

PRIMARY RESEARCH ARTICLE

Iterative model predictions for wildlife populations impacted by rapid climate change

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Abstract

To improve understanding and management of the consequences of current rapid environmental change, ecologists advocate using long-term monitoring data series to generate iterative near-term predictions of ecosystem responses. This approach allows scientific evidence to increase rapidly and management strategies to be tailored simultaneously. Iterative near-term forecasting may therefore be particularly useful for adaptive monitoring of ecosystems subjected to rapid climate change. Here, we show how to implement near-term forecasting in the case of a harvested population of rock ptarmigan in high-arctic Svalbard, a region subjected to the largest and most rapid climate change on Earth. We fitted state-space models to ptarmigan counts from point transect distance sampling during 2005–2019 and developed two types of predictions: (1) *explanatory predictions* to quantify the effect of potential drivers of ptarmigan population dynamics, and (2) *anticipatory predictions* to assess the ability of candidate models of increasing complexity to forecast next-year population density. Based on the explanatory predictions, we found that a recent increasing trend in the Svalbard rock ptarmigan population can be attributed to major changes in winter climate. Currently, a strong positive effect of increasing average winter temperature on ptarmigan population growth outweighs the negative impacts of other manifestations of climate change such as rain-on-snow events. Moreover, the ptarmigan population may compensate for current harvest levels. Based on the anticipatory predictions, the near-term forecasting ability of the models improved nonlinearly with the length of the time series, but yielded good forecasts even based on a short time series. The inclusion of ecological predictors improved forecasts of sharp changes in next-year population density, demonstrating the value of ecosystem-based monitoring. Overall, our study illustrates the power of integrating near-term forecasting in monitoring systems to aid understanding and management of wildlife populations exposed to rapid climate change. We provide recommendations for how to improve this approach.

KEYWORDS

Arctic, climate change, management, near-term forecasting, prediction, ptarmigan, Svalbard, winter temperature

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1 | INTRODUCTION

The climate is currently changing to the extent that ecological systems are moving away from the boundaries of historical variation and established empirical relations, experiencing previously unseen conditions (Malhi et al., 2020). Understanding how species and ecosystems will be impacted by climate change is challenging and requires a combination of different approaches (Turner et al., 2020). However, it is generally recognized that long-term monitoring represents a baseline approach for climate-ecological studies (Gauthier et al., 2013; Hughes et al., 2017; Ims & Yoccoz, 2017; Schmidt et al., 2017). The time series data generated from appropriately designed monitoring systems serve several purposes (Likens & Lindenmayer, 2010). They allow the detection of both fast and slow changes (Hastings et al., 2018). Analyses and modeling of such data provide opportunity to generate both *explanatory predictions* (i.e., those used to test theories) and *anticipatory predictions* (i.e., those used to inform future decisions; Maris et al., 2018; Mouquet et al., 2015).

Because predicting long-term effects of climate change is extremely challenging, and forecasts of future scenarios are affected by high uncertainty (Planque, 2016), ecologists advocate focusing on near-term predictions (Dietze, 2017; Dietze et al., 2018; Petchey et al., 2015; White et al., 2019). This scheme implies routine generation of forecasts of an ecological target, and evaluation of the accuracy of the forecasts by comparing them with new observations as soon as they become available. The iterative nature of the near-term forecasting approach reflects the hypothetico-deductive reasoning of the scientific method (Dietze et al., 2018; Houlahan et al., 2017). The short timescale used for predictions allows analyses to be repeated, models to be validated, and evidence to increase rapidly (Dietze et al., 2018). The near-term forecasting approach has proved especially profitable to deal with ecosystems, species, or populations subject to management (Henden et al., 2020; Nichols et al., 2015), because forecasts are generated at a timescale that can be influenced by decision-making. Near-term forecasting, in fact, constitutes the foundation of adaptive management (Nichols et al., 2015). Arguably, this approach also ought to be particularly useful when integrated in the adaptive monitoring of ecosystems subjected to rapid climate change (Ims & Yoccoz, 2017). Examples of such endeavors, however, are still rare in ecology (Nichols et al., 2019).

The main aim of the present study is to explore and exemplify how state-space models parameterized from time series monitoring data can be used to explain and forecast wildlife population dynamics in environments subjected to rapid change. For this purpose, we use a case study from the high-Arctic Archipelago of Svalbard, Norway (74–81°N, 15–30°E). The Arctic is one of the regions on the Earth experiencing major environmental changes, mostly due to global warming (Ims, Ehrich, et al., 2013). Polar regions warm faster than the rest of the world (Serreze & Barry, 2011) and the trend is projected to continue in the twenty-first century (Koenigk et al., 2020). In Svalbard, higher annual mean temperatures (Nordli et al., 2014), warmer and wetter winters (Hansen et al., 2014), decreased snow cover duration and depth (Descamps et al., 2017), and declined sea ice extent (Dahlke et al., 2020) are indicators of ongoing changes in

the climate system. Svalbard, in fact, is probably the subregion of the Arctic that has experienced the most profound warming during the last decade (Isaksen et al., 2016; Nordli et al., 2014). Climate change impacts on the species belonging to the relatively simple terrestrial food web of Svalbard have already been detected (Descamps et al., 2017; Ims et al., 2013). Most emphasis has been placed on the negative effect of formation of basal ice in winter following rain-on-snow (ROS) events (Rennert et al., 2009), which synchronizes population dynamics across mammal species (Hansen et al., 2013; Stien et al., 2012) and especially among reindeer populations (Hansen, Pedersen, et al., 2019) by hindering forage access. Recent studies have also dealt with climate change impacts on migratory geese in Svalbard (Layton-Matthews et al., 2019; Tombre et al., 2019). Less is known about other phenomena associated with climate change and its impact on other taxa (but see Bjerke et al., 2017; Coulson et al., 2000).

