

## Research

### Stochastic predation exposes prey to predator pits and local extinction

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Understanding how predators affect prey populations is a fundamental goal for ecologists and wildlife managers. A well-known example of regulation by predators is the predator pit, where two alternative stable states exist and prey can be held at a low density equilibrium by predation if they are unable to pass the threshold needed to attain a high density equilibrium. While empirical evidence for predator pits exists, deterministic models of predator–prey dynamics with realistic parameters suggest they should not occur in these systems. Because stochasticity can fundamentally change the dynamics of deterministic models, we investigated if incorporating stochasticity in predation rates would change the dynamics of deterministic models and allow predator pits to emerge. Based on realistic parameters from an elk–wolf system, we found predator pits were predicted only when stochasticity was included in the model. Predator pits emerged in systems with highly stochastic predation and high carrying capacities, but as carrying capacity decreased, low density equilibria with a high likelihood of extinction became more prevalent. We found that incorporating stochasticity is essential to fully understand alternative stable states in ecological systems, and due to the interaction between top–down and bottom–up effects on prey populations, habitat management and predator control could help prey to be resilient to predation stochasticity.

**Keywords:** alternative stable states, carnivores, population dynamics, predator control, ungulates, wildlife management

## Introduction

Predation can be an important factor affecting prey populations. A simple model for the effect of predation is where density-dependent predation causes prey abundance to decline to a single low density equilibrium (Fig. 1a). Another well-known theoretical example of regulation by predation is the predator pit (Fig. 1b). A predator pit occurs when two alternative equilibria (Holling 1973, May 1977) exist and prey can be held at a low density equilibrium, unable to pass a critical threshold ('the pit') needed to reach the higher density equilibrium (Messier 1994, Sinclair and Pech 1996). However, if prey can grow to surpass this critical threshold, both predator and prey will be able to

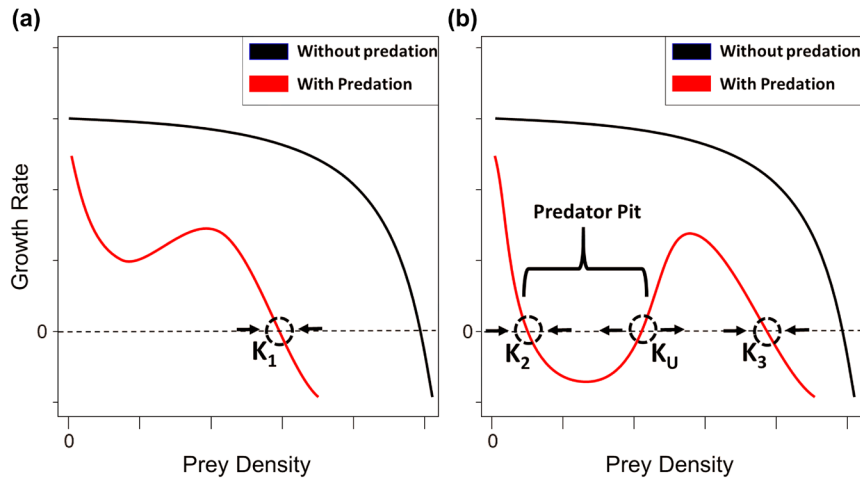


Figure 1. Two conceptual models of prey population regulation. The black lines represent growth rate of prey per density without predation and the red lines represent growth rate of prey per density with predation. When the growth curves cross the dashed black line (growth rate of zero), an equilibrium condition is possible (dashed circles). Arrows pointed towards the circle represent a stable equilibrium, whereas arrows pointed away from the circle represent an unstable equilibrium. (a) Shows that predation can reduce the stable equilibrium to a lower density at  $K_1$ . (b) Shows that predation can reduce the local minima in (a) below the growth rate of zero, resulting in a 'predator pit', where an unstable equilibrium,  $K_U$ , is separated by high and low density stable equilibria,  $K_2$  and  $K_3$ , respectively. If prey density can increase past  $K_U$ , populations will grow to the higher density stable equilibrium,  $K_3$ . Stochasticity may allow the growth curve in (a) to pass below the growth rate of zero, similar to (b), leading to a predator pit.

maintain high density equilibria (Sinclair and Pech 1996). Predator pits are thought to occur when predators maintain prey at low densities via density-dependent predation (Supporting information), whereas at higher prey densities, predation becomes inversely density-dependent (depensatory) due to factors such as predator satiation, handling time and territoriality (Holling 1959, Messier 1994, Sinclair and Pech 1996). Theoretically, predator pits have been shown to occur in complex models such as those with non-monotonic functional responses, alternative prey, feedback loops in trophic structure and age-structured predation (May 1977, Bakun 2006, Smout et al. 2010, Pavlová and Berec 2012). For example, Pavlová and Berec (2012) showed that predator pits may occur if generalist predators only consume one age class of prey with a type II functional response. Predator pits are of concern to applied ecologists, as they present a possible reason for the observed lack of recovery of animals after rapid declines, or low densities of prey species in apparently productive habitat (Courchamp et al. 2008).

