End-user involvement to improve predictions and management of populations with complex dynamics and multiple drivers

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Abstract. Sustainable management of wildlife populations can be aided by building models that both identify current drivers of natural dynamics and provide near-term predictions of future states. We employed a Strategic Foresight Protocol (SFP) involving stakeholders to decide the purpose and structure of a dynamic state-space model for the population dynamics of the Willow Ptarmigan, a popular game species in Norway. Based on local knowledge of stakeholders, it was decided that the model should include food web interactions and climatic drivers to provide explanatory predictions. Modeling confirmed observations from stakeholders that climate change impacts Ptarmigan populations negatively through intensified outbreaks of insect defoliators and later onset of winter. Stakeholders also decided that the model should provide anticipatory predictions. The ability to forecast population density ahead of the harvest season was valued by the stakeholders as it provides the management extra time to consider appropriate harvest regulations and communicate with hunters prior to the hunting season. Overall, exploring potential drivers and predicting short-term future states, facilitate collaborative learning and refined data collection, monitoring designs, and management priorities. Our experience from adapting a SFP to a management target with inherently complex dynamics and drivers of environmental change, is that an open, flexible, and iterative process, rather than a rigid step-wise protocol, facilitates rapid learning, trust, and legitimacy.

Key words: climate change; decision-making; food web; harvesting; near-term forecasting; population cycles; stakeholders; strategic foresight.

Introduction

Sustainable management of wildlife populations can be facilitated by building models that both identify current drivers of natural dynamics and anthropogenic-induced change (Caughley 1994), and provide near-term predictions of future states (Mouquet et al. 2015, Urban et al. 2016, Bradford et al. 2018, Dietze et al. 2018). This is especially relevant in light of the pace of current and future climate change (Mouquet et al. 2015, Urban et al. 2016, Dietze et al. 2018). While ecologists often aim to devise models that can aid environmental decision-making and lead to changes in policy, they often fail to achieve this goal (Dietze et al. 2018). If ecology aims to contribute to policy and management, there is a need to build models and make ecological predictions directly relevant and at a time horizon corresponding to environmental decision-making (Nichols et al. 2007, Pouyat

et al. 2010, Hobbs et al. 2015, Hobday et al. 2016, Dietze et al. 2018). This can be achieved through an integrated approach in which scientists and stakeholders collaborate in the process of deciding on objectives, data, models, and analyses (Nichols et al. 2007, Cook et al. 2014*a*, Parrott 2017) as well as identifying forthcoming problems, opportunities, and surprises (Sutherland et al. 2014). Such participatory or collaborative modeling approaches that involve stakeholders have been forwarded as a way of ensuring direct relevance and uptake of modeling outcomes by end users (Parrott 2017, Reiter et al. 2018, Reiter et al. 2019). This involves all aspects of the research process from simple information and data sharing to development of model structure or interpretation of its output (Parrott 2017, Reiter et al. 2018, Reiter et al. 2019).

A food web consists of directly and indirectly connected species (Wootton 1994). Environmental impact on one species has the potential to propagate through the food web, affecting other species indirectly through multiple pathways (Barton and Ives 2014). Hence, understanding the consequences of environmental

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change and harvesting in complex, natural systems warrants the inclusion of biotic interactions and processes across several trophic levels (O'Connor et al. 2013, Barton and Ives 2014, Urban et al. 2016, Kadin et al. 2019). This is particularly important for harvested species, which are often situated at intermediate trophic levels in food webs, and therefore affected by both lower and higher trophic levels. Harvested species are increasingly recognized to exhibit complex population dynamics (Krebs et al. 2001, Moss and Watson 2001, Glaser et al. 2014), including population cycles, synchrony/travelling waves (Krebs et al. 2018), and transient dynamics (Hastings et al. 2018), expressed as shifts between alternative stable states. Such complex population dynamics may result from high dimensionality in the underlying ecological interactions in combination with strong exogenous environmental drivers (Hastings et al. 2018). Further complications are expected as ecosystems are increasingly subjected to novel climates and food web interactions (Ims et al. 2008). Many harvested populations have been declining in recent decades (Free et al. 2019, Fuglei et al. 2019) and developing predictive models is therefore a more challenging and pressing task than ever.

Case study

The Willow Ptarmigan (*Lagopus lagopus*) is a species known to have complex dynamics. The Willow Ptarmigan has sparked fascination and debate among hunters, managers, and scientists for more than a century (Nansen 1915, Elton 1924, Elton and Nicholson 1942, Moss and Watson 2001), likely due in part to their high-amplitude population cycles (Krebs et al. 2001, Moss and Watson 2001). However, transient dynamics (Hastings et al. 2018), expressed as shifts in cycle period and amplitude, alternation between cyclic and non-cyclic dynamics, or changes in average population density, is also pervasive in most Ptarmigan populations (Moss and Watson 2001). With its circumpolar distribution in mainly sub-Arctic and low-Arctic biomes, the Willow Ptarmigan is also one of the world's most abundant and popular small game species (Potapov and Sale 2013).

Like many other Alpine and Arctic bird species in Europe (Lehikoinen et al. 2014, Lehikoinen et al. 2019), Ptarmigan populations have recently been declining (Fuglei et al. 2019). In Norway, both Rock (*Lagopus muta*) and Willow Ptarmigan were placed on the Norwegian Red List in 2015 as "near threatened" (Henriksen and Hilmo 2015). While climate change has been proposed as the ultimate cause of this decline (Kausrud et al. 2008), the ecological mechanisms involved and consequently how management should respond, remain unresolved both for Ptarmigan and most other Arctic-Alpine bird species that currently are declining (Lehikoinen et al. 2019). The Willow Ptarmigan is preyed upon by different predator guilds and is affected by other herbivores in the ecosystem, some that have recently experienced changed dynamics (see Henden et al. 2017 for an overview). Moreover, several Ptarmigan life cycle stages are thought to be sensitive to climate (Erikstad and Spidsø 1982, Erikstad and Andersen 1983, Wilson and Martin 2012, Henden et al. 2017). Because of the potential multitude of climatic drivers and biotic mechanisms that may be involved, an ecosystem-based approach to data capture, modeling, and forecasting is warranted (Ims and Yoccoz 2017).