Although Svalbard has become a renowned showcase for the impacts of rapid climate warming on wildlife populations (Descamps et al., 2017; Hansen et al., 2013; Hansen, Gamelon, et al., 2019), the present study is the first to apply the approach of iterative near-term forecasting. We focused on the Svalbard rock ptarmigan *Lagopus muta hyperborea*, a high-arctic subspecies of the rock ptarmigan and among the planet's most northerly year-round resident birds. Because the Svalbard rock ptarmigan is an endemic subspecies subjected to harvesting and is predicted to be sensitive to climate change in several ways (Henden et al., 2017; Ims, Jepsen, et al., 2013), it is rigorously monitored to both assess its status and aid its management (Pedersen et al., 2012). However, little is known about what drives its population dynamics and how it is impacted by climate change and harvest in Svalbard (but see Pedersen et al., 2014). The time series of the Svalbard rock ptarmigan population is part of an ecosystem-wide monitoring system that encompasses the period of the most rapid recent climate warming with associated changes in the abiotic and biotic domains of the Svalbard terrestrial ecosystem. The rigorous sampling methods applied to the target population at an extensive spatial scale enabled us to fit dynamic state-space population models to the monitoring data. These models were used to derive two types of predictions: (1) *Explanatory predictions* to quantify the effect of potential drivers of ptarmigan population dynamics, and (2) *anticipatory predictions* to assess the ability of candidate models of increasing complexity to forecast next-year population density. We expected that the combination of the two types of predictions would be particularly suitable in case of populations that are exposed to novel conditions and thereby may exhibit fundamentally changed dynamics.

2 | MATERIALS AND METHODS

2.1 | Sampling design and ptarmigan monitoring protocol

The study area is located in Spitsbergen, Nordenskiöld Land (78°15'N, 17°20'E), within the middle Arctic tundra zone and is centered on the large, glacial valleys of Adventdalen and Sassendalen.

These valleys are characterized by wetland, ridge, and heath vegetation communities and surrounded by peaks reaching 1200 m a.s.l. (Pedersen et al., 2012; Soininen et al., 2016). In April, ptarmigan males establish territories and display territorial behavior (Unander & Steen, 1985). To estimate the pre-breeding population density (males/km²), we used a long-term annual monitoring time series obtained from point transect distance sampling conducted by the Norwegian Polar Institute on calling territorial males during 4 weeks in April (Pedersen et al., 2012). We used data from 2005 to 2019, when a sampling design based on 148 survey points in a study area of ca. 1200 km² was established and systematically perpetuated (Figure S1). Of the 148 survey points, 101 were nonrandomly selected based on altitude and terrain characteristics that are known to be preferred ptarmigan habitats (henceforth “non-random points”). The remaining 47 points were randomly assigned and included in the sampling design to sample also suboptimal ptarmigan habitats (henceforth “random points”; Pedersen et al., 2012). To reduce observer bias during the surveys, each survey point is visited two or three times per season, each time by a different trained observer. Each visit lasts 15 min and the radial distance to birds observed on ground is measured using a laser distance binocular. For details regarding the sampling protocol, see Pedersen et al. (2012). Because ptarmigan calls can travel great distances and increase the risk of double counting, we excluded aural-only detections from the data.

2.2 | Expectations and predictor variables

Expectations regarding potential drivers of the dynamics of Svalbard rock ptarmigan populations were derived from Henden et al. (2017) and Ims, Jepsen, et al. (2013) and are summarized in Figure 1. Because the knowledge about the response of Svalbard rock ptarmigan to environmental fluctuations is limited, expectations are partly based on current evidence from other arctic and alpine ptarmigan populations.

2.2.1 | Abiotic variables

Inclement weather conditions are likely to affect early chick survival, which is regarded as a critical demographic component of several grouse species (Hannon & Martin, 2006; Ludwig et al., 2018). A combination of low temperatures (Ludwig et al., 2010) and heavy rainfall (Kobayashi & Nakamura, 2013; Novoa et al., 2016) is expected to be particularly detrimental by preventing food intake and hindering thermoregulation (Erikstad & Spidsø, 1982, 1983). We obtained local weather data from the Svalbard airport weather station in Longyearbyen (78°14'46"N, 15°27'56"E) collected by the Norwegian Meteorological Institute (available at <http://seklima.met.no>). We extracted data on daily mean temperature and daily maximum precipitation for the first week of July to cover the critical period for early ptarmigan chick survival and calculated mean temperature (°C) and cumulative precipitation (mm).

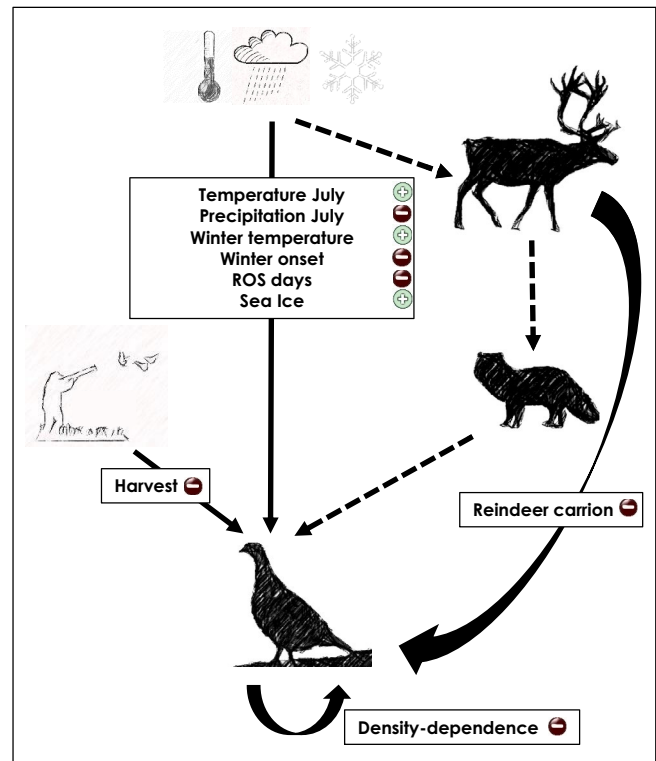


FIGURE 1 Conceptual model depicting potential drivers of Svalbard rock ptarmigan population dynamics. Solid arrows represent direct paths that were included in the models and parameterized, dashed arrows represent the hypothesized mechanisms behind indirect effects. +/- denotes the expected direction of the relationship. Predictors and units of measurement are described in Section 2.2 in the main text. ROS, rain-on-snow