In addition to predator-prey models predicting the existence of predator pits, there is some empirical evidence that predator pits occur in natural populations. For example, the Alaska Dept of Fish and Game controlled gray wolf *Canis lupus* populations in interior Alaska to increase moose *Alces alces* and caribou *Rangifer tarandus* populations for harvest (Boertje et al. 1996). After predator control ended and wolf populations rebounded, prey populations still maintained high densities, consistent with the prediction of predator pit dynamics (National Research Council 1997). Others have found some possible evidence for predator pits (Gascoigne and Lipcius 2004, Regelin et al. 2005, Pimenov et al. 2015 and citations therein), however few have experimentally tested

if prey remain at high densities once predators rebound to high densities, making it difficult to differentiate from simple top-down predation. In light of these empirical examples and others, some wildlife management agencies have managed prey under the explicit or implicit assumption that predator pits are the major regulating mechanism (Boertje et al. 1996, Regelin et al. 2005). Despite the existence of empirical examples, experimental difficulties coupled with complex theoretical mechanisms and similar predictions between simple top-down predation and predator pits (Fig. 1) have led some to conclude that predator pits may not exist in nature (Messier 1994, Oksanen et al. 2001, Andersen et al. 2006).

Bottom-up factors may contribute to the existence of predator pits as much as the nature and shape of predation due to the effect of primary productivity on the prey growth response. Analogously, alternative stable states (e.g. consumer-resource pits) have been found to become more likely at higher carrying capacities (Van Nes and Scheffer 2005). This may be because higher carrying capacities lead to increased energy flux in the system, making predator-prey interactions more top heavy and less stable (Rip and McCann 2011), and therefore increasing the potential for alternative stable states. While there is no information on how bottom-up drivers affect predator pits, examples from simple top-down predation may help to inform these effects. For example, across systems with one equilibrium under predation, Melis et al. (2009) found that predators had a greater impact on roe deer *Capreolus capreolus* populations in habitat with low primary productivity. Moreover, Messier (1994) built theoretical models fit to empirical data of wolf-moose predator-prey dynamics and showed that wolf populations drive moose populations to low density equilibria, not

predator pits, in poorly productive habitat (i.e. low carrying capacity). These examples show that primary productivity can modify the prey growth response when there is one equilibrium, and therefore it is feasible that predator pits (i.e. existence of multiple alternative equilibria) may be modified similarly.

To date, deterministic models have been typically used to search for predator pit dynamics (Pavlová and Berec 2012). However, when realistic parameters are used in these models, even for systems that have demonstrated the likely existence of a predator pit (Boertje et al. 1996), alternative equilibria are not predicted (Messier 1994; Results). To reconcile an apparent discrepancy between empirical observations and theoretical models, we were interested in whether models that incorporated stochasticity in predation rates would change the predictions relative to deterministic models and allow predator pits to emerge. Indeed, research on other consumer–resource systems have shown that when stochasticity is added to deterministic models, these processes can blend to produce emergent dynamics not found in solely deterministic models (Dennis and Costantino 1988, Sharma et al. 2015, Abbott and Nolting 2017). However, these dynamics in higher trophic levels remain largely unexplored. As is the case for many biological processes, predation has been shown to be a stochastic process, driven by predators ranging from large carnivores to piscivorous fish (DeAngelis et al. 1984, Festa-Bianchet et al. 2006, Almaraz and Oro 2011). The predation rate can vary due to abiotic factors such as weather (Post and Stenseth 1998, Hebblewhite 2005, Hegel et al. 2010, Wilmers et al. 2020) or biotic factors such as individual specialization of predators on prey (Festa-Bianchet et al. 2006). In our study, we explored the role of stochastic weather events in mediating predator–prey interactions from both the bottom–up (e.g. carrying capacity) by impacting the prey growth rate and from the top–down (e.g. stochastic predation) by impacting predator behavior. For example, from the bottom–up, as elk *Cervus canadensis* nutritional conditions decline over the winter season, wolf *Canis lupus* kill rates on elk increase (Metz et al. 2012). From the top–down, deep snow leads to higher carnivore predation rates on ungulate populations (Post and Stenseth 1998, Hebblewhite 2005, Hegel et al. 2010, Wilmers et al. 2020).