We develop a dynamic state-space model of Willow Ptarmigan population dynamics tailored to a spatially extensive population monitoring data set, spanning 17 yr and covering the largest management area for Ptarmigan in Norway. Different tools and approaches exist to facilitate model use by management (Gregory et al. 2012, Scheele et al. 2018, Schwartz et al. 2018). However, involvement of end users at the development and research stage, as well as in ongoing engagement and communication, are considered important (Reiter et al. 2018, Reiter et al. 2019). We used a Strategic Foresight Protocol (Cook et al. 2014*a*, Ims and Yoccoz 2017) to incorporate the knowledge, views and needs of major stakeholders in joint decisions on what should be the structure and purpose of the model.

MATERIAL AND METHODS

Target system

The Finnmark Estate (~45,000 km^2) is the largest game management unit for Willow Ptarmigan in Norway. The estate spans sub- and low-Arctic bioclimatic zones (Walker et al. 2005), with steep gradients from the western part, which is relatively mild and wet, to the eastern costal and southern inland parts, which are relatively colder and drier (Hanssen-Bauer 1999). Western Finnmark is topographically most diverse with large islands, steep mountain ranges, deep valleys and fjords (Appendix S1: Fig. S2). The eastern part also contains fjords and large peninsulas, but the relief is gentler. The south-central inland part is topographically the most homogenous with moderately sloped hills and plateaus. Good Willow Ptarmigan habitats. i.e., open sub-alpine/sub-Arctic birch forest and low sub-Arctic/low-Arctic shrub tundra, are well represented across Finnmark (Pedersen et al. 2012), although they are most fragmented in the western part and more continuous in the south-central part.

One major landowner (The Finnmark Estate; FeFo) is responsible for both the management (i.e., hunting regulations) and monitoring (line-transect surveys) of the Willow Ptarmigan in Finnmark. The most extensive land-use in Finnmark is, however, reindeer husbandry, which has profound effects on structure and dynamics of the food web (Ims et al. 2007, Ims and Henden 2012, Henden et al. 2014).

Strategic foresight protocol (SFP)

Stakeholders included in the SFP were the major landowner (FeFo), representatives from the hunters association, governmental management authorities, and conservation bodies (Appendix S1: Section S1). A first heuristic step in the process was to decide on the purpose. The purpose was primarily to develop a data-driven model that could explain past dynamics (i.e., provide explanatory predictions). Later in the process, the stakeholders also expressed a need for using the model for providing near-term forecasts (anticipatory predictions). The key data source stemmed from FeFo's spatially extensive line-transect survey of Willow Ptarmigan across Finnmark.

The opinions of the stakeholder group constituted an integral part of the iterative process of model development (Appendix S1: Section S1: Fig. S1). In this process, the model was updated with predictors to potentially explain both short-term dynamics and more long-term negative trends, as well as pose future threats to Ptarmigan populations (Fig. 2a). Many stakeholders are well acquainted with previous research on Willow Ptarmigan from Scandinavia. Hence, several of the proposed predictors could also have been included on a purely scientific basis. Stakeholders decided that the modeling should be based on a food web approach because of the complexity of the suggested impacts of different drivers on Willow Ptarmigan (Henden et al. 2017, Ims and Yoccoz 2017). A conceptual food web model was built to highlight biotic interactions suspected to affect both short-term population dynamics and long-term trends. Predation on Ptarmigan was considered potentially very important and thought to be driven indirectly by two links involving other herbivores in the food web. One link is due to the cyclic population dynamics of small rodents driving a synchronized alternative prey mechanism (Steen et al. 1988, Ims et al. 2013b). The second link is due to increasing amount of reindeer carcasses subsidizing a guild of generalist predators (Henden et al. 2014). Impact of a recent large-scale geometrid moth outbreak, thought to negatively affect all browsing herbivores (Vindstad et al. 2019) was also included among the biotic predictors. Among abiotic factors, we included the potential effect of severe weather conditions (temperature and precipitation) around hatching, previously shown to be important for Ptarmigan chick survival (Erikstad and Spidsø 1982, Erikstad and Andersen 1983). Moreover, we included the potential negative effect of late onset of winter, due to the camouflage-mismatch effect found for other species that shift to a white plumage in the autumn (Zimova et al. 2016). Finally, we included terms for density dependence and effect of harvest on Ptarmigan population growth (Pedersen et al. 2004). Fig. 1 provides an overview of the annual life cycle of Willow Ptarmigan together with information on when the different drivers have been recorded. Because of a lack of data on some intermediate components of

indirect links in the conceptual model (Fig. 2a, e.g., generalist predators in the reindeer carcass–predators–Ptarmigan path), some of the indirect effects are modeled as direct effects in the statistical model (Fig. 2b). However, these effects (e.g., carcass abundance) are interpreted and referred to according to the expectation from the conceptual indirect effect in the conceptual model (Fig. 2a).

The spatial scale of the model was also discussed in the SFP process. FeFo operates with an eastern, western, and interior Ptarmigan management area (Appendix S1: Fig. S2) based on the contrasts in climate and topography described above (Target system), and their knowledge about gross spatial differences in Willow Ptarmigan dynamics across Finnmark. Hence, it was decided to derive model predictions at this scale, but also to consider higher spatial resolution to the extent that data sources, model specifications, and technical aspects of analyses allowed.

Data sources and variables

Ptarmigan data for modeling population growth rates (response variable) were obtained from transect lines surveyed yearly between 5 and 20 August by trained personnel with pointing dogs according to a distance sampling protocol (Buckland et al. 2001). From 2000 to 2016, a total of 315 lines were surveyed (Appendix S1: Fig. S2). However, the number surveyed ranged from 67 to 229 lines (122 ± 54, mean ± SD) between years. A large part of this variation is due to an intensive study on the effect of hunting conducted in 2008–2010, when extra lines where included in the interior and western part of Finnmark (E. J. Asbjørnsen, *personal communication*). As vegetation structure is likely to influence detection probability, we extracted vegetation data by using a vegetation map for Norway based on Landsat TM/ETM + data (Johansen 2009). From this digital map, we estimated the proportion of vegetation classes reflecting forest and erect woody vegetation within the sampled area (sampled area [km^2] = length [km] × 2width [km]) of each line transect. This proportion entered the modeling of the detection probability.