Based on the extreme physiological adaptation in terms of fat deposition of this subspecies (body fat normally exceeds 30% of the bird body mass at the onset of winter; Grammelvedt & Steen, 1978; Mortensen et al., 1983; Steen & Unander, 1985), it is evident that winter weather is critical in the life cycle of the Svalbard rock ptarmigan. Accordingly, we had strong expectations regarding the influence of changes in winter climate on ptarmigan survival. With increasingly warmer winters (Hanssen-Bauer et al., 2019), ptarmigan are expected to reduce their need for energy consumption, that is, consume less body reserves, thereby improving their winter survival. Changes in winter climate concern also snow duration, which is now shorter than in the past, due to late snow arrival and early snow melt (Descamps et al., 2017; Liston & Hiemstra, 2011). Late onset of winter has been shown to hamper survival of color molting species including ptarmigan (Henden et al., 2020; Melin et al., 2020), likely due to camouflage mismatch resulting in elevated predation rates (Zimova et al., 2016). We used daily temperature data to calculate mean temperature (°C) in the core winter season (December_{t-1}–March_t) and onset of winter (Julian day). The latter is defined as the day when the average of a 10 day forward-moving window was below 0°C for the first time in autumn and remained below 0°C for ≥10 days (Le Moullec et al., 2019).

Rain-on-snow events can cause basal ice formation, which encapsulates ground vegetation and affects ptarmigan by preventing

forage access during winter (Hansen et al., 2013, 2014). Following Hansen et al. (2013), we used daily temperature and precipitation to calculate an index of ROS, that is, the number of rainy days (with rain ≥ 1 mm and temperature $\geq 1^\circ\text{C}$) in the core winter season (December_{*t-1*}–March_{*t*}).

In Svalbard, marine resources dominate the diet of the arctic fox *Vulpes lagopus* (Ehrich et al., 2015; Eide et al., 2005; Prestrud & Nilssen, 1992), the only year-round predator of Svalbard rock ptarmigan. This indicates that sea ice is an important hunting platform for the arctic fox in winter. As sea ice cover in the fjords declines due to global warming (Dahlke et al., 2020), arctic foxes may be forced to rely more on terrestrial prey resources like ptarmigan. Time series of average sea ice extent in the fjords of Svalbard was calculated using ice charts issued by the Norwegian Ice Service since 1969 (Dahlke et al., 2020) and used as a proxy for accessibility of marine resources to arctic fox during winter. We calculated the mean of the monthly average sea ice extent (km²) in the core winter season (December_{*t-1*}–March_{*t*}) for the period 2005–2019 (see Appendix S1 for details).

2.2.2 | Biotic variables

Reindeer carrion constitute an important winter food resource for the arctic fox (Eide et al., 2005; Fuglei et al., 2003). High reindeer mortality can occur following heavy ROS events (Hansen et al., 2013; Hansen, Pedersen, et al., 2019). Abundant reindeer carrion during winter may cause arctic foxes to respond numerically through increased survival and reproduction, eventually leading to higher predation pressure on ground-breeding birds like ptarmigan (Eide et al., 2012; Hansen et al., 2013; Marolla et al., 2019). Counts of reindeer carcasses are carried out every summer (June–July) in the valley of Adventdalen since 1979. Five to six observers walk predefined routes located less than 1 km apart to monitor the whole study area within a week. They scan the area with 10 × 42 mm binoculars and record the position of each spotted reindeer carcass on a map. Reindeer carcasses are easily detected as large, white spots on the treeless tundra. Given the low decomposition rate of reindeer hairs and bones, we assumed that the number of carcasses found in the summer is representative of carrion abundance during the preceding winter. We also assumed that the temporal variation in the number of reindeer carcasses in Adventdalen is representative of the variation in the neighboring valley of Sassendalen. This is supported by the high correlation between annual number of carcasses in two adjacent monitoring areas, Adventdalen and Reindalen (r [95% CI] = 0.93 [0.83; 0.97]).

The population dynamics of Svalbard rock ptarmigan are also likely to be subject to density-dependent processes (e.g., in the form of saturated breeding habitats, Pedersen et al., 2014), and negatively influenced by human harvesting that is regulated by the local government. Harvesting has been regulated since 1998 and today occurs between September 10 and December 23. While hunters must obtain a hunting license from the Governor of Svalbard, there is no limit to the number of issued licenses (Soininen et al., 2016). Hunters—mostly

residents—report the number of birds harvested and an indication of the locality of shooting, while hunting effort is not systematically reported. Hence, bag limits are not based on an assessment of sustainable harvest. For our analysis, we used the number of birds harvested from 2005 to 2018 in the study area. We excluded birds harvested by trappers, who tend to live in remote places far from the study area. Hunting statistics are available at the website of MOSJ (Environmental Monitoring of Svalbard and Jan Mayen; <http://www.mosj.npolar.no>).

Note that the predictor variables were measured at the study area scale rather than at the ptarmigan monitoring scale (i.e., the survey points) because information on spatial variability of predictors was not available. Time series data for all the predictors are shown in Figure S2.