Here, we used stochastic population growth models to investigate how stochastic predation and the effect of changes in carrying capacity influence population dynamics via the likelihood of predator pits and local extinction. We developed models using realistic parameter estimates from large mammal predator–prey systems because of the relevance of the predator pit hypothesis to their applied management (National Research Council 1997). For example, predator pit dynamics predict that if a prey population is managed to be released from predation (e.g. via predator control) and let to grow to high densities out of the ‘pit’, then later relaxation of predator management will let predator populations regrow to achieve both predator and prey populations at high densities (Boertje et al. 1996). We then explored a wider parameter

space using bifurcation analyses to understand how applicable these models were to other predator–prey systems. Because of a potential interaction between the amount of stochastic predation (top–down) and the productivity of the environment (bottom–up), we explored the dynamics of these systems with varying amounts of stochasticity in predation and environments with low and high prey carrying capacities.

## Models and analysis

### Deterministic model of prey growth with predation

First, we explored the equilibria present in population growth with predation in a deterministic framework to understand dynamics in absence of stochasticity. We chose a discrete-time modelling framework because many species have discrete reproductive seasons (Eberhardt 1998). We modeled prey population growth in the absence of predation by a particular predator using the generalized theta-logistic model (Gilpin and Ayala 1973):

$$N_{t+1} = N_t \left( e^{\mu_t} \right) \quad (1)$$

where  $N_t$  is prey population size at time  $t$  and  $\mu_t$  is the population growth rate:

$$\mu_t = r_{\max} \left[ 1 - \left( \frac{N_t}{K} \right)^\theta \right] \quad (2)$$

In Eq. 2  $r_{\max}$  is the maximum growth rate when  $N$  equals 0,  $K$  is the carrying capacity and  $\theta$  is the nonlinear shape parameter governing the nonlinear effect of density on the growth rate. We then included the effect of predation:

$$N_{t+1} = N_t \left( e^{\mu_t} \right) (1 - P_t A) \quad (3)$$

where  $P_t$  is the predation rate (total response; proportion of prey killed by predators), and  $A$  is the proportion of predation that is additive, i.e. that is expected to cause a decline in prey survival. This is to account for the fact that not all predation is additive; predation can be compensatory (e.g. predators kill the ‘doomed surplus’; Errington 1956). To better connect the predation rate to ecological processes, we decomposed the predation rate  $P_t$  into the functional response ( $\Psi_t$ ; no. prey killed/predator as a function of no. prey) and numerical response ( $W_t$ ; no. predators as a function of no. prey), which were modeled using hyperbolic Michaelis–Menten functions (i.e. a variant of Holling’s disc equation; Real 1977):

$$P_t = \Psi_t \left( \frac{W_t}{N_t} \right) \quad (4)$$

$$\Psi_t = \left( \frac{\alpha_0 N_t^{(\alpha_2+1)}}{\alpha_1 + N_t^{(\alpha_2+1)}} \right) \quad (5)$$

$$W_t = \delta_0 + \frac{(\delta_1 - \delta_0) N_{t-1}}{\delta_2 + N_{t-1}} \quad (6)$$

where  $\alpha_0$  is the maximum kill rate,  $\alpha_1$  is the half saturation constant of kill rate,  $\alpha_2$  is the shape parameter (where 0 = type II; 1 = type III functional response),  $\delta_0$  is the minimum predator density,  $\delta_1$  is the maximum predator density and  $\delta_2$  is the half saturation constant of predator density. We modeled the ‘isocline’ numerical response (Eq. 6;  $W_t$ ) phenomenologically based off of previous theoretical and empirical research, assuming alternative prey were available to the predator at low prey densities, and assuming that predator numbers saturate at high prey densities due to nutritional factors or spacing behavior (Supporting information) (Holling 1959, Messier 1994, Bayliss and Choquenot 2002). The numerical response is important for model realism but does not affect the existence of predator pits (Table 2). In the numerical response we assumed a lag of one time-step for prey biomass ( $N_{t-1}$ ) to be converted into predator biomass to allow time for the predator population to grow in response to predation on prey (Eberhardt 1998). Simulations without lags produced similar results.

