instances of lynx moving from areas of relatively higher prey density eastward where prey density had likely already declined, a necessary result for a predator-driven traveling wave in prey. This dispersal result, combined with the relatively consistent survival of resident lynx, creates a scenario in which lynx are likely prolonging the low phase of the cycle. Although our study was not structured to address whether lynx dynamics are facilitating a traveling wave in snowshoe hare, our results are consistent with each characteristic necessary for predators to create traveling waves under theoretical mathematical models.

Beyond the traveling wave, these results also provide insights into hierarchical demographic response to declining prey resources. Declines in reproductive rates were already observed during the 2018 to 2019 season at the easternmost site, likely a result of a concurrent decline in prey density. Similar trends in survival were not observed until the 2020 to 2021 season. Lynx appear to forgo reproduction as a first response to declining resource

**Table 2. ΔWAIC values for candidate survival models for each dispersal status**

| Model structure | WAIC | ΔWAIC |
|---|---|---|
| $h_0(t\|\gamma,\mu,\rho) \sim east\_disp, y_i \sim year$ | 959.20 | 0.00 |
| $h_0(t\|\gamma,\mu,\rho) \sim dispersal, y_i \sim year$ | 961.42 | 2.22 |
| $h_0(t\|\gamma,\mu,\rho) \sim direction\_disp, y_i \sim year$ | 968.11 | 8.91 |
| $h_0(t\|\gamma,\mu,\rho) \sim 1, y_i \sim sex + year$ | 982 | 22.8 |
| $h_0(t\|\gamma,\mu,\rho) \sim dispersal, y_i \sim 1$ | 999.05 | 39.85 |
| $h_0(t\|\gamma,\mu,\rho) \sim 1, y_i \sim dispersal$ | 1,002.43 | 43.23 |
| $h_0(t\|\gamma,\mu,\rho) \sim sex, y_i \sim year$ | 1,008.81 | 49.58 |
| $h_0(t\|\gamma,\mu,\rho) \sim 1, y_i \sim year$ | 1,010.38 | 51.18 |
| $h_0(t\|\gamma,\mu,\rho) \sim 1$ | 1,012.92 | 53.72 |
| $h_0(t\|\gamma,\mu,\rho) \sim age, y_i \sim 1$ | 1,015.73 | 56.53 |
| $h_0(t\|\gamma,\mu,\rho) \sim sex, y_i \sim 1$ | 1,025.35 | 66.15 |

Model selection results with years ranging from April 1 to March 31 of the following year. Covariates may serve as predictors for the underlying hazard or as predictors for survival itself. All models included random effects of refuge and individual.

**Table 3. Coefficient estimates as mean of posterior distribution, SDs, and Bayesian credible intervals for all parameters**

Resident and westward dispersal

| Parameter | Mean | SD | Credible interval |
|---|---|---|---|
| $\mu$ | −0.88 | 1.23 | (−1.21, −0.64) |
| $\rho$ | 0.63 | 0.068 | (0.48, 0.75) |
| $\gamma$ | 0.00007 | 0.00006 | (0.000008, 0.0002) |
| $\beta_{seas\ 2}$ | 2.4 | 0.92 | (0.75, 4.4) |
| $\beta_{seas\ 3}$ | 2.58 | 0.95 | (0.87, 4.63) |
| $\beta_{seas\ 4}$ | 2.72 | 1.11 | (0.65, 5.03) |

Eastward dispersal

| Parameter | Mean | SD | Credible interval |
|---|---|---|---|
| $\mu$ | −1.33 | 0.21 | (−1.67, −0.84) |
| $\rho$ | 0.64 | 1.0 | (0.42, 0.82) |
| $\gamma$ | 0.0008 | 0.0007 | (0.00005, 0.003) |
| $\beta_{seas\ 2}$ | 0.021 | 1.16 | (−2.16, 2.41) |
| $\beta_{seas\ 3}$ | 1.5 | 1.21 | (−0.78, 4.04) |
| $\beta_{seas\ 4}$ | 2.91 | 1.45 | (0.01, 5.93) |

$\mu$, $\gamma$, and $\rho$ come from the wrapped Cauchy hazard function with seasonal $\beta$ coefficients as additive effects of each season. The first season is the reference level for that categorical coefficient with season 2 as 2019 to 2020, season 3 as 2020 to 2021, and season 4 as 2021 to 2022.