2.3 | Models and predictions

2.3.1 | Model structure

We applied a modified version of the Hierarchical Distance Sampling model described by Kéry and Royle (2016) to model point transect distance sampling counts of ptarmigan performed in 2005–2019 over the 148 survey points. This state-space model allows explicit modeling of the spatiotemporal variation in ptarmigan abundance while accounting for detection errors. It consists of two parts, a detection model that estimates detection probability and a dynamic process model that models spatiotemporal variation in population growth rate. The detection process is based on the distance sampling likelihood for point transect data (Buckland et al., 2001). We used a half-normal detection function to describe the decline of detection probability p of an observed bird with the radial distance d from the observer,

$$\log(p) = \frac{d^2}{2\sigma_s^2}, \quad (1)$$

where σ is the half-normal scale parameter at point s . We modeled σ as a log link function of site-specific terrain covariates (terrain ruggedness, aspect, and slope; data obtained from a 20 × 20 m digital elevation model of the study area) to account for their influence on detection probability. To reduce the effect of potential inaccurate distance estimations and movements of birds reacting to observer's presence, we grouped data into eight 50 m distance classes, up to a maximum distance of 400 m from the center of the survey point based on the frequency distribution of detection distances (Kéry & Royle, 2016). The site-specific detection probability pcap_s is then calculated as the integral of the distance function over the distance classes (Kéry & Royle, 2016). The process model consists of a sub-model for the first year (i.e., initial density) and a Gompertz population dynamics model for the consecutive years. In the dynamic part of the model, we used the average detection probability pcap_s to link the sum of observed counts of ptarmigan males y across repeated visits N_{rep} at each point s in year t to the average latent abundance $N_{s,t}$:

$$y_{s,t} \sim \text{binom}(N_{s,t} * N_{\text{rep}_{s,t}}, \text{pcap}_s), \quad (2)$$

where $N_{s,t}$ is assumed to be a Poisson random variable with $E[N_{s,t}] = \lambda_{s,t}$ and $\lambda_{s,t}$ is modeled as the product of ptarmigan density $D_{s,t}$ and the observable size of the surveyed area. The latter was estimated specifically for each survey point by a viewshed analysis that accounted for different terrain morphology affecting the observer's view (Appendix S2). Finally, we assumed log density to be a normal random variable with mean $\mu_{s,t}$ and process error variance σ_{proc}^2

$$\log(D_{s,t}) \sim \text{norm}(\mu_{s,t}, \sigma_{\text{proc}}^2), \quad (3)$$

and modeled $\mu_{s,t}$ as function of a set of a priori-selected predictors

$$\mu_{s,t} = \beta O_{\text{areas}} + rCl + \beta_{\text{DD}} \mu_{s,t-1} + \beta_x X_t, \quad (4)$$

where βO_{areas} is a fixed covariate with three levels (i.e., Adventdalen random, Adventdalen nonrandom, and Sassendalen) accounting for differences between macro-valleys and different survey point selection strategies, rCl is a random cluster effect (i.e., $rCl \sim \text{Norm}(0, \sigma_{\text{Cl}}^2)$) accounting for potential non-independence of observations at points located close to each other (with the number of clusters estimated by a hierarchical clustering algorithm), $\beta_{\text{DD}} \mu_{s,t-1}$ is the density dependence parameter based on the log density the year before, and $\beta_x X_t$ is a set of a priori-selected predictors. The low annual number of random points surveyed in Sassendalen did not allow us to model random and nonrandom points in this valley separately. On the log scale, the classic Gompertz model becomes a linear autoregressive time series model of order 1 (Dennis et al., 2006); thus, effects of predictors are modeled on the growth rate. This model structure was applied

to all years except the first (i.e., initial density, $t = 1$), which had a similar but simpler structure,

$$\mu_{s,1} = \beta 1_{\text{areas}} + rCl_1, \quad (5)$$

where $\beta 1_{\text{areas}}$ and rCl_1 ($rCl_1 \sim \text{Norm}(0, \sigma_{\text{Cl}1}^2)$) have the same significance as in the dynamics model (i.e., $t > 1$).

2.3.2 | Explanatory predictions

To evaluate the effect of the selected predictors on ptarmigan growth rate, we developed a suite of models including different combinations of predictors and assessed the consistency of effect size estimates across models (Table 1). We considered the following predictors: mean temperature and maximum precipitation in the first week of July, mean winter temperature, day of winter onset, number of winter days with ROS, sea ice extent, number of reindeer carcasses, and number of ptarmigan harvested. We also included a trend parameter to account for any excess trend in the data that was not explained by the predictors. While including a phenomenological trend parameter may cause issues of multicollinearity when covariates also exhibit trends, none of our predictors—except for day of winter onset—showed a significant trend in the period we considered (but many of them show trends when longer time series are considered). Except for ROS, winter temperature, and sea ice extent—predicted to influence winter survival and recruitment and thus modeled at time t —all the other variables were modeled at time $t - 1$, because they were expected to influence reproduction and survival during summer and autumn. We point out that, although ROS events can cause high mortality in reindeer, there is no confounding between the variables accounting for ROS and reindeer carrion effects, because the former tests for a

TABLE 1 Combination of predictors in the candidate models. The table indicates also whether a given model was used for explanatory predictions or anticipatory predictions, or both

Variable	WT_Climate	WT_Carrion	WT_Carrion2	SI_Climate	SI_Carrion	SI_Carrion2	PT
Temperature July	X	X	X	X	X	X	–
Precipitation July	X	X	X	X	X	X	–
Winter temperature	X	X	X	–	–	–	–
Winter onset	X	X	X	X	X	X	–
ROS days	X	X	–	X	X	–	–
Sea ice	–	–	–	X	X	X	–
Reindeer carrion	–	X	X	–	X	X	–
Harvest	X	X	X	X	X	X	X
Density dependence	X	X	X	X	X	X	X
Trend	X	X	X	X	X	X	–
Explanatory predictions	Yes	Yes	Yes	Yes	Yes	Yes	No
Anticipatory predictions	Yes	Yes	No	No	No	No	Yes

Abbreviations: PT, Ptarmigan model; ROS, rain-on-snow; SI_Carrion, SI_Climate with the addition of Reindeer Carrion; SI_Carrion2, SI_Carrion without ROS days; SI_Climate, “climate-impact” model including Sea Ice; WT_Carrion, WT_Climate with the addition of Reindeer Carrion; WT_Carrion2, WT_Carrion without ROS days; WT_Climate, “climate-impact” model including Winter Temperature.

direct impact of ROS through inaccessible vegetation, while the latter tests for a delayed, indirect effect of carrion abundance that may be due to ROS events and/or other phenomena (e.g., density-dependent processes; Hansen, Gamelon, et al., 2019).