We now provide a brief overview of the different predictor variables. Detailed descriptions of the different predictor variables can be found in the Appendix S1 (Section S2). Generally, we strove to obtain as high a spatial resolution of the predictor variables as the underlying data allowed.

Harvest statistics for the entire period were available for each municipality that contained transect lines. For the harvest predictor we used the number of shot Ptarmigan per municipality divided by the areas of the municipality since the different municipalities vary greatly in size. Hence, transect lines within the same municipality were given the same value of the predictor. Note that the scale of the harvest predictor (number of
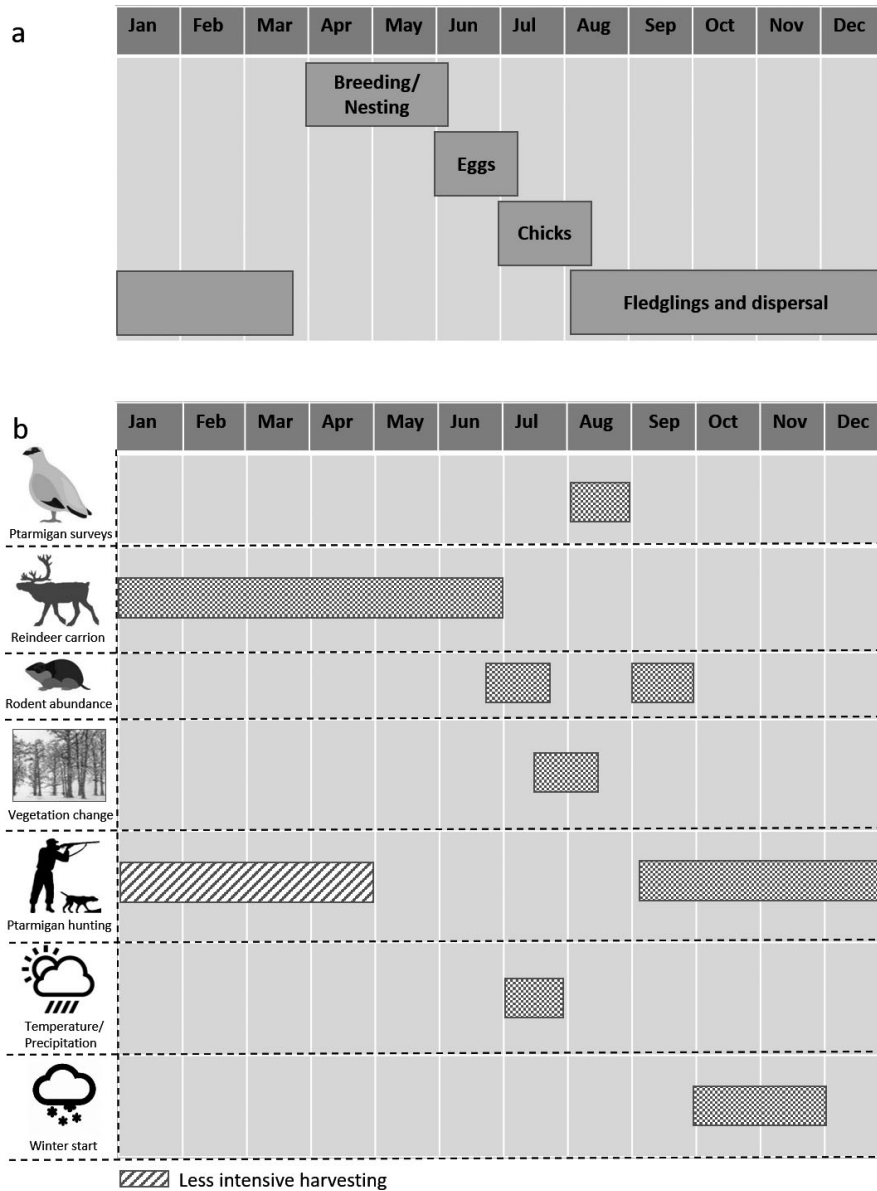
Fig. 1. (a) Annual life cycle of Willow Ptarmigan in Finnmark, denoting the breeding/nesting, egg, chick, and fledgling and dispersal phases. (b) Annual life cycle of data collection for the different drivers included in the model. Note that, while hunting may proceed well into late winter, the majority of hunting is performed in the autumn.

Ptarmigan harvested/km^2) corresponds to the scale of the response variable (change in the Ptarmigan density/km^2).

The two predictors linking Ptarmigans indirectly to predators (Fig. 2a) have different spatial scales. The spatial resolution of the rodent data is at the scale of the three main regions of Finnmark (western, interior, and eastern), while for reindeer carrion the scale is the entire county of Finnmark. Annual rodent density indices from each of the three regions were obtained from two ongoing monitoring programs (Yoccoz and Ims 2004, Ims et al. 2011), with constant effort across years and areas.

We used the number of small rodents trapped in standardized programs conducted in each of the three regions as the predictor. Annual counts of reindeer carcasses were retrieved from a national database at the scale of Finnmark (database *available online*).[5] We used the sum of the number of reindeer found dead across municipalities in Finnmark during winter (January–June) every year as an index of the carcass abundance.

