Title: ***A Priori*** **Prediction of Population Growth of** ***Parnassius smintheus.***

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Abstract

A priori testing of a model, *i.e.*, predicting an event before it happens, is the gold standard for model validation. This model testing approach steps up ecological modeling beyond simply explaining the past to proactive predictive modeling by challenging the ability of theories to make accurate forecasts before new data are collected, a litmus test of how well we understand the systems we study. The present research aims to test a model based on temperature at ground level by predicting population growth (year-to-year adult population size among 17 sub-populations) of the Rocky Mountain Apollo Butterfly *Parnassius smintheus,* from 2025 to 2026. We built a generalized linear model using subpopulation density and accumulated warm (> 6°C) ground temperatures from November to December (early overwintering period) from 2010 to 2024 as predictors of subpopulation growth rate ($F_{1,70}$ =6.615619, P=1.22e-02). Adult subpopulation growth rate was calculated by using $r_t = \ln(\frac{N_{t+1}}{N_t})$, where N_{t+1} is the current year's peak population while N_t is the peak population size of the previous year. While the model significantly explains past population growth, its predictive ability remains untested. Despite the critical need to accurately predict the effects of climate change on populations, population models have rarely been tested in this manner.

Introduction

Ecological models are simplified versions of reality that capture the main processes and factors influencing how ecological processes work within a particular system. Because ecological models empower researchers and policymakers to examine the potential outcomes of different strategies or management options across various areas, they serve as essential tools for guiding environmental decisions, such as habitat and species conservation and protection of endangered species (Schmolke 2010).

A priori testing of a model, *i.e.*, predicting an event before it happens, is the gold standard for model validation (Popper 1963). This form of prediction is increasingly treated as the clearest operational demonstration of scientific understanding (Houlahan et al. 2017). In ecology, several influential papers have argued that the field of ecology has often privileged post hoc explanation over risky, forward-looking prediction, even though near-term forecasts offer a direct way to test theory, learn from errors, and inform management under changing conditions. *A priori* testing of a model emphasizes archived forecasts, uncertainty quantification, validation against future observations, and continuous model updating. That forecasting perspective is particularly relevant for alpine insects; these species live in some of the most climate-sensitive ecosystems on Earth. For species like *Parnassius smintheus*, which occupies alpine and subalpine meadow systems in the Rocky Mountains, where local population dynamics are shaped by winter weather, especially early winter, waiting until populations have already declined may leave little time for conservation action.

Earlier work on this species showed that winter, especially early winter, is the most influential season for population dynamics. Roland and Matter (2016) found that extreme November minimum and maximum temperatures, together with snowfall, predicted annual population growth better than broad climatic indices and that fine-scale early-winter snow cover across meadows can explain a large fraction of local annual demographic variation. Later work suggests that overwintering eggs experience substantial mortality when exposed to extreme cold temperatures (Matter & Roland 2017). Mechanistic follow-up experiments by Turnbull et al. (2026) indicate that early winter warming increases the likelihood of precocious hatch, that precocious larvae are less cold-tolerant than eggs, and that lethal risk rises when cold snaps occur without persistent snow cover. These preliminary studies point to the fact that optimum winter temperature is beneficial, and this makes winter thermal accumulation a biologically plausible forecasting target.

Degree-day approaches are widely used in insect ecology because they summarize heat accumulation above a lower developmental threshold and often capture the temperature dependence of development, survival, and phenology (Arnold 1959). However, the best threshold is usually species- and stage-specific, and one of the core forecasting tasks is to compare alternative thermal thresholds rather than assume the correct value.

The goal of this preprint is therefore to present an *a priori* prediction of population growth of *Parnassius smintheus* for year 2026. Using historical meadow data, I ask this question: Can a simple model combining meadow density and accumulated winter warmth generate meadow-specific forecasts of next-year (2026) growth rate (R_t)?

Methods

Study design

The Rocky Mountain Apollo butterfly, *P. smintheus*, is native to the Rocky Mountains. At our site, they are found in alpine meadows (Fig. 1) where they constitute a spatial population network. Adults emerge in mid-to-late July and nectar on their host plant, *Sedum lanceolatum,* and a variety of plants with yellow flowers within the meadows (Matter et al. 2009). There is one generation per year, and females lay eggs singly near, but not on, the host plants (Fownes & Roland 2002). Larvae eclose from eggs shortly after snowmelt and feed on the leaves of *Sedum lanceolatum*. This species overwinters as pharate larvae within the eggs, a process critically dependent on early-winter snow cover for survival.

In our previous study, temperature threshold comparison (DTM0–DTM20) from 0 to 20 °C identified the 6°C candidate base temperature (DTM6) as producing the greatest proportion of deviance explained among all candidate models, indicating that winter thermal accumulation above a 6°C base temperature was the most informative predictor of annual population growth. While the model significantly explains past population growth ($F_{1,70}$ =6.615619, P=1.22e^{-02}), its predictive ability remains untested. Adult subpopulation growth rate was calculated by using $r_t = \ln\left(\frac{N_{t+1}}{N_t}\right)$, where N_{t+1} is the current year's peak population while N_t is the peak population size of the previous year.

Forecasting model and uncertainty

The model used for prediction is Rt~($\log_{10}$ (Meadow Density)+DTM6). The fitted equation from the data was: $R_t = 0.5050070 - (0.1901451)\log_{10}(Meadow\ Density) - (0.0002393)\text{DTM6}$.

Forecast uncertainty for each meadow in 2026 was quantified using 95% prediction intervals from the fitted model, which capture both uncertainty in the estimated mean response and residual variability around that mean. In practical terms, the reported intervals are the relevant quantities for *a priori* prediction because they indicate where new observations should plausibly fall, not just the uncertainty in the mean.

