Integrated Population Modeling Provides the First Empirical Estimates of Vital Rates and Abundance for Polar Bears in the Chukchi Sea

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Large carnivores are imperiled globally, and characteristics making them vulnerable to extinction (e.g., low densities and expansive ranges) also make it difficult to estimate demographic parameters needed for management. Here we develop an integrated population model to analyze capture-recapture, radiotelemetry, and count data for the Chukchi Sea subpopulation of polar bears (*Ursus maritimus*), 2008–2016. Our model addressed several challenges in capture-recapture studies for polar bears by including a multievent structure reflecting location and life history states, while accommodating state uncertainty. Female breeding probability was 0.83 (95% credible interval [CRI] = 0.71–0.90), with litter sizes of 2.18 (95% CRI = 1.71–2.82) for age-zero and 1.61 (95% CRI = 1.46–1.80) for age-one cubs. Total adult survival was 0.90 (95% CRI = 0.86–0.92) for females and 0.89 (95% CRI = 0.83–0.93) for males. Spring on-ice densities west of Alaska were 0.0030 bears/km² (95% CRI = 0.0016–0.0060), similar to 1980s-era density estimates although methodological differences complicate comparison. Abundance of the Chukchi Sea subpopulation, derived by extrapolating density from the study area using a spatially-explicit habitat metric, was 2,937 bears (95% CRI = 1,552–5,944). Our findings are consistent with other lines of evidence suggesting the Chukchi Sea subpopulation has been productive in recent years, although it is uncertain how long this will continue given sea-ice loss due to climate change.

Managing wildlife populations often requires knowledge of demographic parameters such as reproduction, survival, and density or abundance. This information is particularly important for species of conservation concern due to direct human impacts (e.g., harvest1, habitat fragmentation7) or changes in phenology, distribution, or population dynamics resulting from climate change1. Many species of large carnivores are imperiled1 and face accelerating declines3. Some of the characteristics that make these species vulnerable to extinction also make demographic parameters difficult to estimate, including low population densities, high mobility, expansive range requirements, and complex life histories. Resulting challenges include small sample sizes, heterogeneous detection probabilities6, non-random temporary emigration relative to a localized study area7, unobservable life history states8, and estimates of abundance that may not be referenced to the region of interest9. These issues can increase bias, reduce precision, and complicate interpretation of demographic parameters, limiting their value for management and conservation.

Polar bears (*Ursus maritimus*) occur at low densities throughout ice-covered waters of the Arctic (e.g., 0.0041 bears/km²)10 and typically have large annual activity areas (e.g., >100,000 km²)11. The global population of polar bears is divided into 19 subpopulations that currently exhibit variable demographic status, although up-to-date...
and accurate estimates of abundance and trend are often lacking\textsuperscript{12}. In 2008, polar bears were listed as threatened range-wide under the U.S. Endangered Species Act (ESA) due to projected population declines associated with loss of sea-ice habitat resulting from climate change\textsuperscript{13}. Estimates of demographic parameters are required for population projections\textsuperscript{14}, compliance with protected species legislation (e.g., assessment of recovery criteria under the ESA)\textsuperscript{15}, conservation assessments\textsuperscript{16}, and management of subsistence harvest\textsuperscript{17}. Given that habitat loss is projected to continue\textsuperscript{18}, accurate and timely information will become increasingly important for state-dependent management (e.g., adjusting harvest based on current environmental conditions)\textsuperscript{19} and detection of potentially rapid or nonlinear population responses to climate change\textsuperscript{20}.

The Chukchi Sea (CS) subpopulation of polar bears inhabits the Bering, Chukchi, and East Siberian seas\textsuperscript{21}. Capture-recapture studies conducted 1986–1993 did not provide adequate information to estimate demographic parameters due to low recapture rates and the movement of bears in to and out of the study area\textsuperscript{22}. The only previous estimate of abundance was based on a rough extrapolation of the number of maternity dens on Wrangel Island, an important denning area located north of mainland Russia, in the 1970s and 1980s\textsuperscript{23}. Although recent research has suggested positive nutritional condition and reproduction despite sea-ice loss\textsuperscript{24,25}, abundance has never been estimated using empirical methods with a clear spatial and temporal reference, and the IUCN Polar Bear Specialist Group lists abundance and trend of the CS subpopulation as unknown\textsuperscript{26}.

In this study, we develop an integrated population model (IPM)\textsuperscript{27} to analyze several types of count data together with multistate capture-recapture and telemetry data that include uncertainty in the true state (e.g., reproductive class) of individuals\textsuperscript{28}. After fitting the model, we use estimates of abundance referenced to the study area, together with polar bear movement data and a habitat-quality metric\textsuperscript{29}, to extrapolate density throughout the subpopulation range\textsuperscript{30}. Our objectives were to (i) estimate abundance for the CS subpopulation using data collected in a geographically-limited study area; (ii) estimate vital rates (e.g., reproduction and survival) concurrently analyzing multiple types of data, including parameters that would be unobservable or confounded if data types were analyzed separately; (iii) reduce bias in demographic parameters by modeling the movement of animals in to and out of the study area\textsuperscript{31,32}; and (iv) develop a flexible modeling framework that addresses key analytical challenges for CS polar bears, and can be adapted to other subpopulations or species. Our findings represent the first rigorous estimates of demographic parameters for the CS polar bear subpopulation, providing information needed for management and serving as a baseline to evaluate future population change.

**Methods**

**Study Area and Data Collection.** The CS region is seasonally covered by sea ice that extends south into the Bering Sea at its maximum extent in March and retreats north towards the polar basin at its minimum extent in September\textsuperscript{33}. We physically captured polar bears in an offshore study area located west of Alaska (Fig. 1) from mid-March to early May in 2008–2011, 2013, and 2015–2016, using standard chemical immobilization techniques\textsuperscript{34}. For use in some analyses, we defined a multiyear core sampling area of approximately 25,000 km\textsuperscript{2} based
We defined breeding for a female polar bear as consisting of fertilization in the spring of year $t$, implanting the blastocyst and entering a maternal den in autumn or winter, and emerging with at least one C0 in the spring of year $t+1$. We included two female breeding probabilities: $B_t$ for females without cubs or with C2 (i.e., females that are available to breed per a typical three-year reproductive cycle), and $B_t$ for females with C0 or C1. We did not enforce any relationship between these parameters, thereby allowing for Markovian movements.