Moth outbreak intensity was estimated using a cumulative defoliation score based on NDVI data from
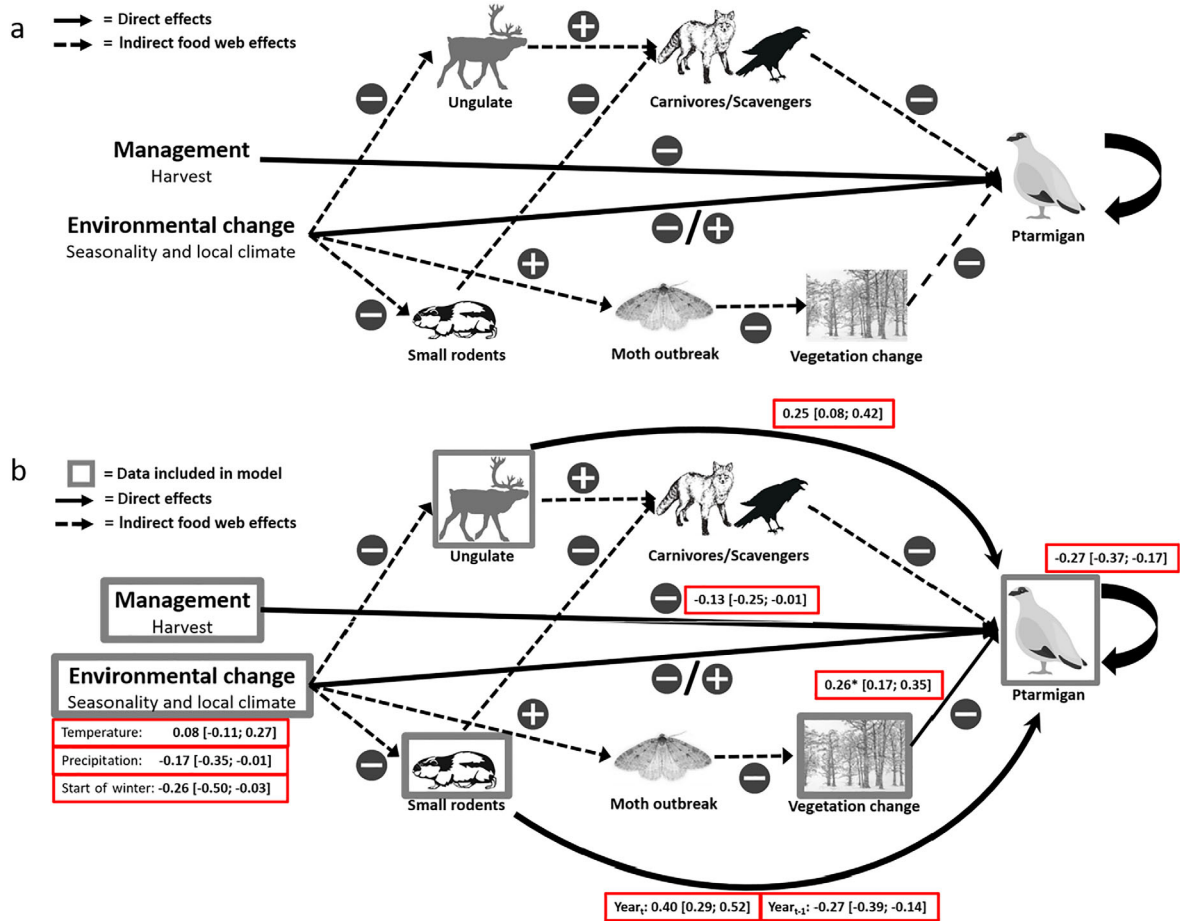
[5] www.rovbase.no

FIG. 2. (a) Conceptual model denoting the main mechanism and drivers of Willow Ptarmigan dynamics coming out from the Foresight process. Solid lines denote direct effects, while stippled lines denote indirect effects of different drivers on Ptarmigan population growth and density. Boxes with gray perimeter lines denote predictor and response data included in the model. (b) Conceptual model denoting the main mechanism and drivers modeled in the state-space model. Values with red perimeter lines denote estimated coefficients with 95% credible intervals of specific paths of the conceptual model. Note that as we used an inverse measure of moth outbreak intensity, the model estimate represents a negative effect. Note also that the moth effect shown is the residual effect, which mostly represents a temporal effect.

MODIS v6 (Jepsen et al. 2009). The cumulative defoliation score estimates the degree to which the annual peak plant productivity in an area is lower than the maximum across the time period 2000–2017. We used the mean cumulative defoliation score for each line-transect survey area, including a 6-km buffer zone, as a measure of local outbreak intensity. Larger negative values of the cumulative defoliation score denote more intense moth outbreaks and hence increased negative impacts on Willow Ptarmigan habitats.

Climate-related predictors were all quantified as the mean at the scale of the line-transect survey area using interpolated gridded data (1-km^2 pixel size) from the Norwegian meteorological institute (MET Norway; see Lussana et al. 2016). Mean temperature and max precipitation during the first week of July were used as predictors for the conditions affecting chick survival. The

seasonality predictor (onset of winter), related to the camouflage-mismatch hypothesis, was obtained from remote sensing data (Appendix S1: Section S2.3).

Statistical model

To assess the effect of different predictors of Willow Ptarmigan growth rate, we used a modified version of the Hierarchical Distance Sampling (HDS) model from Kéry and Royle (2016). This model consists of a detection model, which estimates an average detection probability based on the observed distances from each transect line, and a process model, which models the spatial-temporal variation in population density as a function of a set of predictors. 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. All covariates (except year) were scaled (over all locations and time points) to mean = 0 and SD = 1 to ease convergence and interpretation of effect sizes. Note that since small rodent data where acquired using different sampling methods, the data from different regions were scaled separately. The temperature, precipitation, start of winter, and moth outbreak intensity data were all split into three components in the analyses: a temporal component that captured the overall average between-year variation, a spatial component that captured the overall average between-sites variation, and a residual component that represented the interaction between the temporal and spatial components (Oedekoven et al. 2017). Consequently, the three management-area-specific intercepts denote the growth rate at average values of the covariates. Our models were fitted using Markov Chain Monte Carlo (MCMC) methods as implemented in JAGS (Plummer 2003). A detailed description of the state-space model as well as the JAGS code is given in Appendix S1 (Section S2.5) and Data S1.

Near-term forecasting

According to the stakeholders' desire to obtain anticipatory predictions (i.e., forecasts), we used the full food web model to forecast a given year's survey counts (P_s) by using the estimated model coefficients based on data sources from previous years and predictors available in early summer the same year. In order to see to what extent the forecasts improved with more years of data, we ran the model with $t = 10$ to $t = 16$ yr of prior data. We then compared the predicted (P_s) and observed (O_s) survey counts by calculating the symmetric mean absolute percentage error (sMAPE; Makridakis 1993, Makridakis et al. 2018).

In order to assess the contribution of measurement error to our models' predictive ability, we calculated the potential "theoretical" minimum prediction error based on a "perfect" Poisson process model (see Appendix S1: Section S2.6, for details and Data S1 for the R code). We assessed the contribution of a potential hunting ban as a management action, by comparing predictions of observed counts of the full model (hereafter FoodWeb model) with and without harvest for 2016.