availability in an effort to maximize their own survival (27, 28). This strategy appears to be successful in mitigating survival declines for another year, at which point conditions begin to influence survival. Throughout the population decline, survival rates for residents and westward dispersers remained relatively stable with evidence for ∼20% survival decline following the first year, as the proportion of individuals dispersing increased. Given the cessation of reproduction, resident populations will still see declines even with relatively low mortality rates ($\leq$25%), as emigration rates exceeds 40%. These local population declines would then result mostly from emigration (and subsequent mortality during dispersal) (29) than mortalities in resident lynx. We suspect that a few dominant resident lynx may exclude subdominant lynx thus forcing dispersal. During periods of low snowshoe hare density, prey switching is a commonly documented phenomenon in lynx across North American. Diets can shift from almost exclusively hares during peak phase to largely alternative prey (red squirrels, grouse, ungulates, and scavenging) during a low (30). We hypothesize that subdominant lynx are typically younger, but given the difficulty in accurately aging lynx beyond their first year of life, any age-based model was not well supported.

These results imply a hierarchically shifting life history pattern that begins with reduced reproduction, followed by increased dispersal, and finally by directionally biased decreases in survival. This strategy underscores the need to conserve local populations in protected, high-quality refugia where some individuals will survive the population low, from which population expansions can occur following increases in prey population. Although not stable in the long term due to lack of reproduction, these resident populations decline at a much slower rate than dispersing populations, increasing the chances of persistence through a population low.

Here we provide empirical evidence, from a perspective based in individual movement and reproduction, of the underlying life history mechanisms driving the lynx-snowshoe hare wave in North America (17, 24, 31). Moving forward we hope to see further research into the dynamics governing population increases following a cyclic low, wherein we would expect to see the inverse of the trends observed here, with higher survival in the east followed by a spatially asynchronous increase in reproduction. Documentation of inverse trends during a population upswing would provide even further support for this hypothesis and provide overall stronger evidence of the mechanisms driving this traveling wave. Additionally extending the spatial scale of this research would provide more insights into the full spatial form of these cycles as well as information on where they originate.

## Materials and Methods

**Data Collection.** Lynx capture was conducted across five study sites spanning interior Alaska's boreal forest including Tetlin, Koyokuk, Yukon Flats, and Kanuti National Wildlife Refuges and Gates of the Arctic National Park (Fig. 5). National Wildlife Refuge (NWR) lands were located in boreal forest lowlands characterized by low relief stretches of mixed coniferous and deciduous forest with intermittent wetlands. Capture efforts near Gates of the Arctic National Park were conducted out of Wiseman (just outside park boundaries) located in the Brooks Range (and thus, this site was much more topographically variable). Although lynx harvest is legal at all study sites, Gates of the Arctic was the only location with significant human-caused mortality as the remote nature of the NWR sites precluded any harvest mortality. Each site operated 1 to 3 traplines consisting of a mix of box traps and foot snares. Capture efforts took place between 2018 and 2022, which coincided with a lynx population high in 2018 and subsequent population decline over the following years.

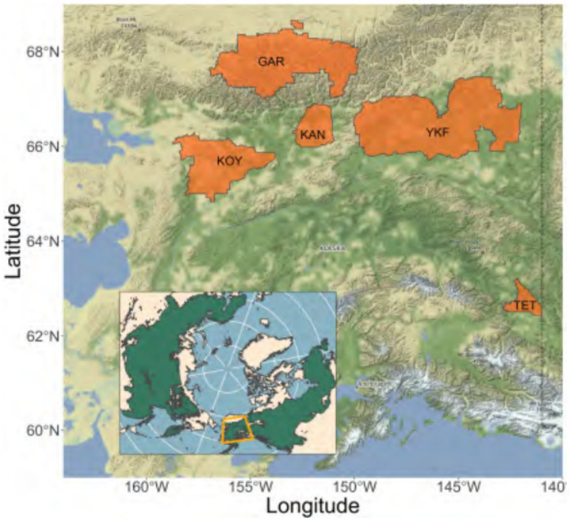

**Fig. 5.** Perimeters of five study sites [Tetlin (TET), Yukon Flats (YKF), Kanuti (KAN), Koyokuk (KOY) National Wildlife Refuges, and Gates of the Arctic National Park (GAR)] with location within global extent of boreal forest on inlaid map.