For males, the population projection model included states representing age-classes for subadults (2–3 years; states F2Y and F3Y), after which bears were considered adults ($\geq 4$ years; state AM; Fig. 2)35. The model allowed for temporary emigration by including versions of each state that were in and out of the study area. Transitions among states were determined by subadult survival ($\phi_{SM}$), adult survival ($\phi_{AM}$), and movement probabilities that allowed individuals outside of the study area in year $t$ to either remain outside ($\psi_{SM}$) or move into the study area ($\psi_{SM}$) in year $t+1$. Similarly, individuals inside the study area could remain inside ($\psi_{AM}$) or move outside ($1 - \psi_{AM}$) by including versions of each state that were in and out of the study area. Transitions among adult female states were determined by subadult survival ($\phi_{SM}$), adult survival ($\phi_{AM}$), and movement probabilities that allowed individuals outside of the study area in year $t$ to either remain outside ($\psi_{SM}$) or move into the study area ($\psi_{SM}$) in year $t+1$. We did not enforce any relationship between these parameters, thereby allowing for Markovian movements.

### Figure 2.

Male life cycle matrix in the integrated population model for polar bears. Rows and columns represent life cycle states. The parameters in cell $ij$ define the probability of transitioning from the state in column $j$ at year $t$, to the state in row $i$ at year $t+1$. Life cycle states and parameters are described in the main text and Supplementary Table S1. Superscripts $I$ and $O$ on movement probabilities ($\psi$) designate states that are inside and outside the study area, respectively. Male recruitment (not shown) matches female recruitment (Fig. 3) assuming an equal sex ratio.

|                | $M2Y_{in}$ | $M2Y_{out}$ | $M3Y_{in}$ | $M3Y_{out}$ | $M4Y_{in}$ | $M4Y_{out}$ | $AM_{in}$ | $AM_{out}$ |
|----------------|------------|-------------|------------|-------------|------------|-------------|-----------|------------|
| $M2Y_{in}$     | 0          | 0           | 0          | 0           | 0          | 0           | 0         | 0          |
| $M2Y_{out}$    | 0          | 0           | 0          | 0           | 0          | 0           | 0         | 0          |
| $M3Y_{in}$     | $\phi_{SM} \psi_{I}^{1}$ | $\phi_{SM} (1 - \psi_{O}^{0})$ | 0          | 0           | 0          | 0           | 0         | 0          |
| $M3Y_{out}$    | $\phi_{SM} \psi_{I}^{1}$ | $\phi_{SM} (1 - \psi_{O}^{0})$ | 0          | 0           | 0          | 0           | 0         | 0          |
| $M4Y_{in}$     | 0          | 0           | $\phi_{SM} \psi_{I}^{1}$ | $\phi_{SM} (1 - \psi_{O}^{0})$ | 0          | 0           | 0         | 0          |
| $M4Y_{out}$    | 0          | 0           | $\phi_{SM} \psi_{I}^{1}$ | $\phi_{SM} (1 - \psi_{O}^{0})$ | 0          | 0           | 0         | 0          |
| $AM_{in}$      | 0          | 0           | 0          | 0           | 0          | 0           | $\phi_{SM} \psi_{I}^{0}$ | $\phi_{SM} \psi_{O}^{0}$ |
| $AM_{out}$     | 0          | 0           | 0          | 0           | 0          | 0           | $\phi_{SM} \psi_{I}^{0}$ | $\phi_{SM} \psi_{O}^{0}$ |

$\phi_{SM}$ and $\phi_{AM}$ are time constant due to small sample sizes, and were defined relative to biologically relevant sex, age, and reproductive classes as established by other polar bear studies13,35. A general description of the model is provided here, with additional details in the Supplementary Methods. The IPM is graphically displayed in Supplementary Fig. S1. A complete list of parameter, data, and indexing definitions is provided in Supplementary Table S1.
Supplementary Methods. Reproductive status was uncertain. Details of the observation component of the IPM are provided in the main text and Supplementary Table S1. Superscripts I and O on movement probabilities (ψ) designate states that are inside and outside the study area, respectively. In addition, but not shown, is a single absorbing dead state.

![Figure 3. Female life cycle matrix in the integrated population model for polar bears in the Chukchi Sea. Rows and columns represent life cycle states. The parameters in cell ij define the probability of transitioning from the state in column j at year t to the state in row i at year t + 1. Life cycle states and parameters are described in the main text and Supplementary Table S1. Superscripts I and O on movement probabilities (ψ) designate states that are inside and outside the study area, respectively. In addition, but not shown, is a single absorbing dead state.](image)

expected \( B_c < B_s \), because \( B_s \) requires that a female lose her entire C0 or C1 litter in time to breed again in the same spring.26

Data. For state-specific count data, we modeled the number of individuals physically captured in state \( s \) and year \( t (n_{s,t}) \) as binomially distributed random variables, with capture probability \( p \) and latent state-specific abundance \( N_{s,t} \):

\[
n_{s,t} \sim \text{Binomial} \left( p_{s,t}, N_{s,t} \right),
\]

where \( I_j \) is an indicator variable equal to 1 if state \( s \) is an inside state (i.e., inside the study area) and 0 otherwise. Capture probability was constant across states and years except that it was fixed to 0 in 2012 and 2014 when there was no sampling.

We modeled annual counts of C1 litter sizes \( \left( n_{1[1:3]} \right) \), observed during physical captures, as multinomial random variables. Parameters of the multinomial \( \left( \phi_{1[1:3]} \right) \) described the probability that an AFC1 has 1, 2, or 3 cubs. Following the methods of Hunter et al.28 and Regehr et al.19, the parameters \( \omega_{0[1:3]} \) were modeled as a function of C0 litter size probabilities \( \left( \phi_{0[1:3]} \right) \) and C0 survival \( \left( \phi_{0C0} \right) \). These multinomial probabilities were modeled as conditional on at least one C0 surviving \( \left( \phi_{0C0} \right) \) (Supplementary Methods). That is, if at least one cub in a female’s C0 litter was predicted to have survived, we modeled the probability that she had 1, 2, or 3 C1s. Expected C0 and C1 litter sizes \( \left( l_{L0} \right) \) and \( \left( l_{L1} \right) \) were then derived parameters. The number of dependent and independent C2s provided information on the probability \( W \) that C2s were weaned (i.e., separated from their mothers) prior to the spring sampling period. Here, we assumed:

\[
n_{\text{weanC2}} \sim \text{Binomial} \left( W, n_{C2,t} \right),
\]

where \( n_{\text{weanC2}} \) is the number of observed independent C2s in year \( t \), \( n_{C2,t} \) is the total number of observed C2s, and \( W \) is the probability that a C2 was weaned prior to our sampling period.