Finally, we assessed the importance of the food web approach by comparing predictive ability of the FoodWeb model with a model containing only Ptarmigan data (including direct density dependence [DD] and harvest, hereafter called PtarmiganOnly) and a model containing Ptarmigan and local climate data (DD, harvest, temperature, precipitation and time of winter, hereafter called PtarmiganClimate). We did this to assess the value of collecting additional extensive and potentially costly food web and local climate data for the management of Ptarmigan. To assess whether predictive ability was different between management regions, we also decomposed predictive ability of the three alternative models into management-area-specific predictive ability.

RESULTS

The SFP process produced two major purposes (i.e., deliveries) of the modeling: (1) explanatory predictions to yield a more comprehensive (i.e., ecosystem-based) understanding of the main mechanisms and drivers of Willow Ptarmigan dynamics as a basis for devising efficient monitoring and management strategies and (2) anticipatory predictions to inform stakeholders about the near future state of the population as a basis for adaptive annual management decisions with respect to the Ptarmigan hunt.

Explanatory predictions: Drivers of Ptarmigan population dynamics

The coefficients of the temporal predictors of the full FoodWeb model are given in Fig. 2b (see Appendix S1: Section S3, for more details about less central covariates and parameters).

Most of the temporal climatic predictors significantly influenced Ptarmigan population growth. Increased precipitation around the time of hatching (i.e., first week of July) had a negative effect, while the effect of temperature at the same time had a positive, but non-significant effect. Consistent with the expectation from the camouflage-mismatch hypothesis, there was reduced population growth associated with a later start of winter.

All the predictors reflecting food web interactions were significant. Both a high reindeer carcass abundance and a high rodent abundance the same year had a positive effect on Ptarmigan population growth, while high rodent abundance the previous year had a negative effect. Intensive moth outbreak had a strong negative effect on Ptarmigan population growth.

As expected, harvest had a negative effect on population growth, albeit with a small estimated coefficient relative to the coefficients of the food web predictors and the negative density dependence in Ptarmigan population growth. There was a small negative temporal trend in population growth not accounted for by the covariates in the model.

Annual density estimates were highest in the western part of Finnmark (except for initial density), while the density estimates for inner and eastern part were lower (Fig. 3). There was large variation among transects within each region (Appendix S1: Section S3), and several of the spatial predictors contributed significantly to this variation (see Appendix S1: Section S3, for estimates of the spatial predictors). Despite the significant spatial and residual effects (interaction between spatial and temporal predictors), there was a high degree of synchrony in Willow Ptarmigan population dynamics between the three parts of Finnmark (Fig. 3). As indicated by the coefficients of the direct and delayed rodent

predictors (Fig. 2b), there was also some synchrony between Ptarmigan and rodents (Appendix S1: Fig. S5), in particular during the peaks and crashes in 2011–2012 and 2015–2016. The link between Ptarmigan and rodents was not at all clear during 2002–2008, when there was a strong and steady decline in the Ptarmigan populations across Finnmark. This period coincided with an extensive moth outbreak in Finnmark (Jepsen et al. 2013).

Regarding the detection part of the state-space model, average transect level detection probability varied little between transect lines and was generally low (mean = 0.171, SD = 0.019, range = [0.134, 0.195]). As expected, there was a negative relationship between detection probability and the proportion of erect woody vegetation in the surveyed area of the transect lines.

Anticipatory predictions: Near-term forecasting

Short-term predictive performance of the FoodWeb model generally increased (i.e., improved iterative short-term predictive performance) with increasing length of the time series used to parameterize the model (Fig. 4a). This trend was also apparent for the two alternative models. Moreover, predictive performance was on average higher (i.e., lower prediction error) for the FoodWeb model compared to both the PtarmiganOnly and PtarmiganClimate models, even though there were some exceptions in single years (Fig. 4a). After 2014, the prediction error of most candidate models was only 10–25% greater than the theoretical minimum prediction error. While all candidate models predicted next years observed density fairly well (Fig. 4b), the predictions from the FoodWeb model were on average as close or closer to the observed (compared to the two other models). There was, however, one big exception (year 2014), in which both the FoodWeb and PtarmiganClimate models performed poorly. This poor performance is most likely due to extreme values of three predictors

(Start of winter 2013, Carcass 2014, and Rodents 2013 and 2014) leading to greatly overestimated predicted densities in 2014, compared to the observed data.

The contribution of harvest to predictive performance of the FoodWeb model was marginal, accounting for only a 5% (~1.2 individuals/km^2) difference in observed density in 2016 (with harvest 22.56, without harvest 23.77).

DISCUSSION

In an era of rapid and extensive changes in ecosystems worldwide, ecology is increasingly challenged by policy-makers, managers, and everyday citizens with questions about the future state of species and ecosystems. We cannot rely on our understanding of dynamics based on historic variability alone for forecasting future ecosystem change (Groffman et al. 2006, Jackson and Hobbs 2009), as the current pace of environmental change results in increasing novelty of ecological drivers. Hence, decision-makers will need data and predictions, at a time horizon relevant for environmental decision-making, to support and adapt effective mitigating management decisions for the benefit of both wildlife and users. Without adequate models to foresee future impacts of environmental change and guide decisions, we may risk that changes accumulate without a proper understanding of their effects (Halpern and Fujita 2013). Exploring potential impacts and predicting short-term future states, such as in our case study of game populations in a rapidly changing Arctic, provides the basis for collaborative learning, refined data collection, monitoring designs, and management priorities. Coupled with a quantitative objective function, this approach is a required step for building adaptive management programs in a time of rapid and uncertain change (Nichols et al. 2011, Williams and Brown 2016).