### Stochastic model of prey growth with predation

We added stochasticity to the deterministic model (Eq. 3) in two ways. We first added environmental stochasticity to prey population growth in the absence of predation:

$$\mu_t = r_{\max} \left[ 1 - \left( \frac{N_t}{K} \right)^\theta \right] + E_t \quad (7)$$

where  $E_t \sim \text{normal}[0, \sigma^2]$ . Second, we modeled stochasticity in the predation rate by adding a normally distributed error term  $F_t \sim \text{normal}[0, \tau^2]$  to the logit-transformed predation rate  $\text{logit}(P_t A) + F_t$  and then back-transforming to get the stochastic predation rate. These transformations were necessary so that stochasticity could be added to the predation rate and still be bounded from 0 to 1, as it is the proportion of prey killed. Thus:

$$N_{t+1} = N_t \left( e^{r_{\max} \left[ 1 - \left( \frac{N_t}{K} \right)^\theta \right] + E_t} \right) \left( 1 - \text{invlogit}(\text{logit}(P_t A) + F_t) \right) \quad (8)$$

### Model parameterization

To explore how adding stochasticity changes the predictions of a deterministic predation model with realistic conditions, we first parameterized our model using a well-studied system of wolf predation on elk and then explored a wider range of parameter space using sensitivity analyses. Parameterization for the wolf–elk system are as follows (Table 1). The parameter  $r_{\max}$  for elk was obtained from Eberhardt (1996), who observed that the maximum intrinsic growth rate could be as high as 0.28. We used elk abundance data which were gathered from the northern Yellowstone elk herd, WY-MT, USA, from 1968 to 1980, where elk were naturally regulated without predation by wolves (Coughenour and Singer 1996), to estimate  $\theta$ . We estimated  $\theta$  to be 4.0 by holding  $r_{\max} = 0.28$  and  $K = 13\,000$  (assumed to be the apex of elk population size based on data) constant in fitting the theta-logistic model to these Yellowstone data using a nonlinear least-squares procedure (Supporting information). This  $\theta = 4.0$  is consistent with biological evidence that elk have slow life histories representative of convex nonlinear density-dependent growth (Bonenfant et al. 2009). For Eq. 5 and 6, we assumed  $\alpha_0$ ,  $\alpha_1$  and  $\delta_1$  were 20, 1 and 35, respectively, by averaging across

Table 1. Parameter values for deterministic and stochastic models (Eq. 3 and 8, respectively) for the wolf–elk system.

Parameter	Meaning	Value(s)	Source(s)
$r_{\max}$	Intrinsic growth rate of prey	0.28	Eberhardt 1996
$K$	Carrying capacity of prey	5; 20	NA
$\theta$	Nonlinear shape parameter of density-dependence of prey	4	Coughenour and Singer 1996
$A$	Proportion of prey mortality which is additive	0.7	Ballard et al. 2001
$\alpha_0$	Maximum of kill rate for functional response, $\Psi_t$	20	Hayes and Harestad 2000, Smith et al. 2004, White and Garrott 2005, Vucetich et al. 2011
$\alpha_1$	Half-saturation constant of kill rate for functional response, $\Psi_t$	1	Hayes and Harestad 2000, Smith et al. 2004, White and Garrott 2005, Vucetich et al. 2011
$\alpha_2$	Shape parameter of kill rate for functional response, $\Psi_t$	0	Vucetich et al. 2002, Hebblewhite 2013, Zimmermann et al. 2015
$\delta_0$	Minimum predator density of numerical response, $W_t$	5	Vucetich et al. 2002, Hebblewhite 2013, Zimmermann et al. 2015
$\delta_1$	Maximum predator density of numerical response, $W_t$	35	Hayes and Harestad 2000, Smith et al. 2004, White and Garrott 2005, Vucetich et al. 2011
$\delta_2$	Half-saturation constant of predator density for numerical response, $W_t$	1	Vucetich et al. 2002, Hebblewhite 2013, Zimmermann et al. 2015
$\sigma^2$	Environmental stochasticity	0.1	NA
$\tau^2$	Predation stochasticity	0–2	Vucetich et al. 2011