Capture-recapture and telemetry data were jointly analyzed using a multievent model39 with true latent states matching those defined by the population projection matrices, excluding the recruitment component. Conditional on first capture, we assumed the state of an individual in year \( t \) was a categorical random variable:

\[
z_{i,t} | z_{i,t-1} \sim \text{Cat}(\Theta_{z_{i,t-1}}),
\]

where \( \Theta_{z_{i,t-1}} \) is the vector of state transition probabilities for an individual that was in state \( z_{i,t-1} \) in year \( t-1 \), as defined by parameters in the projection matrices (Figs 2 and 3).

We modeled observation data for individual \( i \) in year \( t \), \( y_{i,t} \) as a function of its state in year \( t \) as well as individual- and time-specific factors (e.g., presence of a functional collar). We assumed \( y_{i,t} \) is a categorical random variable:

\[
y_{i,t} | z_{i,t} \sim \text{Cat}(\Pi_{i,t|z_{i,t}}),
\]

where \( \Pi_{i,t|z_{i,t}} \) is the vector of detection probabilities for individual \( i \) in year \( t \). For males, only direct observation data were available, thus individuals inside the study area were detected with probability \( p \), and individuals outside the study area were detected with zero probability (i.e., could not be observed). For females, the observation process included both direct and telemetry observations, where the true state may be partially identified from remote telemetry observations (e.g., a collared individual was known to be alive and outside the study area, but its reproductive status was uncertain). Details of the observation component of the IPM are provided in the Supplementary Methods.

We calculated the total number of individuals that used the study area in year \( t (N_{\text{study}}) \) as the sum of the number of bears in all inside states, plus the estimated number of dependent cubs associated with adult females:
where \( s[\text{in}] \) denotes all inside states. Annual abundances of C0s (\( N_{C0[\text{in},t]} \)) and C1s (\( N_{C1[\text{in},t]} \)), which were always with their mothers and therefore not included as independent individuals, were calculated as the product of average C0 and C1 litter sizes and the total (latent) number of females in each reproductive state inside the study area (\( N_{AFD[\text{in},t]} \) and \( N_{AFC[\text{in},t]} \), respectively). A multiyear average study area abundance (\( N_{\text{study}[t]} \)) was calculated within the IPM as the mean of annual estimates. Details of abundance estimation are provided in the Supplementary Methods.

**Model Implementation.** To fit the IPM, we used informative Beta priors for subadult and adult survival, corresponding to mean values and standard deviations on the probability scale of 0.89 (sd = 0.05), 0.93 (sd = 0.02), 0.82 (sd = 0.10), and 0.89 (sd = 0.05) for \( \phi_{SM} \), \( \phi_{AM} \), \( \phi_{AFC} \), and \( \phi_{AFD} \), respectively. These priors were developed using moment matching methods based on point estimates of total survival (i.e., including harvest mortality) from capture-recapture studies for 12 polar bear subpopulations with available data (Supplementary Methods, Supplementary Table S3). We used an informative Beta(2.1,1.14) prior for \( B_2 \) as it was only weakly identifiable from the data. Vague priors were used for all other parameters. We fit the model in a Bayesian framework using JAGS40 and the jagsUI package41 accessed through R version 3.3.1 (R Core Team 2016). Further details about priors, sensitivity of estimated parameters to choice of priors, model goodness-of-fit, and implementing the IPM are provided in Supplementary Methods. We report results as posterior modes and 2.5th and 97.5th quantiles unless otherwise noted.

**Density Extrapolation.** After fitting the model, we used a previously developed, spatially- and temporally-explicit habitat-quality metric29 to extrapolate density estimates from the study area to the CS subpopulation boundary. First, we estimated a multiyear, average density within the core sampling area, after correcting for lack of geographic closure (\( \overline{\delta}_{\text{Sampling}} \)), as follows:

\[
\overline{\delta}_{\text{Sampling}} = \overline{N}_{\text{study}} \times \frac{\hat{q}}{A_{\text{Sampling}}}.
\]

where \( \hat{q} \) is the average proportion of the individual areas used by collared females during the spring sampling season (Supplementary Methods) that occurred within the core sampling area; and \( A_{\text{Sampling}} \) is the size (km2) of the core sampling area42. Second, we calculated an adjusted value of local density that excluded AFC0 and C0 (\( \overline{\delta}_{\text{Sampling}}^{\text{Adj}} \)), by replacing \( \overline{N}_{\text{study}} \) in equation (6) with a multiyear average abundance estimate that excluded \( N_{AFD[\text{in},t]} \) and \( N_{C0} \). Because AFC0 and C0 rarely used the study area in the spring (i.e., there were only 3 direct observations of AFC0), we used \( \overline{\delta}_{\text{Sampling}}^{\text{Adj}} \) to extrapolate densities of bears in other states, and subsequently added in approximate numbers of AFC0 and C0 (see below; Supplementary Methods). Third, we overlaid the region with 25 × 25 km grid cells. For each grid cell \( x \), we used a habitat-quality metric (\( h_x \)) representing the relative probability of use by polar bears during March and April, averaged over the years 2009–2011, 2013, and 2015–2016, as estimated from non-denning adult female polar bear location data and environmental covariates (e.g., sea-ice concentration and characteristics, ocean depth) using resource selection functions29. Fourth, we extrapolated abundance to the entire CS subpopulation boundary area (\( \overline{N}_{\text{CS}}^{\text{Adj}} \)) by assuming a 1:1 proportional relationship between habitat quality and density30, as follows:

\[
\overline{N}_{\text{CS}}^{\text{Adj}} = (\overline{\delta}_{\text{Sampling}}^{\text{Adj}} \times A_{\text{Sampling}}) \times \sum_{x=1}^{X_{\text{CS}}} h_x / \sum_{x=1}^{X_{\text{Sampling}}} h_x,
\]

where \( \overline{N}_{\text{CS}}^{\text{Adj}} \) is an extrapolated estimate of abundance, excluding AFC0 and C0, referenced to the CS subpopulation boundary; and \( X_{\text{Sampling}} \) and \( X_{\text{CS}} \) are the number of grid cells overlaying the core sampling area and CS subpopulation boundary, respectively. We used bootstrapping methods to estimate variance and account for uncertainty in the proportions of AFC0 and C0 that occurred within the total subpopulation (Supplementary Methods).

**Age-One Cubs per Adult Female.** Separate from other analyses, we used the physical capture data to estimate and evaluate temporal trends during the period 2008–2016 in the number of C1s per adult female, a metric that integrates cub production and first-year survival35. We assumed the annual numbers of C1s were Poisson distributed random variables with an offset for the numbers of adult females, and compared the fit of constant and linear trend models. The models were fit in JAGS following the same specifications as the IPM.