Because winter temperature and sea ice extent were highly correlated (r [95% CI] = -0.74 [-0.91 ; -0.34]), we modeled their effect in two separate “climate-impact” models containing all the other climate variables (WT_Climate and SI_Climate models in Table 1). Moreover, we extended the two climate-impact models by the inclusion of the effect of reindeer carrion abundance (WT_Carrion and SI_Carrion models in Table 1). However, because the number of reindeer carcasses was somewhat correlated with winter temperature, sea ice extent, and ROS, we also run WT_Carrion and SI_Carrion without ROS (WT_Carrion2 and SI_Carrion2 models in Table 1) to evaluate the consistency of estimates. We scaled the values of all predictor variables by subtracting their mean and dividing by their standard deviation to ease interpretation of coefficients and model convergence. We fitted the models using Markov Chain Monte Carlo methods implemented in JAGS (Plummer, 2003) through the R package jagsUI (Kellner, 2015), assigning vague priors to the parameters. We run 400,000 iterations on four chains at a thinning rate of 50, burn-in of 4000, and adaptation phase of 80,000, yielding 31,680 samples. Convergence of parameter estimates was evaluated by ensuring that the Gelman–Rubin convergence statistics R -hat was below 1.1 (Brooks & Gelman, 1998). We provide the JAGS code in Appendix S3.

2.3.3 | Anticipatory predictions

We implemented the near-term forecasting approach by using our model to predict next-year ptarmigan density, following Henden et al. (2020). We sequentially fitted the models to the time series of ptarmigan counts spanning $t = 10$ – 14 years of prior data. For each time step, we predicted next-year point-specific density ($t + 1$) using the estimated model parameters from previous years of data (Appendix S4). We assessed whether the addition of abiotic and biotic predictors improved model's forecasting ability by comparing a climate-impact model (WT_Climate) and its extension including reindeer carrion abundance (WT_Carrion) to a simpler model containing only ptarmigan data (i.e., density dependence and harvest; PT). We then compared predicted densities to observed densities for each survey point by calculating the symmetric mean absolute percentage error (sMAPE, Makridakis et al., 2018; Appendix S4). A fundamental aspect of iterative near-term forecasting is the opportunity to update the models not only with new data but also with incoming evidence about model parameters. At each model run, therefore, we used the parameter estimates generated from the previous model run to initiate the MCMC chains, thereby providing the model with an indication of plausible parameter values. To address the contribution of measurement error to the predictive performances of the models, we compared each sMAPE to a theoretical minimum prediction error expected from a “perfect”

Poisson process model (Appendix S4). Finally, we assessed whether the WT_Climate and WT_Carrion models were better than the PT model at forecasting next-year mean density, which is a measure of practical management value. It was not possible to perform this whole analysis for the SI_Climate and SI_Carrion models because parameters of the latter failed to reach convergence when it was fitted to reduced time series.

3 | RESULTS

3.1 | Density and detection probability

Estimated average model-based densities of territorial ptarmigan males ranged between 0.4 and 6.1 individuals/km² (Figure 2a; Figure S3). As could be expected, nonrandom points in Adventdalen exhibited the highest densities, but overall densities were similar in Adventdalen and Sassendalen given the high proportion of nonrandom points in Adventdalen. Both valleys showed an increasing trend in density from 2014 regardless of the point selection strategy, but with substantial between-year variation especially toward the end of the series.

Detection probability was generally low and did not vary substantially across survey points (mean = 0.34; SD = 0.02; range = [0.29–0.39]). There was no evidence of terrain covariates influencing detection probability, except for a small negative effect of terrain aspect (mean [95% CI] = -0.032 [-0.063 ; -0.002]).

3.2 | Explanatory predictions

Most of the estimates of predictor effects on ptarmigan growth rate pointed in the expected directions. However, due to large uncertainty in effect sizes across models, the evidence was far from conclusive for most of them (Figure 3; Table S1). Mean winter temperature consistently showed the strongest effect on ptarmigan growth rate, with highly coherent positive estimates across models. Sea ice extent, as could be expected from the high negative correlation with winter temperature, had a strong negative effect. Among the other predictors, the negative effects of ROS and reindeer carrion abundance were the most consistent, despite large uncertainty. The effect of mean temperature in the first week of July was always positive and the effect of cumulative precipitation in the same week mostly negative, but effect sizes varied across models and credible intervals tended to overlap zero. Similarly, the effect of winter onset was always negative but with low consistency of estimates. While there was no evidence for an influence of harvest on ptarmigan growth rate, there was evidence of negative density dependence, albeit large credible intervals limited the inference about the strength of the effect. Finally, a positive estimate of the trend parameter denoted a small excess temporal trend in the growth rate. This suggests that the predictors in the model and/or the model structure did not account for all the variation in population growth rate.