Snowshoe hare pellet data were collected at ∼8 transects from the Tetlin study site and ∼7 transects from the Wiseman site. Each transect consisted of 50 quadrats. At each quadrat, pellets were counted along a 2-inch wide strip and removed to prevent double counting between years. Due to complications with the COVID-19 pandemic hare pellet data collection stopped during the 2020 season. Since snowshoe hare pellets build up over a year, pellet counts are a lagging abundance index of the prior year, thus data end during the 2019 season for some Tetlin transects.

Captured lynx were fitted with Telonics TGW-4277-4 Argos/GPS collars (∼200 g) programmed to 4 h fix rates. At this sampling rate, the collar batteries were able to last ∼1 to 2 y. Argos satellite uplink allowed data collection without recapture. Juvenile lynx were fitted with collars modified with foam inserts to allow future growth. Lynx were aged based on morphometrics collected during capture including mass, ear tuft length, girth, and hind foot length, along with presence of a family group. Using these measures, we were only able to classify lynx of one year old or less as juveniles with all other lynx categorized as adults.

Mortality data were collected by the onboard accelerometers which transmitted a mortality signal after 10 consecutive hours of collar inactivity. Given the vast study area and distances traveled by collared individuals, we were unable to investigate every mortality, however those that we did visit were all confirmed as true mortalities with no instances of slipped collars. Source of mortality was also unidentifiable given how quickly carcasses were scavenged and time to travel to mortality locations. Denning data were derived from presence of seasonal GPS clusters in female lynx. Denning was clear as female movements would drastically reduce and center on 2 to 3 clusters for several weeks. Given the remote nature of these dens, approximately half of the dens were visited, but all visited dens were active and contained between 1 and 8 kittens. Since we were unable to visit each den site, reproduction for each individual was categorized as a binary denning/not denning classification every year as opposed to quantifying reproductive output in number of kittens. Lynx kittens stay with their mothers for $\leq$10 mo, thus females have the capacity to reproduce annually, so reproductive rate was calculated as the number of female lynx that denned divided by the total number of female lynx at a given site.

We evaluated the impact of dispersal on survival by dividing individual movement data into two statuses: "dispersing" or "resident." The dispersal state was defined as an extended (1 wk or more) extraterritorial movement that was $\geq$25 km from home range center. We felt that these requirements for dispersal were sufficient to exclude small extraterritorial forays, a common behavior wherein territorial animals briefly explore extraterritorial areas without giving up their own territory. The cutoff of 1 wk continuous extraterritorial movement was chosen as sufficient time for a territory to be identified by other territorial con-specifics and likely filled, as loss of territory is an important part of dispersal. This duration came from several instances of vacant territories being filled after

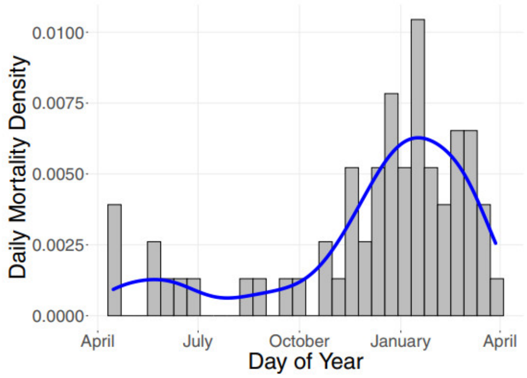

**Fig. 6.** Density of lynx mortalities by day of year. Years begin on April 1 and end on March 31. Seasonal mortalities appear to peak during the winter during the month of January. Density curve overlay as an approximation for wrapped Cauchy fit.

less than one week. Additionally, this definition allowed dispersal status to be time-varying if an individual returned to occupy their former home range or moved to a different directional dispersal state. Dispersal rarely occurred after October, as individuals overwinter in a local territory even if they continued to disperse the following year. Some individuals would disperse to a new location and remain there for multiple years, thus all dispersing individuals were reclassified as residents at the beginning of each year. We labeled this covariate *dispersal*.

Additionally, we built a separate covariate that divided dispersal state into three categories, building on the previously described states. To assess whether direction of dispersal affected survival, we differentiated dispersal directions resulting in three categories: resident, eastward dispersal, and westward dispersal. Dispersal state was defined as above and thus resident state is identical, but dispersing individuals were divided by direction of dispersal. Dispersal paths ending west of their origin were defined as westward dispersal state and those ending east of the origin were defined as eastward dispersal. We labeled this covariate *direction_disp* for the three directional state (east, west, and resident) and *east_disp* for the east vs. combined west and resident states.