**Ethics statement.** This research was approved by and carried out in accordance with (i) the U.S. Marine Mammal Protection Act and ESA, under U.S. Fish and Wildlife Service (USFWS) permit number MA046081; and (ii) animal handling protocols established by the USFWS Region 7 Institutional Animal Care and Use Committee.

**Results**

A total of 166 unique males (annual mean = 24, sd = 5) and 135 unique females (annual mean = 19 bears, sd = 5 bears) were physically captured and released in 2008–2011, 2013, and 2015–2016. These numbers do not reflect captures of C0s and C1s, which were not included as individuals in the capture-recapture model. Among adult females, 103 individuals (annual mean = 15, sd = 3) received telemetry collars. The complete dataset consisted of 403 direct and remote observation events (Supplementary Table S2), 39 observations of C1 litters (Supplementary Table S4), and 61 observations of independent and dependent C2s (Supplementary Table S5).
The separate analysis of the number of C1s per adult female provided no evidence for a linear trend during the period 2008–2016 (slope = 0.02, 95% credible interval = −0.07–0.10). The time-constant model resulted in an estimate of 0.64 (0.49–0.80) C1s per adult female.

**Vital Rates and Movement Probabilities.** Survival probability modes varied by sex and age, with overlapping credible intervals (Fig. 4). Adult female and male survival probabilities were 0.90 (0.86–0.92) and 0.89 (0.83–0.93), respectively (Table 1). Subadult female and male survival were 0.79 (0.68–0.87) and 0.71 (0.59–0.81), respectively. Age-zero cub survival was 0.62 (0.45–0.86). Litter survival probabilities for C0 (φL0) and C1 (φL1) were 0.87 (0.82–1.00) and 0.96 (0.83–1.00), respectively.

Breeding probability for states AFNC and AFC2 (B1) was 0.83 (0.71–0.90; Table 1). As expected, this was higher than breeding probability for states AFC0 and AFC1 (B2 = 0.10; 0.02–0.39). The average size of C0 and C1 litters was 2.18 (1.71–2.82) and 1.61 (1.46–1.80) individuals, respectively. The probability that a C1 in year t would be weaned prior to the sampling period in year t + 1 (W) was 0.34 (0.24–0.44).

Denning females were generally outside the study area during the sampling period, as indicated from previous studies of reproductive ecology in this subpopulation36. Specifically, females entering state AFC0 moved out of the study area (ψII2) with probability 0.99 (0.88–1.00) or remained outside (ψOO2) with probability 0.98 (0.89–0.99; Table 1). Bears not transitioning into state AFC0 exhibited a tendency to stay where they were the previous year, either remaining in the study area (ψII1) with probability 0.59 (0.40–0.73) or remaining outside the study area (ψOO1) with probability 0.78 (0.64–0.89). Estimated detection probabilities and assignment parameters for the multievent capture-recapture data are provided in the Supplementary Results.

### Table 1. Vital rates for polar bears in the Chukchi Sea. Values are posterior modes and 95% credible intervals (CRI). Parameters included survival probabilities (φ), movement probabilities (ψ), breeding probabilities (B), weaning probability (W), and average litter size (l). Detailed parameter definitions are provided in the main text and Supplementary Table S1.

| Parameter | Mode (95% CRI) |
|-----------|----------------|
| φC0       | 0.62 (0.45–0.86) |
| φC1       | 0.92 (0.71–0.99) |
| φAF       | 0.79 (0.68–0.87) |
| φSM       | 0.90 (0.86–0.92) |
| φAM       | 0.71 (0.59–0.81) |
| φSF       | 0.69 (0.83–0.93) |
| φCl       | 0.59 (0.40–0.73) |
| φCl0      | 0.78 (0.64–0.89) |
| φCl1      | 0.01 (0.00–0.12) |
| φCl2      | 0.98 (0.89–0.99) |
| ψII1      | 0.83 (0.71–0.90) |
| ψII2      | 0.10 (0.02–0.39) |
| ψOO1      | 0.34 (0.24–0.44) |
| ψOO2      | 2.18 (1.71–2.82) |
| B1        | 1.61 (1.46–1.80) |
| B2        | 0.34 (0.24–0.44) |
| W         | 0.34 (0.24–0.44) |
| lL0       | 2.18 (1.71–2.82) |
| lL1       | 1.61 (1.46–1.80) |

**Figure 4.** Apparent survival of polar bears in the Chukchi Sea. Life stages are age-zero cubs (C0), age-one cubs (C1), subadult females (SF), adult females (AF), subadult males (SM), and adult males (AM). Posterior distributions (violin plots), modes (squares), and 95% credible intervals (error bars) are shown. Note that cub survival is conditional on adult female survival (i.e., survival of the mother).
Density and Abundance. Annual estimates of the number of bears that used the study area \( (N_{\text{study}}) \) ranged from 167 (94–312) in 2008 to 350 (208–589) in 2011, with a multiyear mean \( \bar{N}_{\text{study}} = 296 \) (176–513; Fig. 5). The average proportion of time that collared adult females spent inside the core sampling area, over the approximate 6-week duration of the sampling period, was \( \hat{q} = 0.25 \) (0.16–0.36). Multiyear average density within the core sampling area was \( \hat{D}_{\text{sampling}} = 0.0030 \text{ bears/km}^2 \) (0.0016–0.0060). The multiyear average estimate of abundance, extrapolated to the area within the CS subpopulation boundary and adjusted to include approximate numbers of AFC0 and C0, was \( \hat{N}_{\text{CS}} = 2,937 \) (1,552–5,944). This corresponds to an average density of 0.0036 bears/km\(^2\) (0.0019–0.0073) within the CS subpopulation boundary.

Discussion

Many large carnivores have experienced range retractions, are threatened with extinction, or both. Factors that contribute to vulnerability include intrinsic biological traits (e.g., complex life histories with extended maternal care) and characteristics that increase contact with humans (e.g., high mobility and expansive range requirements), both of which can pose challenges for research. In this paper we develop an IPM that combines multiple data types into a single, integrated analysis of abundance and demographic processes\(^43\). We used telemetry data to model animal movements in and out of the study area, with a multievent structure\(^48\) to account for state uncertainty. After fitting the IPM, we used a habitat-quality metric calculated from resource selection functions to extrapolate densities. This allowed large-scale inference from geographically-limited sampling\(^45,46\), producing estimates of abundance with a clear spatial and temporal definition (i.e., as opposed to estimates of “superpopulation” size from open capture-recapture models, which can be difficult to interpret)\(^9\).