Strategic foresight protocol (SFP)

Although it has for decades been advocated for the great value of involving stakeholders in the ecological research process has been advocated for decades, a core ingredient in adaptive management (Walters and Holling 1990) and monitoring (Lindenmayer and Likens 2010), there are not many examples of applying structured protocols for doing so. Here we adopted the Strategic Foresight Protocol (SFP) that has been proposed for tackling rapidly emerging problems in applied ecology (Cook et al. 2014a). The SFP is very similar to other stakeholder-oriented processes, such as group model building (Otto and Struben 2004), collaborative modeling for decision support (Langsdale et al. 2013), participatory modeling (Beall and Zeoli 2008), and mediated modeling (Van den Belt 2004), although they use slightly different methods for structured involvement of stakeholders. In the case of the recently red-listed, but still harvested, population of Willow Ptarmigan in Northern Norway,
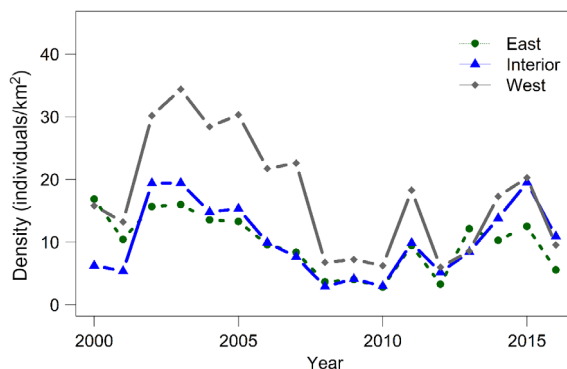

FIG. 3. Willow Ptarmigan population dynamics given as the average model-based density estimates from the FoodWeb model for each of the three parts of Finnmark (east, west, and the interior part).
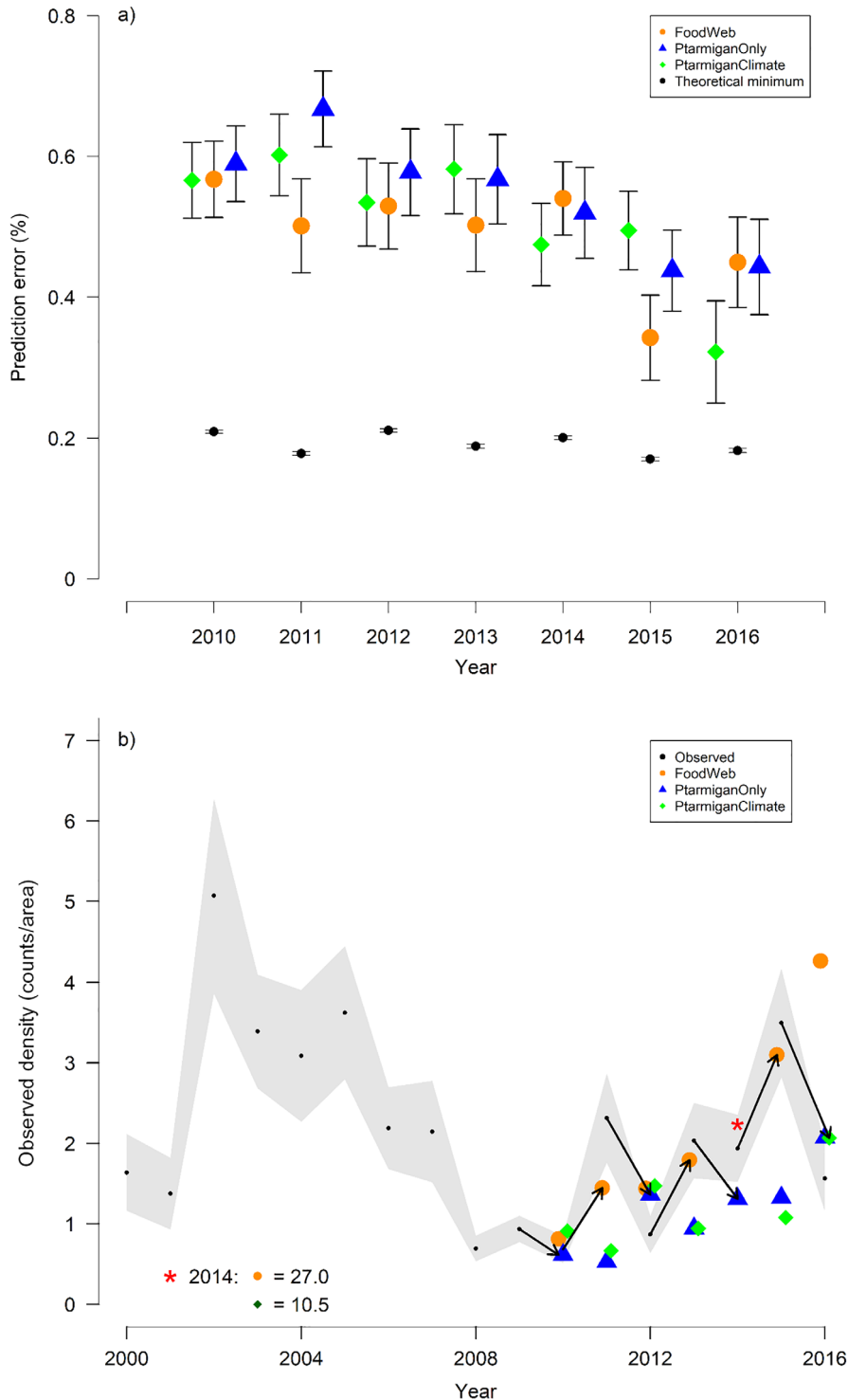
FIG. 4. Prediction error and near-term prediction of line-transect survey counts at the scale of Finnmark. (a) Show iterative percent (percent/100) prediction error (sMAPE) for the three candidate models. (b) Show the three candidate models' ability to predict next year's mean observed density (counts/sampling area). Note (inset) the poor ability of the FoodWeb and the PtarmiganClimate model to predict observed density in 2014. Arrows point to the model that each year predicts next years observed density best. Equivalent graphs for each of the three parts of Finnmark separately (west, interior, and east) is provided in Appendix S1: Fig. S4.1 and S4.2.

we experienced that the SFP constituted a highly functioning framework for involving stakeholders in modeling efforts for the purpose of identifying drivers of past and current dynamics as well as for deriving prediction of the near future state of the population. Our positive experience may have been aided by the traditionally high interest in Ptarmigan as a game species in Norway and the enhanced attention created by the recent red-listing. The SFP also likely benefitted from stakeholders that were well acquainted with previous research on Willow Ptarmigan from Scandinavia.