**Data Analysis.** Mortality status was transmitted along with GPS fixes. Collar fix rates were ~96% for all collars resulting in complete survival datasets with no need for interval censoring from missed GPS fixes. We consolidated survival data from the 4-h fix rates into daily survival rates. Given the seasonal nature of our data, we felt it was appropriate to examine survival on a recurrent time horizon. We chose April as the start for this time horizon as all dispersal events occurred during the spring and summer after the breeding season in March. This timescale captured dispersal first, followed by reproduction within a single year, capturing our definition of a truly successful dispersal event. When examined on an annually recurrent time horizon, lynx mortality appeared to have a single consistent peak in January of each year (Fig. 6). Given this single seasonal peak in mortality, we chose to model survival using a wrapped Cauchy hazard function (Eq. **1**).

$$h_0(t|\gamma,\mu,\rho,\tau) = \frac{\gamma(1-\rho^2)}{1+\rho^2-2\rho\cos(\frac{2\pi(t-\mu)}{\tau})} \qquad \textbf{[1]}$$

Under the wrapped Cauchy framework each parameter defines a different feature of the hazard function: $\gamma$ is the average annual hazard, $\rho$ defines the duration of the peak, and $\mu$ defines the timing of the hazard peak. The $\tau$ parameter dictates the number of peaks in cases where there may be multiple peaks over one year, however since our data only showed a single peak, this parameter was kept at one and will be omitted for the remainder of the analysis. We chose to use a Bayesian counting process (Eq. **2**)

$$y_{it} \sim Poisson(h_0(t|\gamma,\mu,\rho,\tau)\cdot e^{\mathbf{X}\boldsymbol{\beta}}) \qquad \textbf{[2]}$$

to model survival as this allowed the use of the parametric wrapped Cauchy daily hazard. Use of this specific distribution is not possible under the semiparametric Cox model and has never been used under existing parametric model analyses (32–34). Additionally collar battery failures resulted in right censored data, which is readily accounted for under this model formulation. Given the hypothesis that a traveling wave was moving across the population, we included a random effect of refuge to account for spatial differences in survival.

Model formulation in this way allows the inclusion of covariates influencing survival ($y_i \sim covariate$), or as separate hazard functions ($h_0(t|\gamma,\mu,\rho) \sim covariate$). The difference between these approaches comes from the assumptions we make about the underlying hazard function governing the system. Fixed-effect covariates used to model survival assume a single underlying hazard function with an additive effect of covariates (*age*, *sex*, *dispersal status*, and *dispersal direction*), whereas covariates modeled on hazard assume separately parameterized hazard functions, allowing for varying peaks, durations, and average hazard by covariate, each with additive covariate effects. We chose to include *dispersal status* (resident vs. dispersal), *dispersal direction* (east dispersal, west dispersal, resident), *age*, *sex*, and a categorical factor of *year* as predictors for both hazard and survival in our model selection. Biologically speaking there was no reason to model separate hazard functions by *year* so this was only included as a categorical fixed effect of survival. Model selection was conducted using Widely Applicable Information Criterion (WAIC) (35).

Given the lack of previously collected survival data from the study region, we chose to use uninformative priors for the model parameters and coefficients. Hazard function parameters priors were modeled as $\rho \sim Uniform(0,1)$, $\mu \sim Uniform(-2\pi, 2\pi)$, and $\log(\gamma) \sim Normal(0,10)$. Fixed-effect parameters of *year* and *sex* took the form $\beta \sim Normal(0,10)$ while random effects of refuge and individual were modeled using $r \sim Normal(0,\tau)$ with $\tau \sim Uniform(0,5)$ hyperpriors. Markov-chain Monte Carlo was conducted for 100,000 updates using 4 chains. We used a burn in of 25,000 and all models converged with R-hat values between 1 and 1.05. All analyses were conducted using Numerical Inference for statistical Models using Bayesian and Likelihood Estimation (NIMBLE) in program R (36, 37).

**Data, Materials, and Software Availability.** Data is available and can be directly accessed at ServCat database (38). Code is available at ServCat (39).

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