Vital Rates. Survival rates for independent bears in this study represented total apparent survival (i.e., the probability of remaining alive, considering all sources of mortality, and not permanently emigrating from the study area). We did not estimate harvest mortality because only five animals were captured as independent bears and subsequently known to be killed by humans, which was too few to justify additional model complexity. Based on an average harvest from 2008–2015 of approximately 24 bears per year in Alaska\(^45\) and 32 bears per year in Chukotka\(^46\), and a total abundance of 2,937 bears (this study), the median proportion of the CS subpopulation removed by humans each year would be approximately 1.8% (0.9–3.6%). This is likely below the 4.5% harvest rate, at a 2:1 male-to-female harvest sex ratio, that has been commonly applied to polar bear subpopulations under favorable environmental conditions\(^45\), noting that 1.8% likely represents a minimum estimate due to incomplete harvest reporting\(^45,46\).

We used telemetry data to model animal movements and thereby mitigate potential bias in demographic parameters due to non-random temporary emigration\(^7\). We found that the probability of being in the study area in year \( t \) differed for bears that were in vs. out in year \( t-1 \), and was a function of reproductive state (i.e., adult females with COs had very low probability of being in). In a review of the demographic status of 13 Canadian subpopulations, York et al.\(^33\) suggested that incomplete geographic sampling was significantly correlated with negative bias in demographic parameters. Furthermore, a data-based simulation study for the Southern Beaufort Sea subpopulation identified non-random temporary emigration and movement-related heterogeneity in recapture probability as key factors contributing to bias when the study area is smaller than the subpopulation range\(^31\). Although we took an important step toward addressing this challenge, estimates of survival for independent bears in this study should be interpreted with caution. Recapture probabilities \( (p) \) were conditional on presence in the study area, as determined by movement probabilities \( (\psi) \). Due to sample size limitations, estimates of both \( p \) and \( \psi \) were restricted to be constant across time and multiple life cycle states. Also, estimates of \( \psi \) were informed primarily by data on adult females because other sex and age classes did not provide telemetry data, which contributed more to estimation of movements than did direct captures. Polar bears are mobile animals that exhibit individual and interannual variation in site fidelity and activity area sizes\(^31\). Although net movement patterns appear broadly similar for adult males and females\(^47\), seasonal movements may reflect sex-specific behavioral

**Figure 5.** Annual estimates of the number of Chukchi Sea polar bears that used the study area during the sampling period. Violin plots represent the full posterior distributions, squares are modes, and error bars are 95% credible intervals. The multiyear mean estimate is shown in red.
Estimates of reproductive parameters provide context for the current status of the CS subpopulation. Relative to 12 polar bear subpopulations with available data as summarized in Regehr et al., our estimates of breeding probability and age-zero cub (C0) survival were average (Bt = 0.83 compared to mean point estimate for bears age ≥6 years = 0.81, range = 0.44–1.0; and φC0 = 0.62 compared to mean point estimate = 0.63, range = 0.34–0.90, respectively), and our estimates of C0 litter size and age-one cub (C1) survival were high (tL = 2.16 compared to mean point estimate = 1.64, range = 1.49–1.76; and φC1 = 0.92 compared to mean point estimate = 0.81, range = 0.32–0.98, respectively). Detailed comparisons are complicated by methodological differences and lack of information on subpopulation sizes relative to environmental carrying capacity (K), which determines the strength of density-dependent regulation. It is possible that the CS subpopulation size is currently above its maximum net productivity level, which Regehr et al. suggested occurs at approximately 0.69K for polar bears, due to (i) relatively low harvest in recent years, and (ii) loss of approximately 8.9 ice-covered days per year for the period 1979–2014, which is likely correlated with reduced on-ice foraging opportunities for polar bears and may cause reductions in K or intrinsic growth rate. However, it is unknown whether unquantified, but likely high, illegal harvest in Russia during the period 1994–2003 caused reductions from which the CS subpopulation is still recovering.

Our point estimate of average C0 litter size >2, and observations of females with three C1s (Supplementary Table S4), is interesting because triplet litters are thought to be rare in most polar bear subpopulations except for Western Hudson Bay. Higher litter size may reflect maternal body condition prior to entering the den and sufficient post-denning prey availability to support larger family groups. However, the CS region is experiencing high rates of sea-ice loss. During the period 1979–2014, the open water period increased by 80 days and large declines in summer sea-ice extent are projected to continue. Although several studies (including this one) have suggested that the CS polar bear subpopulation has not been negatively affected by ice loss to date, telemetry data indicate that twice as many collared females are spending the summer on shore, and are remaining there 30 days longer, compared to two decades ago. As sea-ice loss continues it is uncertain how much additional time polar bears can spend in poor foraging habitats (e.g., land, sea ice over less-productive waters of the polar basin) without experiencing negative nutritional and demographic effects. The availability of supplemental nutrition in the form of stranded carcasses of gray whales (Eschrichtius robustus), bowhead whales (Balaena mysticetus), and other marine mammals along the coastlines of the CS region may become increasingly important as sea-ice loss continues, although these resources are unlikely to compensate for the effects of sea-ice loss in the long term.

Density and Abundance. Estimates of density and abundance from the current study appear broadly consistent with previous estimates for the CS subpopulation, although methodological differences preclude direct comparisons. Estimated density within the core sampling area (Dsampling) was 0.0030 bears/km2 (0.0016–0.0060). This is similar to a spring on-ice density of 0.0031 bears/km2 (SE = 0.0019) estimated using distance-sampling methods in 1987 for the area around Cape Lisburne, Alaska, which spatially overlaps our study area (Fig. 1). Our estimated abundance within the CS subpopulation boundary (2,937) is within the range of 2,000–5,000 bears that still recovering.

The need to estimate abundance for a management area or population range that is larger than the region where sampling occurs is a common challenge in wildlife research and management. Our approach of extrapolating local densities based on habitat metrics has been used in other studies, and is supported by a recent meta-analysis suggesting positive relationships between indices of habitat selection and abundance. The CS polar bear subpopulation is likely to meet key assumptions of density extrapolation, including that a population is relatively stable and at equilibrium with its environment. First, polar bears are long-lived animals characterized...
by high adult survival, and thus unlikely to exhibit large annual fluctuations in abundance. Although there is evidence for declines due to sea-ice loss in some polar bear subpopulations, others are stable or increasing and recent case studies suggest that multiple interacting factors influence when and how the effects of sea-ice loss will occur.