Implementing the SFP was more time intensive (>3.5 yr) than we expected, even for the first four of six stages of the SFP (Appendix S1: Fig. S1), as they required the commitment of much time from both managers, stakeholders, and researchers. The SFP can appear as a rigid linear stage-by-stage process (Cook et al. 2014a), where each stage is completed before moving to the next. However, we decided to adopt a more dynamic approach whereby new views and hypotheses could be implemented in the modeling at every meeting in the stakeholder group. While the process has not yet reached the stage of decision-making on management actions, consensus has been reached about what the likely drivers of Ptarmigan dynamics are, which data sets are to be used, and how models should be used to explore the near future. Several positive and useful experiences have come from the collaborative process. Early involvement of all major stakeholders was decisive in providing legitimacy and trust in the objectives of the process and thereby for the focus and progress of the work. An informal kick-off meeting, governed by an external moderator, enabled stakeholders the opportunity to voice their needs, views, and opinions, as well as take active part in setting the scope of the work, discussing lack of data, data needs, and suitability of available data sources. This increased the understanding of the basis for different stakeholders' viewpoints and counteracted potential conflicts (Redpath et al. 2015). The adopted flexibility in the process, i.e., flexible in the sense that we moved back and forth between stages 2, 3, and 4 of the SFP (see Appendix S1: Section S1), reduced the potential for missed opportunities, and increased the likelihood that stakeholders' views were incorporated as collaborative learning evolved. In summary, the SFP has increased the trust and understanding of different viewpoints among stakeholders as well as between stakeholders and scientists, and thereby increased the likelihood for a positive future outcome with regard to management decisions and actions.

Explanatory predictions: Drivers of Ptarmigan population dynamics

Our model highlights several environmental drivers, acting directly and indirectly, that are important in explaining Ptarmigan population growth and thereby the recent decline of Norwegian Ptarmigan populations (i.e., later winter start, increased precipitation around hatching, intensified moth outbreaks, and potentially a weaker link to small rodent peak years). Some of the effects have been documented in previous studies based on other data sources and time periods. Those include the classic link between Ptarmigan dynamics and the population cycles of sympatric rodents (Myrberget 1984, Steen et al. 1988), the negative impact of severe weather conditions for early chick survival (Erikstad and Spidsø 1982, Erikstad and Andersen 1983) and the weak compensation of harvest despite strong density-dependent growth (Pedersen et al. 2004, Sandercock et al. 2011). However, several of the food web effects documented here have not been previously documented for Ptarmigan, such as the indirect effects of carrion abundance, moth outbreak intensity, and the potential effect of increased camouflage-mismatch on Ptarmigan population growth.

It has been argued that increased abundance of carrion could lead to a resource-driven mesopredator release (Killengreen et al. 2011), negatively impacting tundra-breeding birds (Henden et al. 2014, Henden et al. 2017). A recent study on Lesser White-fronted Goose in Finnmark (Marolla et al. 2019) found a negative impact of carrion abundance on Goose reproductive performance. Hence, the positive effect of carrion abundance on Willow Ptarmigan growth found in this study was unexpected. Future studies should aim to uncover whether and how an increase in carrion abundance may affect Willow Ptarmigan growth rate positively. The timing of a resource pulse relative to the timing of predation-sensitive life-stages of alternative prey might tip such relationships from apparent competition to apparent mutualism (Abrams and Matsuda 1996, 2004).

The duration and severity of outbreaks by geometrid moths in northern Fennoscandian mountain birch forests have intensified due to climate warming (Jepsen et al. 2013). The most recent moth outbreak in Finnmark (2002–2008) resulted in large-scale defoliation of birch trees and shrubs as well as a region-wide state shift of the understory vegetation from shrubs to grass (Jepsen et al. 2013). Interestingly, Jepsen et al. (2013) showed that these effects cascaded to affect the abundance of both rodents and ungulates. Since Willow Ptarmigan diet consists mainly of shrubs (*Salix* and *Vaccinium* spp.) (Weeden 1969, Williams et al. 1980), the large-scale defoliation of these preferred forage plants has likely resulted in less forage for Ptarmigan in areas of intense outbreaks. Insect outbreaks in northern-boreal forests are expected to intensify due to climate warming (Jepsen et al. 2013) and may even extend into the shrub tundra (Karlsen et al. 2013). Therefore, this may constitute a future threat to low- and sub-Arctic Ptarmigan populations.

One of the key manifestations of climate change in Arctic and alpine regions is the increasingly later onset of snow cover in autumn and an advanced spring with earlier snowmelt (Ims et al. 2013a, Derksen et al. 2017).

For Ptarmigan, this implies longer periods with white plumage against dark bare ground, and thereby likely increased predation risk as has been documented for boreal hares (Zimova et al. 2016). Considering that predation constitutes the main form of juvenile and adult mortality in most Ptarmigan populations (Smith and Willebrand 1999, Martin 2001, Munkebye et al. 2003) and the autumn season is when Ptarmigan mortality is the highest (Smith and Willebrand 1999), the impact of a mismatch between molt and onset of winter snow cover can be high. The strong negative effect of late onset of winter on population growth is in accordance with the proposed mechanism of increased predation in years of larger mismatch between plumage color and snow cover in autumn (Henden et al. 2017). Hence, in the absence of an adaptive response, such mortality costs could result in strong population-level declines of Ptarmigan populations as snow cover in autumn is predicted to be further delayed due to climate change (Derksen et al. 2017).

Finally, it should be noted that Ptarmigan (both Rock Ptarmigan and Willow Ptarmigan) are presently declining together with a host of other ground-nesting bird species in alpine and Arctic ecosystems (Lehikoinen et al. 2014, Lehikoinen et al. 2019). This trend points toward drivers of change that are not exclusively linked to species-specific traits or management, but rather to general changes in the ecosystem such a climate-warming-induced increased primary productivity (greening) and increased nest predation rates (Kubelka et al. 2018, Ims et al. 2019). This may also explain the declining trend in the Willow Ptarmigan population that was not accounted for by any of the predictors included in our model.