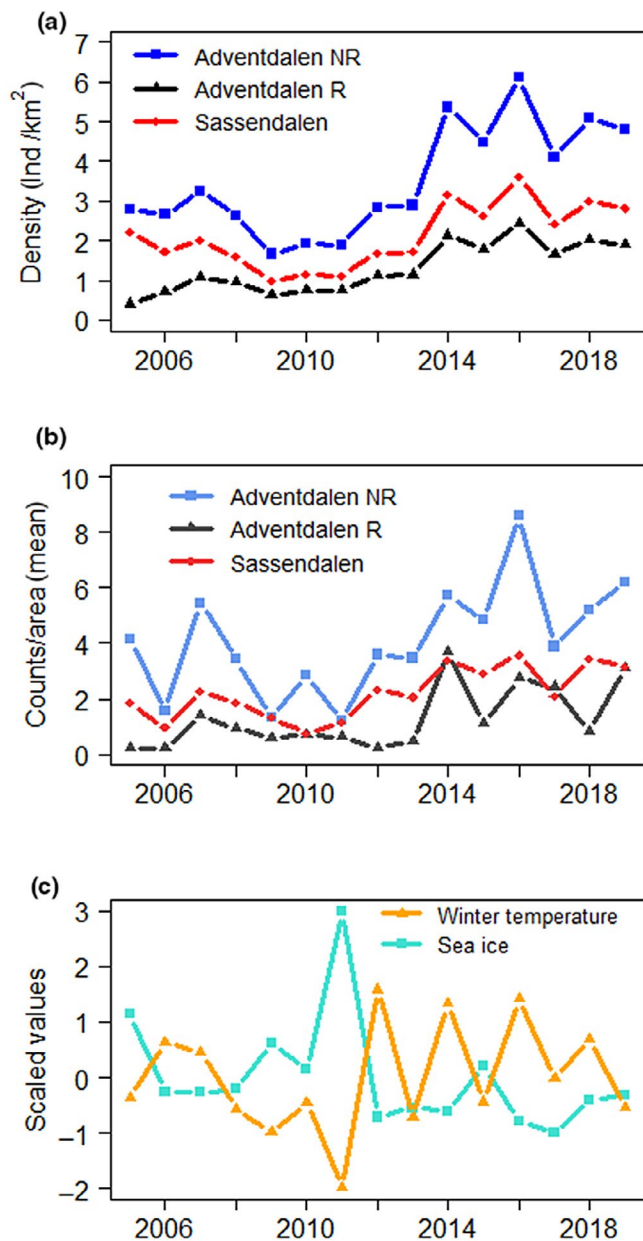


FIGURE 2 (a) Average area-specific model-based estimates of Svalbard rock ptarmigan male population density (males/km²) for the period 2005–2019 from the WT_Climate model (“climate-impact” model including Winter Temperature). Sassendalen includes random and nonrandom points together. (b) Average area-specific observed density for the period 2005–2019. Legend abbreviations as in panel (a). Note the scale on the y-axis differs between panels (a) and (b). (c) Time series of winter temperature and sea ice extent in the study area. Values are scaled to ease comparison. NR, nonrandom survey points; R, random survey points

3.3 | Anticipatory predictions

The near-term predictive performances of the three candidate models used for anticipatory predictions (i.e., PT, WT_Climate, and WT_Carrion; Table 1) tended to increase with more years of

data (i.e., the length of the time series; Figure 4). On average, the sMAPE of our models was approximately 30% higher than that expected from a “perfect” Poisson process model (Figure 4). However, there was a small trend toward lower prediction error with more years of data. At the end of the time series, the discrepancy between models' prediction error and minimum prediction error was approximately 20%. While, in the end, the PT model displayed the lowest sMAPE, the WT_Carrion model showed the largest improvement from 2015 to 2019 (Δ sMAPE_{PT} ≈ 12%; Δ sMAPE_{WT_Climate} ≈ 12%; Δ sMAPE_{WT_Carrion} ≈ 16%).

In general, the models predicted next year's density fairly well, at least in the sense of anticipating population increase and decrease (Figure 5). Overall, the WT_Climate model performed slightly better compared to the PT and the WT_Carrion model. Although predictions from the PT model were closer to the observed density in some years (i.e., 2015 and 2019), the WT_Climate model displayed greater ability to predict larger changes in ptarmigan density in consecutive years (i.e., 2016 and 2017).

4 | DISCUSSION

We have here used rock ptarmigan population monitoring data from high-arctic Svalbard with the aim of showing more generally how the combination of explanatory and anticipatory model predictions may promote efficient learning about the impact of rapid climate change on wildlife populations. We did this by first exploring whether state-space models could identify the drivers of a recent trend in the target population (Fuglei et al., 2020) and next by assessing whether these models (and drivers) could yield reasonable near-term forecasts of population states in an era of rapid climate warming. Benefitting from a spatially extensive and statistically rigorous monitoring design of the target populations and access to other relevant ecosystem data that could be fitted as predictors, we were able to parameterize state-space models that indeed achieved these goals.

4.1 | Explanatory predictions

Among the four seasons, winter temperature shows the largest increase in Svalbard, alongside spring temperature. In the period 1971–2017, the increase in average winter temperature ranged between 3 and 5°C (Hanssen-Bauer et al., 2019), with at least six of the 10 warmest winters occurring after 2000 (Isaksen et al., 2016; Nordli et al., 2014). In the years following 2012, ptarmigan density fluctuated in remarkable synchrony with winter temperature (Figure 2). Svalbard rock ptarmigan's adaptations to the harsh conditions of the arctic winter are exceptional and involve behavioral, morphological, and physiological adjustments (Nord & Folkow, 2018). Among these, deposition of fat stores plays a fundamental role in terms of energy store and thermal insulation (Mortensen & Blix, 1986; Stokkan et al., 1985). Our results add support to the notion that warmer winters

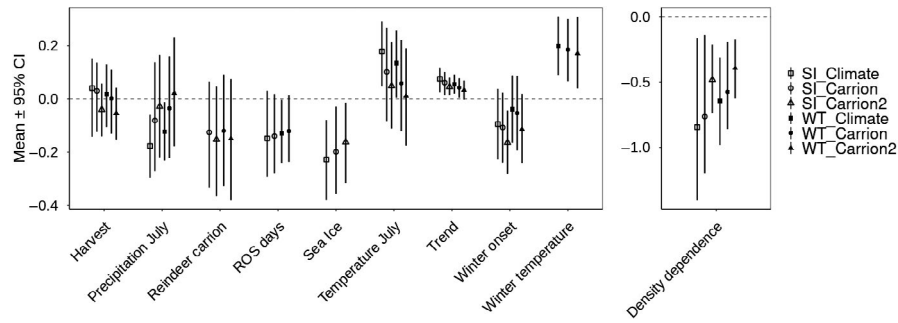


FIGURE 3 Mean \pm 95% credible intervals of estimated posterior distributions of scaled predictors. Abiotic and biotic effects and density dependence are reported separately for graphical purposes. Note the scale on the y-axis differs between (a) and (b). Effects should be interpreted as change in ptarmigan population growth rate for an increase of 1 SD in the predictor. The number of bars differs among predictors because not all predictors were included in each model. SI_Carrion, SI_Climate with the addition of Reindeer Carrion; SI_Carrion2, SI_Carrion without ROS days; SI_Climate, “climate-impact” model including Sea Ice; WT_Carrion, WT_Climate with the addition of Reindeer Carrion; WT_Carrion2, WT_Carrion without ROS days; WT_Climate, “climate-impact” model including Winter Temperature