Second, harvest mortality was likely relatively low and well-distributed throughout the region, precluding human-caused source-sink dynamics. Third, our habitat-quality metric was based on contemporary data and included functional responses in habitat selection patterns. Nonetheless, estimates of abundance from the current study should be interpreted with caution. Temporal and individual heterogeneity in recapture probabilities, discussed above and not accounted for in our model, are common sources of bias in estimates of abundance. Also, information on the density and distribution of prey species was not available for inclusion as covariates in the resource selection functions underlying our habitat-quality metric. Polar bears collared in the study area west of Alaska moved throughout the entire region, but few locations were available in the far western portion of the subpopulation boundary in the spring. As a result, our analyses applied to the CS subpopulation boundary 26. We did not estimate abundance within a larger reference area for CS polar bears as defined under the Agreement between the Government of the United States of America and the Government of the Russian Federation on the Conservation and Management of the Alaska-Chukotka Polar Bear Population (U.S.-Russia Agreement; United States T. Doc. 107–10), a bilateral treaty signed in 2000. Although circumpolar resource selection functions suggest that sea ice over the continental shelf north of Siberia includes high-value polar bear habitats, the area under the U.S.-Russia Agreement extends west into the Eastern Siberian Sea, which is characterized by lower in situ primary production that could influence species abundance at higher trophic levels.

Integrated Population Model. Integrated population models offer several advantages including improved precision, reduced bias, estimation of otherwise confounded parameters, and the ability to use all available data to make the best possible inference on a population. To date, many IPMs have focused on populations with relatively simple life histories (e.g., only juvenile and adult stages). Here we demonstrate the usefulness of IPMs for mobile, long-lived species by incorporating a complex multistate projection model that reflects sex-specific life history characteristics and explicitly models movement patterns. Our model allowed for extended maternal care, variable reproductive intervals, hidden or partially observable states, sex-specific projection matrices that share information, estimation of parameters that lack direct data (e.g., C0 litter size), and integration of capture-recapture and satellite telemetry data. The model did not meet the assumption of independent datasets previously specified for IPMs, because capture data were used to estimate vital rates in the multievent portion of the model, and to estimate abundance in the count portion of the model. However, simulations suggest that violation of the independence assumption has relatively minor effects on estimates of sampling variance, while IPMs offer clear benefits in terms of precision and accuracy. Additional work is needed to better understand effects of violation of the independence assumption for species with complex life histories.

We used quantitative and qualitative information from the scientific literature and Traditional Ecological Knowledge (TEK) to establish informative Bayesian priors on some parameters. This can be beneficial when data are limited. For instance, breeding probability of adult females with C0s or C1s (β1) was weakly identifiable because it is a rare event for CS polar bears. As such, we included an informative prior based on previously published estimates, which improved parameter identifiability. Similarly, it can be advantageous to utilize prior information for population processes that are well documented. Polar bear survival has been estimated from multiple demographic case studies, which improved parameter identifiability. We included informative priors based on previously published estimates, which improved parameter identifiability. Similarly, it can be advantageous to utilize prior information for population processes that are well documented. Polar bear survival has been estimated from multiple demographic case studies (Supplementary Table S3). In developing our informative priors we assumed that these estimates were approximately unbiased and were informative about survival of CS bears. This was justified by ecological studies and TEK indicating that CS bears have exhibited good nutritional condition and reproduction in recent years, which suggests that survival has not been depressed through density-dependent mechanisms; and by the fact that human-caused removal rates were within the typical range for the species and we were not aware of other, atypical density-independent sources of mortality. Because our priors were based on survival estimates for subpopulations with variable demographic status and across a wide geographic range, they did not correspond to a specific demographic status (e.g., a negative or positive population growth rate) but rather represented empirical evidence for the range of survival rates exhibited by the global population of polar bears in recent decades. Although survival probabilities were estimable from the data alone, use of informative priors reduced the lower range of posterior distributions, which sometimes were implausible for a long-lived mammal when vague priors were used. Estimates of other vital rates and subpopulation abundance were robust to the choice of priors on survival, and the IPM framework is sufficiently flexible to accommodate changes to the sampling and analytical design that may improve parameter estimates and allow investigation of temporal variation. Extending our approach to an integrated spatially explicit capture-recapture framework should be an area of continued research, as it may better address the interconnectedness between animal movements, the dynamic nature of sea ice, detection probabilities, and demographic processes. Other potential future directions include: (i) increased sample size and expanded geographic distribution of sampling effort; (ii) using re-sightings of individuals within a sampling season to develop a robust design, providing more reliable estimates of survival and movements; (iii) developing telemetry tags that have a low failure rate, are worn for multiple years, and can be applied to all sex and age classes; and (iv) extrapolating densities using a habitat metric that reflects the distribution of prey, or integrating additional count data for the target species, to improve abundance estimates.

Summary. We developed a model that builds upon previous findings and incorporates prior information, and integrates multiple data types to estimate vital rates and provide the first empirical estimates of abundance for the CS polar bear subpopulation. Our analysis provides information that is urgently needed for conservation
planning and co-management of subsistence harvest by federal and Native partners under the U.S.-Russia Agreement. It also identifies study design considerations to help reduce future analytical assumptions, uncertainties, and potential biases. The methods presented here are broadly applicable to researchers interested in IPMs, particularly for large carnivores and other species that present similar research challenges.

Data Availability
Data for the CS polar bear subpopulation and computer code for the IPM are available in the Dryad Digital Repository repository: https://doi.org/10.5061/dryad.692jb15.