Result

For the *a priori* 2026 forecast, predicted Rt values were generally close to zero but varied meaningfully among meadows. The positive central forecasts were for meadow J (R_t = 0.106214497), L (R_t = 0.060731375), M (R_t = 0.134535518), and Z (R_t = 0.002936038). The negative central forecasts were for meadows I (R_t = -0.177414575), K (R_t = -0.001452434), F (R_t = -0.0157185), G (R_t = -0.083912676), O (R_t = -0.214391308), P (R_t = -0.179908056), and Q Peak (R_t = -0.218114104). The forecasts provide information about the most likely direction of population change, but the wide prediction intervals indicate substantial uncertainty. Because every meadow's prediction interval overlaps Rt = 0, no meadow can be classified with complete confidence as either increasing or declining before validation with the observed 2026 data.

Forecast archiving and validation plan

This preprint of my *a priori* predictions will be published before butterfly mark-recapture studies to establish a credible, transparent, and time-stamped record of the model's predictions and expected outcomes. Following adult emergence, mark-recapture methods will be done as described in Matter et al. (2014). Craig's method (Craig 1953) will be used to estimate abundance in each sub-population. Result validation will proceed in four steps, I will: 1. compute observed Rt for each meadow using 2025 and 2026 counts 2. evaluate point forecast error using Root Mean Square Error (RMSE) and mean signed error 3. evaluate interval calibration by checking the proportion of observations falling within the 95% prediction intervals, 4. rerun the degree day threshold comparison with the new data.

Discussion

Science is a structured inquiry involving prediction, experimentation, and modification of hypotheses to provide a better understanding of the natural world. Most scientific research, including in ecology, focuses largely on explaining patterns in outcomes. Scientists gather data, identify patterns, and then build models to explain observed results. This descriptive approach has greatly expanded our understanding of nature, but it cannot test how well our ideas can predict what will happen next. *A priori* prediction steps up science by challenging the ability of theories to make accurate forecasts before new data are collected. This method is a litmus test of how well we understand the systems we study.

Parnassius smintheus is especially well suited for *a priori* prediction because its populations occur in clearly defined meadows whose ecological relationships are well understood, its winter sensitivity has empirical support, and the overwintering stage is now better connected to specific thermal and snow-related risks than in many insect systems. The literature suggests that winter conditions can transmit through survival and development to affect adult abundance in the subsequent summer, which makes winter microclimate a natural leading indicator for the next year's population growth (Roland and Matter 2013). Ecological forecasting literature increasingly emphasizes that structural and input uncertainty can dominate prediction error if ignored. Our *a priori* forecasts explicitly account for both sources of uncertainty. By testing model performance against ecological patterns that have not yet been observed, our research moves ecological modeling beyond explaining historical phenomena toward making genuinely prospective predictions, thereby enabling proactive and evidence-based conservation decisions.

Conclusions

When scientists make predictions before collecting data, they demonstrate transparency about the expected outcomes of their research. When those predictions are confirmed, it builds confidence in scientific understanding; however, when they fail, it is a step toward revision that guides the inquiry in a new direction. As described by Popper 1963, science advances through continuous questioning and refinement of hypotheses and not through asserting perfection.
Our study introduces a publication-ready a priori prediction paper for *Parnassius smintheus* which is built around a simple and interpretable forecasting workflow: measure or model winter thermal accumulation, fit annual growth as a function of previous meadow density and winter thermal accumulation, issue meadow-level predictions with quantified uncertainty, and validate them after the next field season.

The core contribution of the eventual empirical paper will be demonstrating whether an ecologically informed model can accurately predict where populations will grow, stabilize, or decline before the counts are known. Regardless of the outcome, comparing these *a priori* forecasts with subsequent observations will identify where the model performs well and where it requires refinement, thereby turning ecological understanding into an iterative, testable forecasting framework.

Meadow	N_t	Area	DD6	Predicted_R_t	Lower_ R_t	Upper_ R_t	N_{t+1}	Lower_ N_{t+1}	Upper_ N_{t+1}
I	26.5	1.48	559.3265	-0.177414575	-0.972628	0.617799	22.19196	10.01933	49.15329
J	68.7	15.96	506.7145	0.106214497	-0.689614	0.902043	76.39855	34.47158	169.3203
K	85.7	7.82	214.0625	-0.001452434	-0.796402	0.793498	85.57562	38.64627	189.4927
L	58.6	8.28	301.6693	0.060731375	-0.733197	0.854659	62.26915	28.14974	137.7436
M	85.6	20.29	404.3311	0.134535518	-0.661027	0.930098	97.92685	44.19705	216.9753
F	27.8	2.42	236.2553	-0.0157185	-0.810564	0.779127	27.36644	12.36008	60.59199
G	20.5	2.235	700.1254	-0.083912676	-0.878678	0.710853	18.84999	8.514297	41.73239
O	47.8	2.53	671.1858	-0.214391308	-1.010316	0.581534	38.57615	17.40416	85.50368
P	68.7	6.01	926.3775	-0.179908056	-0.977979	0.618163	57.38834	25.83604	127.474
Q	190.3	9.12	607.8134	-0.218114104	-1.01428	0.578052	153.0076	69.01485	339.2216
Z	76.6	13.398	712.7943	0.002936038	-0.793352	0.799224	76.82523	34.64818	170.3442

Table 1: Meadow Growth Rate and Population Size predictions with 95% prediction intervals for Year 2026

Fig.1: *P. smintheus* subpopulations along Jumpingpound Ridge in Canada during snow cover (50.95° N, 114.91° W, 2100m). Seventeen meadows and corresponding subpopulations are shown.

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