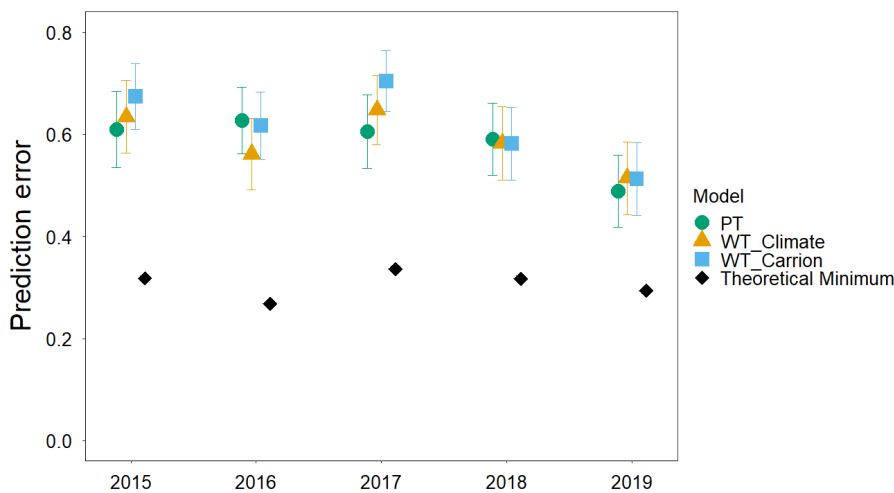


FIGURE 4 Prediction error (symmetric mean absolute percentage error) for the three candidate models used for anticipatory predictions. Theoretical Minimum is the expected prediction error under a Poisson process model. PT, Ptarmigan model; WT_Carrion, WT_Climate with the addition of Reindeer Carrion; WT_Climate, “climate-impact” model including Winter Temperature

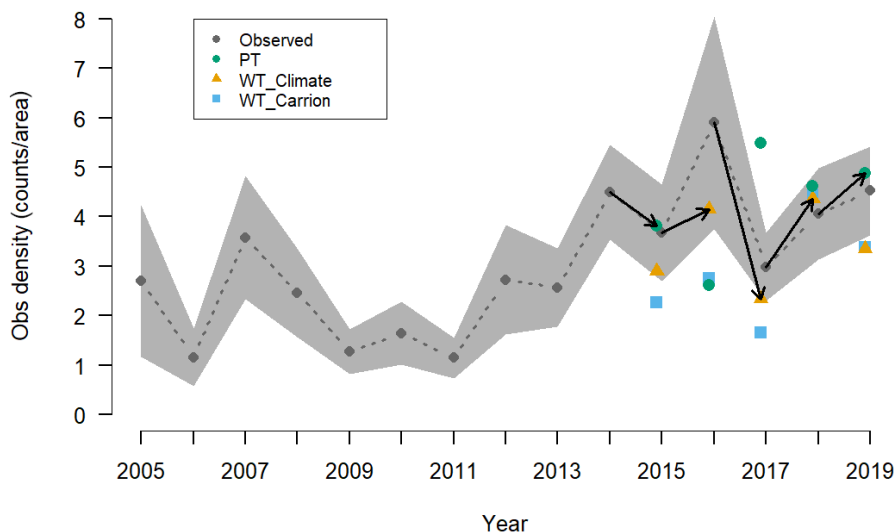


FIGURE 5 Ability of candidate models to predict next-year mean population density of the Svalbard rock ptarmigan in the study area. Predicted next-year mean densities are compared to observed densities. Arrows point at the model that provided the best prediction. PT, Ptarmigan model; WT_Climate, “climate-impact” model including Winter Temperature; WT_Carrion, WT_Climate with the addition of Reindeer Carrion

contribute to reduce the total energy consumption of ptarmigan, that is, lower the need for thermoregulation, thereby sustaining their body conditions and improving survival throughout the winter. The body condition of hens is regarded as the most important factor

for chick production in this species (Steen & Unander, 1985). Our analysis, therefore, suggests that increased winter temperature may constitute the aspect of changing arctic climate that contributed the most to the positive ptarmigan population trend. Notably, sea ice

shrinkage (Dahlke et al., 2020) likely promotes a positive feedback due to more open water that can cause temperatures on land to be even higher (Isaksen et al., 2007).

The drastic increase in winter temperature has also resulted in increased frequency of ROS events (Hansen et al., 2014; Peeters et al., 2019). Despite considerable uncertainty, the average negative effect of the number of ROS days is consistent with Hansen et al. (2013). They showed that if ROS events are associated with ice crust formation at the ground level that hinders access to vegetation, they might cause sudden population crashes in resident herbivore species. Our result is relevant because their analysis did not include data from the most recent warming period. It may be that the winters in Svalbard now have become so warm that the positive effect of high temperature on ptarmigan population growth overrides the negative effects of ROS. This underscores the importance of frequent updating of such explanatory analyses in ecological systems subjected to rapid climate change.

Although the estimates tended to be in the expected directions, large uncertainty and poor consistency of effect sizes characterized most of the other predictors in our model. Making strong inference about their effects, therefore, is difficult. Given the relatively short time series available for the Svalbard rock ptarmigan, it is possible that the strong winter temperature effect overrode other effects. Notably, we could not detect any impact of harvest on the breeding component of the ptarmigan population. Combined with evidence of relatively strong density dependence, this result suggests that the population is currently able to compensate for the harvest, likely due to higher survival in recent years as compared to estimated survival from the 1980s (Unander et al., 2016) and the existence of a surplus of floater birds that occupy vacant breeding territories (Pedersen et al., 2014). However, strong inference on the effect of density dependence and harvest is not warranted because they may be partially confounded. Moreover, harvest may affect ptarmigan at a smaller spatial scale or through changes in the demographic structure of the population.