References
1. Rivera, C. J. Exploitation of endangered mammals in the United States. *Endanger Spec Res* 34, 185–190 (2017).
2. Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C. & Boitani, L. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos Trans R Soc Lond B Biol Sci* 366, 2642–2651 (2011).
3. Walther, G.-R. et al. Ecological responses to recent climate change. *Nature* 416, 389–393 (2002).
4. Ripple, W. J. et al. Status and Ecological Effects of the World’s Largest Carnivores. *Science* 343, 1241484 (2014).
5. Di Marco, M. et al. A Retrospective Evaluation of the Global Decline of Carnivores and Ungulates. *Conserv Biol* 28, 1109–1118 (2014).
6. Fletcher, D. et al. Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. *Methods Ecol. Evol.* 3, 206–216 (2012).
7. Peñalosa, C. L., Kendall, W. L. & Langtimm, C. A. Reducing bias in survival under nonrandom temporary emigration. *Ecol Appl* 24, 1155–1166 (2014).
8. Kendall, W. L. et al. Sampling design considerations for demographic studies: a case of colonial seabirds. *Ecol Appl* 19, 55–68 (2009).
9. Kendall, W. L., Nichols, J. D. & Hines, J. E. Estimating temporary emigration using capture-recapture data with Pollock’s robust design. *Ecology* 78, 563–578 (1997).
10. Taylor, M. & Lee, J. Distribution and abundance of Canadian polar bear populations: a management perspective. *Arctic* 48, 147–154 (1995).
11. Amstrup, S. C., Durner, G. M., Stirling, I., Lunn, N. J. & Messier, F. Movements and distribution of polar bears in the Beaufort Sea. Can J Zool 78, 948–966 (2000).
12. Wiig, Ø. et al. *Ursus maritimus*. The IUCN Red List of Threatened Species 2015: e.T22823A14871490, https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T22823A14871490.en. Accessed 06 January 2016 (2015).
13. USFWS (U.S. Fish and Wildlife Service). Endangered and threatened wildlife and plants; determination of threatened status for the polar bear (Ursus maritimus) throughout its range; final rule. *Federal Registrar* 73, 28211–28303 (2008).
14. Lunn, N. J. et al. Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. *Ecol Appl* 26, 1302–1320 (2016).
15. USFWS (U.S. Fish and Wildlife Service). Polar Bear (Ursus maritimus) Conservation Management Plan, Final, 59 pp (2016).
16. Regehr, E. V. et al. Conservation status of polar bears (Ursus maritimus) in relation to projected sea-ice declines. *Biol Lett* 12, https://doi.org/10.1098/rsbl.2016.0556 (2016).
17. Laidre, K. L. et al. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv Biol* 29, 724–737 (2015).
18. Atwood, T. C. et al. Forecasting the relative influence of environmental and anthropogenic stressors on polar bears. *Ecosphere* 7, 14–24 (2016).
19. Regehr, E. V., Wilson, R. R., Rode, K. D., Runge, M. C. & Stern, H. Harvesting wildlife affected by climate change: a modeling and management approach for polar bears. *J Appl Ecol* 54, 1534–1543 (2017).
20. Derøcher, A. E. et al. Rapid ecosystem change and polar bear conservation. *Conservation Letters* 6, 368–375 (2013).
21. Wilson, R. R., Horne, J. S., Rode, K. D., Regehr, E. V. & Durner, G. M. Identifying polar bear resource selection patterns to inform offshore development in a dynamic and changing Arctic. *Ecosphere* 5, https://doi.org/10.1890/14-00193.1 (2014).
22. Garner, G. W., McDonald, L. L. & Robson, D. S. Challenges in the estimation of population size for polar bears in western Alaska. *North American Wildlife and Natural Resources Conference* 59, 180–188 (1994).
23. Belikov, S. E. Number, distribution, and migrations of the polar bear in the Soviet Arctic. *Krupnye Khishniki (Big Predators)*. Moskva, CNIL Glavokhoty RSSSR, 74–84 (1992).
24. Rode, K. D. et al. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Glob Change Biol* 20, 76–88 (2014).
25. Rode, K. D. et al. Spring fasting behavior in a marine apex predator provides an index of ecosystem productivity. *Glob Change Biol* 1–14 (2017).
26. Durner, G. M., Laidre, K. L. & York, G. S. Polar Bears: Proceedings of the 18th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 7–11 June 2016, Anchorage, Alaska. Gland, Switzerland and Cambridge, UK. IUCN. xxx + 267pp (2018).
27. Besbeas, P., Freeman, S. N., Morgan, B. J. T. & Catchpole, E. A. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58, 540–547 (2002).
28. Pradel, R. The Stakes of Capture-Recapture Models with State Uncertainty in Modeling Demographic Processes in Marked Populations, *Environmental and Ecological Statistics* Vol 3 (eds. Thomson, D. L., Cooch, E. G. & Conroy, M. J.) 781–795 (New York: Springer, 2009).
29. Wilson, R. R., Regehr, E. V., Rode, K. D. & St Martin, M. Invariant polar bear habitat selection during a period of sea ice loss. *Proc R Soc Biol Sci Ser B* 283, 20160380, https://doi.org/10.1098/rspb.2016.0380 (2016).
30. Boyce, M. S. & McDonald, L. L. Relating populations to habitats using resource selection functions. *Trends Ecol Evol* 14, 268–272 (1999).
31. Regehr, E. V., Ben-David, M., Amstrup, S. C., Durner, G. M. & Horne, J. S. Chapter 4. Quantifying bias in capture-recapture studies for mobile species: a case study with polar bears; in Polar bear (Ursus maritimus) demography in relation to Arctic sea ice decline. PhD thesis, University of Wyoming (2009).
32. York, J., Dowsley, M., Cornwell, A., Kuc, M. & Taylor, M. Demographic and traditional knowledge perspectives on the current status of Canadian polar bear subpopulations. *Ecol. Evol* 6, 2897–2924 (2016).
33. Douglas, D. C. Arctic sea ice decline: projected changes in timing and extent of sea ice in the Bering and Chukchi Seas. *U.S. Geological Survey Open-File Report* 2010–1175 (2010).
34. Stirling, I., Spencer, C. & Andriashek, D. Mobilization of polar bears (Ursus maritimus) with Telazol® in the Canadian Arctic. *J Wildl Dis* 25, 159–168 (1989).
35. Regehr, E. V., Hunter, C. M., Caswell, H., Amstrup, S. C. & Stirling, I. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. *J Anim Ecol* 79, 117–127 (2010).
36. Rode, K. D. et al. Increased land use by Chukchi Sea polar bears in relation to changing sea ice conditions. *PLoS ONE* https://doi.org/10.1371/journal.pone.0142213 (2015).
37. Ramsay, M. A. & Stirling, I. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *J Zool* (Lond.) **214**, 601–634 (1988).

38. Hunter, C. M. *et al.* Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* **91**, 2883–2897 (2010).

39. Pradel, R. Multi-event: An extension of multistate capture-recapture models to uncertain states. *Biometrics* **61**, 442–447 (2005).

40. Plummer, M. JAGS version 3.3.0 user manual, http://mcmcs.jags.sourceforge.net/ (2012).

41. Kellner, K. jagsUI: a wrapper around rjags to streamline JAGS analyses. *R package version 1* (2015).

42. Ivan, J. S., White, G. C. & Shenk, T. M. Using auxiliary telemetry information to estimate animal density from capture-recapture data. *Ecology* **94**, 809–816 (2013).

43. Zipkin, E. F. & Saunders, S. P. Synthesizing multiple data types for biological conservation using integrated population models. *Biol Conserv* **217**, 240–250 (2018).

44. Weber, M. M., Stevens, R. D., Diniz, J. A. F. & Greille, C. E. V. Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography* **40**, 817–828 (2017).