prior estimates of kill rates and maximum wolf densities (Smith et al. 2004, White and Garrott 2005, Vucetich et al. 2011). The parameters  $\alpha_2$ ,  $\delta_0$  and  $\delta_2$  were set to 0, 5 and 1, respectively, allowing for type II functional and numerical responses, which have been found to characterize wolf predation on elk (Vucetich et al. 2002, Hebblewhite 2013, Zimmermann et al. 2015). Elk and wolf abundance were on different spatial scales (elk/1 km<sup>2</sup> and wolves/1000 km<sup>2</sup>), so elk abundance ( $N_1$ ) was multiplied by 1000 within the predation rate equation (Eq. 4). Predation rate (total response;  $P$ ) was density-dependent, then became inversely density dependent at a density of 0.75 elk km<sup>-2</sup> (Supporting information), consistent with simulations from type II functional and numerical responses (Holling 1959, Messier 1995). The parameter  $A$  was suggested to be 0.7 from the proportion of predation that is expected to contribute to additive mortality (Ballard et al. 2001). We modeled the relationship between prey density and prey growth rate using Eq. 3 in simulations with and without predation and with high and low carrying capacity ( $K=20$  or 5 elk km<sup>-2</sup>, respectively) in relation to the initial condition of population density,  $N_1=3$ . Varying initial conditions did not change the dynamical results found in Eq. 3 or 8.

To examine the interaction among stochasticity and the effects of top-down (predation) versus bottom-up (resource limitation; proxied by  $K$ ) regulation, we ran simulations of population growth (Eq. 8) where both carrying capacity ( $K=5$  or 20) and predation stochasticity ( $\tau^2=0-2$ ) were varied. We set environmental stochasticity on prey to a relatively low level ( $\sigma^2$  to 0.1), as we were primarily interested in the effects of predation stochasticity on prey dynamics. Other values did not change our primary findings (Table 2). Predation stochasticity ( $\tau^2$ ) was varied between 0 and 2 due to high variability observed in predation rates of wolves on elk (Vucetich et al. 2011). Simulations showed that under the maximum predation stochasticity ( $\tau^2=2$ ), predation rate ( $P$ ) had a mean standard deviation of 0.207, which is within the standard deviation found for wolf-elk predation rates, 0.277, in Banff National Park, Alberta, Canada (Vucetich et al. 2011). Here, we hypothesized that predation stochasticity was driven by stochastic weather events, which have been shown to mediate predator-prey interactions (Post and Stenseth 1998, Hebblewhite 2005, Wilmers et al. 2020),

and suggests that  $E_t$  and  $F_t$  are correlated. Therefore, we drew  $E_t$  and  $F_t$  from a bivariate normal distribution with means of 0, variances of  $\sigma^2$  and  $\tau^2$ , respectively, and correlation of 0.7. Alternative correlation values produced qualitatively similar results (Supporting information). Initial conditions for density ( $N_1$ ) were set to 3, and 1000 replications were run per simulation. Simulations were run for 500 years until  $N$  reached a stationary distribution, where local modes/antimodes are fixed and equivalent to the stable/unstable equilibria of deterministic population models (Dennis and Costantino 1988, Dennis et al. 2016). We recorded qualitative changes in stationary distributions (known as P-bifurcations (Arnold 1998, Bashkirtseva and Ryashko 2018)) as a function of both  $\tau^2$  and  $K$ .

### Bifurcation and sensitivity analyses

As has been the case for many systems, the deterministic model (Eq. 3) using our particular parameterization of the wolf-elk system did not predict a predator pit. To evaluate if alternative parameterizations would have resulted in a deterministic predator pit across a wider range of parameter space, we conducted bifurcation analyses. We simultaneously varied all parameter values by taking 10 000 random draws from uniform distributions from -30 to +30% of each original parameter value. We then recorded the proportion of draws in which predator pits occurred. To evaluate how uncertainty in parameter values affected the predicted equilibrium (there was only one for our deterministic model), we varied all parameters by  $\pm 5\%$ ,  $\pm 15\%$  and  $\pm 30\%$  and measured the population size at  $t=500$ .