It is also important to acknowledge other aspects of climate change that were not included in the analysis. For instance, not only winters but also summers are becoming warmer and longer. This may benefit ptarmigan through increased plant productivity (van der Wal & Stien, 2014) and a prolonged grazing season, as observed for the Svalbard reindeer (Albon et al., 2017; Le Moullec et al., 2019). A hint of this effect may be the small excess positive population trend that we detected in our study. Climate warming-induced changes that show trends but happen at a slow pace, like summer lengthening and prolonged grazing seasons, will deserve attention in the imminent future in terms of their potential effects on ptarmigan population dynamics.

4.2 | Anticipatory predictions

Assessing the predictive ability of ecological models of different complexity is not only a strategy to validate models and gather

evidence efficiently but also to align management of populations, species, and communities to current environmental change (Nichols et al., 2019). The Svalbard rock ptarmigan is the most popular recreational game species in Svalbard (Soininen et al., 2016), and there is concern that harvest may affect the populations at least at the local level. The Svalbard Environmental Protection Act and harvesting regulations for Svalbard allow harvest on the condition that the total offtake does not have an appreciable impact on the population. Hence, tools capable of accurately forecasting next-year population density and providing insights on the effect of harvest would be useful to adapt harvesting strategies in the face of current and future climate change (Nichols et al., 2015).

The difference between the prediction error of our models and a theoretical minimum expected under a "perfect" Poisson process was similar to that found by Henden et al. (2020), who used the same metric for the same purpose. Although none of our models outperformed the others with respect to forecasting next-year mean population density, the inclusion of local climate and food web predictors was important for predicting large changes between years (e.g., 2016 and 2017). A more complex model, therefore, may be better suited for the Svalbard rock ptarmigan population, although simpler models can perform as well in some cases (cf. Gerber & Kendall, 2018). A noticeable exception was 2019, when the more complex models (i.e., WT_Climate and WT_Carrion) underestimated densities, likely due to the strong influence of the winter temperature predictor that showed a low value in 2019 (i.e., average temperature from December 2018 to March 2019; Figure 2c). Overall, we deem the predictive ability of our models sufficient for iterative forecasting on a yearly basis. There is, however, scope for improved predictions, which will be possible with better spatial matching of predictor variables and ptarmigan monitoring (i.e., accounting for spatial variation) and a longer time series.

Although our study area in Svalbard is relative small compared to the size of the Svalbard archipelago, the geomorphology of the glacial valleys and the fact that some parts are considerably distant from the coast can cause substantial variation in local temperatures and precipitations (Isaksen et al., 2016). Because the sMAPE is the mean of the per-survey site prediction error, not accounting for spatial variation in weather covariates may have influenced the predictive performance of the models. The current installation of new weather stations throughout the study area, combined with the development of modeling systems that reconstruct spatial weather by interpolation techniques, provides scope for more accurate gridded data of local climate variables. With more data and better predictors, we expect confidence to rise in models that perform well and decrease in those that perform poorly. This will likely lead to more precise and useful predictions with respect to which drivers of population dynamics are most important. Iterating the forecasting process in the next years will elucidate whether some of the strong effects we found are real or occurred by chance (e.g., the effect of winter temperature). Moreover, as our models do not account for potential interaction effects between some of the drivers (e.g., between population density and ROS as shown for Svalbard reindeer,

Hansen, Gamelon, et al., 2019; Hansen, Pedersen, et al., 2019), more sophisticated, hypothesis-specific models could be developed. This should be aligned to the implementation of methods to formally accumulate evidence and develop increasing confidence in the models that perform better (e.g., using model weights to address specific objective functions as in Nichols et al., 2019). Generating predictions from several hypothesis-specific models and using appropriate metrics to formally assess the confidence in the models' predictive ability may improve the understanding of the mechanisms governing the population dynamics of the Svalbard rock ptarmigan.

5 | CONCLUSIONS AND PERSPECTIVES

We have here provided the first assessment of a general protocol of combining explanatory and anticipatory predictions for generating rapid knowledge about the fate of high-arctic wildlife populations. By doing this, we have responded to the call for making ecology more predictive in the face of global-scale environmental change (Houlahan et al., 2017) and to the recent movement among ecologists toward implementing iterative near-term forecasting as integral part of long-term studies and monitoring systems (Dietze, 2017; Dietze et al., 2018). In a situation of limited prior knowledge, such as for the Svalbard rock ptarmigan population, committing to validate predictions from hypothesis-driven models against new data will allow more frequent hypothesis testing and thus more robust explanatory science about the impact of climate change. With respect to our assessment of iterative near-term forecasting, it was encouraging to find that our dynamic state-space models yielded good forecasts of ptarmigan population state even though the time series was relatively short. Our case study also provides support for value of ecosystem-based monitoring in the era of rapid climate change (Ims & Yoccoz, 2017), because our most complex models performed the best in years with sharp changes in the ptarmigan population.

Near-term forecasting plays an important role in guiding management of harvested populations (Jensen et al., 2013; Nichols et al., 2015). In the case of the Svalbard rock ptarmigan population, no influence of current harvest levels was detected. However, the ongoing, rapid climate change may have yet unknown effects on wildlife's ability to tolerate harvesting. Hence, continuing the iterative protocol of updating the model with new data is necessary for maintaining sustainable management in the future (Nichols et al., 2019). We also suggest that the formal integration of stakeholders' views in the modeling process through standardized protocols should be implemented in the future (cf. Henden et al., 2020). This will help generating more nuanced hypotheses about drivers of change as well as devising practically feasible and socially acceptable management strategies.

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AUTHOR CONTRIBUTIONS

F. Marolla, J-A. Henden, E. Fuglei, and Å. Ø. Pedersen conceived the idea; F. Marolla and J-A. Henden designed methodology; E. Fuglei and Å. Ø. Pedersen provided ptarmigan data, Å. Ø. Pedersen provided reindeer carrion data, M. Itkin made calculation of sea ice coverage; F. Marolla and J-A. Henden prepared and organized the ptarmigan data; F. Marolla analyzed the data; F. Marolla led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

None of the authors has conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.ngf1vhht0>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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