45. Schliebe, S. *et al.* Co-management of the Alaskan harvest of the Alaska–Chukotka polar bear subpopulation: How to implement a harvest quota. *Wildlife Technical Bulletin ADF&G/DWC/WTB-2016-15* (Division of Wildlife Conservation, Alaska Department of Fish and Game, Juneau, Alaska, 2016).

46. Kochnev, A. & Zdor, E. *Harvest and Use of Polar Bears in Chukotka: Results of 1999–2012 Studies*. (Published in partnership with WWF-Russia, Association of Traditional Marine Mammal Hunters of Chukotka, Pacific Fisheries Research Center, and the Institute of Biological Problems of the North, Far East Branch, Russian Academy of Sciences, 2016).

47. Amstrup, S. C., Durner, G. M., McDonald, T. L., Mulcahy, D. M. & Garner, G. W. Comparing movement patterns of satellite-tagged male and female polar bears. *Can J Zool* **79**, 2147–2158 (2001).

48. Laidre, K. L. *et al.* Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). *Proc R Soc Biol Sci Ser B* **280**, https://doi.org/10.1098/rspb.2012.2371 (2013).

49. Stern, H. L. & Laidre, K. L. Sea-ice indicators of polar bear habitat. *The Crysopher* **10**, 2027–2041 (2016).

50. Bromaghin, J. F. *et al.* Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecol Appl* **25**, 634–651 (2015).

51. Grebmeier, J. M., Cooper, L. W., Feder, H. M. & Sirenko, R. I. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amurian Arctic. *Prog Oceanogr* **71**, 331–361 (2006).

52. Crawford, J. A., Quakenbush, L. T. & Citta, J. J. A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas. *Prog Oceanogr* **136**, 133–150 (2015).

53. Derocher, A. E. Latitudinal variation in litter size of polar bears: ecology or methodology? *Polar Biol* **22**, 350–356 (1999).

54. Molnár, P. K., Derocher, A. E., Thiemann, G. W. & Lewis, M. A. Predicting survival, reproduction and abundance of polar bears under climate change. *Biol Conserv* **143**, 1612–1622 (2010).

55. Noyce, K. V. & Garshelis, D. L. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *International Conference of Bear Research and Management* **91**, 481–496 (1994).

56. Serreze, M. C., Crawford, A. D.; Stroeve, J. C., Barrett, A. P. & Woodgate, R. A. Variability, trends, and predictability of seasonal sea ice retreat and advance in the Chukchi Sea. *Journal of Geophysical Research-Oceans* **121**, 7308–7325 (2016).

57. Rode, K. D., Robbins, C. T., Nelson, L. & Amstrup, S. C. Male and female polar bears use terrestrial foods to offset lost ice-based hunting opportunities? *Front Ecol Environ* **13**, 138–145 (2015).

58. Whitman, J. P. *et al.* Phenotypic plasticity and climate change: can polar bears respond to longer Arctic summers with an adaptive fast? *Oecologia*, https://doi.org/10.1007/s00442-017-4023-0 (2017).

59. Laire, K. L., Stirling, I., Estes, J. A., Kochnev, A. & Roberts, J. Historical and potential future importance of large whales as food for polar bears. *Front Ecol Environ*, https://doi.org/10.1002/fee.1963 (2018).

60. McDonald, L. L., Garner, G. W. & Robertson, D. G. Comparison of aerial survey procedures for estimating polar bear density: Results of pilot studies in northern Alaska in *Marine mammal survey and assessment methods* (eds. Garner, G. W. et al.) 37–51 (Rotterdam, Netherlands: A.A. Balkema Publishers, 1999).

61. Evans, T. J. *et al.* Polar Bear Aerial Survey in the Eastern Chukchi Sea: a Pilot Study. *Arctic* **56**, 359–366 (2003).

62. Hebblewhite, M., Miguele, D. G., Murzin, A. A., Aramilev, V. V. & Pukinov, D. G. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biol Conserv* **144**, 2403–2413 (2011).

63. Boyce, M. S. *et al.* Can habitat selection predict abundance? *J Anim Ecol* **85**, 11–20 (2016).

64. Durner, G. M. *et al.* Predicting 21st-century polar bear habitat distribution from global climate models. *Ecol Monogr* **79**, 25–58 (2009).

65. Hill, V., Ardyna, M., Lee, S. H. & Varela, D. E. Decadal trends in phytoplankton production in the Pacific Arctic Region from 1950 to 2012. *Deep-Sea Research II* **152**, 82–94 (2018).

66. Schaub, M. & Abadi, F. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J Ornithol* **152**, 227–231 (2011).

67. Arnold, T. W., Clark, R. G., Koons, D. N. & Schaub, M. Integrated Population Models Facilitate Ecological Understanding and Improved Management Decisions. *J Wildl Manage* **82**, 266–274 (2018).

68. Abadi, E., Gimezene, O., Arletzetta, R. & Schaub, M. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* **91**, 7–14 (2010).

69. Braund, S. C. *et al.* Polar Bear TEK: A Pilot Study to Inform Polar Bear Management Models. *Research Report NSB.DWM.RR.2018-01* (North Slope Borough Department of Wildlife Management, Utqiagvik, Alaska, 2018).

70. Derocher, A. E. & Taylor, M. K. Latitudinal variation in litter size of polar bears: ecology or methodology? *Polar Biol* **22**, 350–356 (1999).

71. Eberhardt, L. L. Survival rates required to sustain bear populations. *J Wildl Manage* **54**, 587–590 (1990).

72. Chandler, R. B. & Clark, J. D. Spatially explicit integrated population models. *Methods Ecol Evol* **5**, 1351–1360 (2014).

73. Kendall, W. L. *et al.* Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods Ecol Evol* **4**, 828–835 (2013).

74. USFWS (U.S. Fish and Wildlife Service). Co-Management of Subsistence Use of Polar Bears by Alaska Natives; Conservation of the Alaska-Chukotka Polar Bear Population. *Federal Register R18(216)*, 78560–78564 (2016).

75. Regehr, E. V., Hostetter, N. J., Rode, K. D., St. Martin, M. & Converse, S. J. Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.692zb15 (2018).

76. Waterson, K., Meier, W., Savoie, M. & Windnagel, A. K. Sea Ice Index, Version 3.0. Boulder, Colorado USA NSIDC: National Snow and Ice Data Center, https://doi.org/10.7265/N5K072F8 (2017, updated daily).
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Author Contributions

E.V.R., K.D.R. and R.R.W. conceived and designed the study. E.V.R., M.S.M., R.R.W. and K.D.R. performed the fieldwork. N.J.H., E.V.R., S.J.C., R.R.W. and K.D.R. analyzed the data. All authors contributed to and reviewed the manuscript.

Additional Information

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