Anticipatory predictions: Near-term forecasting

One of the main needs arising from the foresight process was to assess the performance of models in making *anticipatory predictions* (Bradford et al. 2018, White et al. 2019); i.e., based on the desire of managers and hunters to have near-term forecast of Ptarmigan dynamics prior to the line transect census in late summer. Predictive performance was fairly good compared to what can be theoretically expected given a "perfect" Poisson model, even though predictions in some years were not as good as might be desired (cf. Nichols et al. 2015). There was no clear difference among the different candidate models with regard to predicting next year's survey counts or improving iterative predictive performance, although the FoodWeb model performed better in most years. Hence, there is currently no strong support for including biotic interactions and thereby embarking on large-scale sampling of food web interactions to aid prediction and management decisions. However, this is not unexpected, given the relatively short time series and low quality and/or resolution of those variables that represented some of the indirect food web interactions such

as carcass dynamics, moth outbreak intensity, and small rodent dynamics. However, it may also reflect that simpler models might be preferred to complex models for making decisions (Gerber and Kendall 2018). With more and better data from coming years, our expectation is that confidence will rise in models that perform well and decrease in those that perform poorly. This process will allow us to attain more precise and useful predictions with respect to which drivers of population dynamics are most important (Nichols et al. 2015).

If ecology is to become more relevant for society, we need to be willing to contribute to anticipating and mitigating expected environmental changes, i.e., ecology needs to be more predictive (Evans et al. 2012, Mouquet et al. 2015). Hence, there has recently been an increasing focus on conducting near-term ecological forecasts that operate on timescales relevant to decision-makers (cf. Dietze et al. 2018; Ecological Forecasting Initiative [EFI], *available online*).[6] To our knowledge, we are among the first (Mäntyniemi et al. 2013) to adopt this approach to harvested species while simultaneously addressing the effect of alternative model complexity on short-term forecast ability. In the long run, we think a food web approach to modeling will be most suited for species with complex population dynamics such as many small game populations. This is because more mechanistic models will better accommodate shifting dynamical regimes due to ecological interactions that change over time than simpler phenomenological models (Urban et al. 2016).

Scopes for improved predictions

Although the overall outcome of the SFP has been satisfactory with respect to its purpose, there remains scope for improving on predictive ability. For example, there are limitations regarding what time series of annual population density estimates can explain in terms of mechanisms affecting population growth rates. Demographic data can provide better insights about such mechanisms.

While few studies on harvested species have been able to assess the effect of environmental change by means of demographic models, such approaches will likely provide a richer understanding of the complex effects of climate change (Jenouvrier 2013). Indeed, it has been argued that such understanding is key for the development of more mechanistic models to promote robust predictions (Evans et al. 2012, Urban et al. 2016). However, acquiring individual-based demographic data from Arctic-alpine Ptarmigan populations are logistically and methodologically challenging, and hardly achievable on the temporal and spatial scales relevant for management. However, there is scope for future studies that are able to combine intensive demographic studies

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[6] http://ecoforecast.org/

conducted on a relatively small scale with survey-type population monitoring data acquired on a large scale.

Another scope for improving predictions is in data quality. More transect lines and a spatially extended effort to survey Ptarmigan populations could yield more spatially resolved predictions, for instance, at the scale of local municipalities in a management region. Also, higher precision could be gained by better spatial matching of response and predictor variables. In particular, some of the predictor variables that entered our state-space model were spatially interpolated proxies with unknown measurement errors. Increasing sampling efforts to reduce the extent of interpolation and conducting trials to assess measurement errors would likely contribute improved predictive ability.

CONCLUSION

We used a Strategic Foresight Protocol (Cook et al. 2014*a*, Schwartz et al. 2018), that included several interest groups, to integrate the views and needs of stakeholders. Importantly, drivers that proved to be influential in the modeling were taken into account because of stakeholder involvement, drivers that would not have been included in a purely researcher-driven process. Interestingly, some of these drivers were related to outcomes of recent climate change (e.g., novel pest insect outbreaks and Ptarmigan plumage color mismatch) observed by local stakeholders. Hence, the SFP facilitated the inclusion of recently acquired local knowledge about rapid environmental change. The incentive for conducting near-term forecasting was due to the management's need to have time to prepare, organize, and inform about upcoming harvest regulations. Thus, the ability of the dynamical state-space model to predict population increases and decreases will provide the landowner extra time to consider appropriate harvest regulations as well as early communication of hunting expectations for both local and visiting hunters. The feedback from the landowner indicated that such predictions would be desired and valuable. In general, the modeling approach and access to extensive population and ecosystem data, offer a suitable framework for implementing the views of stakeholders as alternative hypotheses that can be confronted with data. Moreover, the approach forms a structured basis for making short-term predictions that can be iteratively updated and improved as more and new data become available.

Our collaborative modeling approach widens the scope for potential mitigating actions, by highlighting several novel and manageable drivers of Ptarmigan population dynamics and changes. While our results indicate that protection against hunting or reduced hunting quotas would have a positive effect, it appears that the current harvest quotas are not among the key drivers of Ptarmigan population dynamics in the management region and time period considered in the present study. One should be aware that the effect of harvest could to some extent be confounded with the strong negative effect of winter onset, as late snowfall may lead to a longer hunting season compared with years of early snowfall. However, our results suggest that other management actions could be more effective, such as forest management after moth outbreaks. Given that multiple drivers impact the population dynamics, potential management actions are diverse and complicated by the uncertainty in how the drivers act in concert, especially if acted upon by management. Considerations are further complicated by uncertainty about whether the population is in a transient state or at its natural attractor (Hastings et al. 2018), that itself may be moving due to climate change. Furthermore, the community and continent-wide decline in ground-nesting birds (Lehikoinen et al. 2014, Lehikoinen et al. 2019) also urge for consideration of general drivers of change in alpine-Arctic ecosystems (Ims et al. 2019).

Our experience supports the growing evidence of the potential for SFP to aid ecological decision-making (Cook et al. 2014*a, b*, Schwartz et al. 2018). However, our experience also emphasizes the need for appropriate time and funding in order to be successful, as well as long-term ongoing involvement from all involved (Reiter et al. 2018). It is difficult to assess the potential benefit of SFP in leading to positive biodiversity change in the long term (Young et al. 2013). Our experience is that an open and flexible process, where all stakeholders' views and opinions are included and treated as "alternative" hypotheses confronted with data, will promote social learning, trust and legitimacy of conservation programs (Young et al. 2013, Sterling et al. 2017). This will increase the likelihood of positive future biodiversity outcomes, which is especially important in light of the current and rapid changes to the natural world (Young et al. 2013, Sterling et al. 2017).

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Supporting Information

Data Availability