We conducted a similar numerical bifurcation analysis to explore a wider range of parameter space in the stochastic model (Eq. 8). However, due to the intractability of simultaneously varying and exploring the 12-dimensional parameter space of our stochastic model, we performed a restricted bifurcation analysis for all parameters in the stochastic model and more thorough bifurcation analyses with the most sensitive and relevant life-history parameters ( $K$ ,  $\tau^2$ ,  $r_{\max}$ ) to extend our results to other predator-prey relationships. In our restricted bifurcation analysis, we varied each parameter value by  $\pm 5\%$ ,  $\pm 15\%$  and  $\pm 30\%$  while holding  $K=20$  and other parameters constant. We then recorded dynamical changes

Table 2. Bifurcation analysis for Eq. 8 at  $t=500$  over 1000 simulations. Parameter values were varied from -30% to +30% and changes in dynamical predictions were recorded. 'High Eq.' shows that one stable equilibrium near  $K$  is found; 'Low Eq.' shows that one stable equilibrium near or at 0 is found; and 'Predator Pit' shows two stable equilibria separated by one unstable equilibrium are found in the corresponding parameter space.

Change in parameter	$r_{\max}$	$K$	$\theta$	$\sigma^2$	$\alpha_0$	$A$	$\tau^2$	$\delta_1-\delta_0$
-30%	Low Eq.	Pred-Pit	Pred-Pit	Pred-Pit	High Eq.	High Eq.	High Eq.	Pred-Pit
-15%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit
-5%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit
0%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit
5%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit
15%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Low Eq.	Pred-Pit
30%	Pred-Pit	Pred-Pit	Pred-Pit	Pred-Pit	Low Eq.	Pred-Pit	Low Eq.	Pred-Pit

in stationary distributions (P-bifurcations) as a function of these varied parameters (Bashkirtseva and Ryashko 2018). To explore the influence of top-down versus bottom-up effects on predator pit dynamics, we conducted a more thorough bifurcation analysis by simultaneously varying  $K$  from 0 to 20, and  $\tau^2$  from 0 to 2. Lastly, to explore how slow-fast life history traits affect the emergence of predator pits, we performed a more thorough bifurcation analysis by simultaneously varying  $r_{\max}$  from 0.1 to 0.6, and  $\tau^2$  from 0 to 2, thereby encompassing a relatively wider range of animal prey species.

## Results

### Deterministic model predicts no predator pit

Using realistic parameters for elk in the northern Rocky Mountains, USA, we found that without predation, prey population growth followed a convex nonlinear density-dependent path with one equilibrium at carrying capacity (Fig. 2). Importantly, although there was a basin of prey population growth, the predation rate was not high enough to predict a predator pit in this system (two stable equilibria separated by one unstable equilibrium, Fig. 1b), and only one stable equilibrium near  $K$  in these deterministic models was observed. For more results on the sensitivity of this single equilibria to changes in parameters (Supporting information). Only 1.04% of simulations in the bifurcation analysis of the deterministic predator-prey model (Eq. 3), across a wide range of parameter combinations, indicated predator pit dynamics (Fig. 2c).

### Stochastic model predicts a predator pit

In contrast to straightforward predictions from the deterministic model, we found that prey population dynamics,

including the presence of predator pits and the location of equilibria, depended on the level of predation stochasticity and the prey carrying capacity. Similar to deterministic models, we found a low likelihood for predator pits for simulations with low predation stochasticity, as shown by unimodal stationary distributions with one stable equilibrium near the carrying capacity (modes: low  $K=4.53$ ; high  $K=18.98$ ) and 0% likelihood of low densities and extinction (Fig. 3e–f, 4a). As predation stochasticity increased, predator pits were found in both carrying capacity scenarios (Fig. 3e–f). Under the high carrying capacity scenario, there was a higher likelihood for predator pits (local modes = 0.293 and 18.57 elk km<sup>-2</sup>) that were separated by an unstable equilibrium (critical threshold; antimode = 6.68 elk km<sup>-2</sup>) and a low likelihood (0.045) of extinction (defined as  $N_{500} < 0.1$ ; Fig. 3a, c, e, 4a). However under the low carrying capacity scenario and high levels of predation stochasticity, predator pits became less likely, with one stable equilibrium at low densities (mode = 0.047) more prevalent far away from  $K$  and a higher likelihood of extinction (0.325; Fig. 3b, d, f, 4a).

When stochasticity in predation was included, we found predator-pits across a wider range of realistic parameter values using numerical bifurcation analyses (Table 2). We found predator pits across realistic ranges of  $r_{\max}$  for many animal prey, with higher rates of growth allowing for higher likelihoods of high density equilibria and lower rates of growth allowing for higher likelihoods of low density equilibria and extinction (Fig. 4b).

## Discussion

With the inclusion of stochasticity, we found emergent dynamic properties (e.g. predator pits) that were not predicted in deterministic models. Although the importance of stochasticity in ecological systems with alternative stable

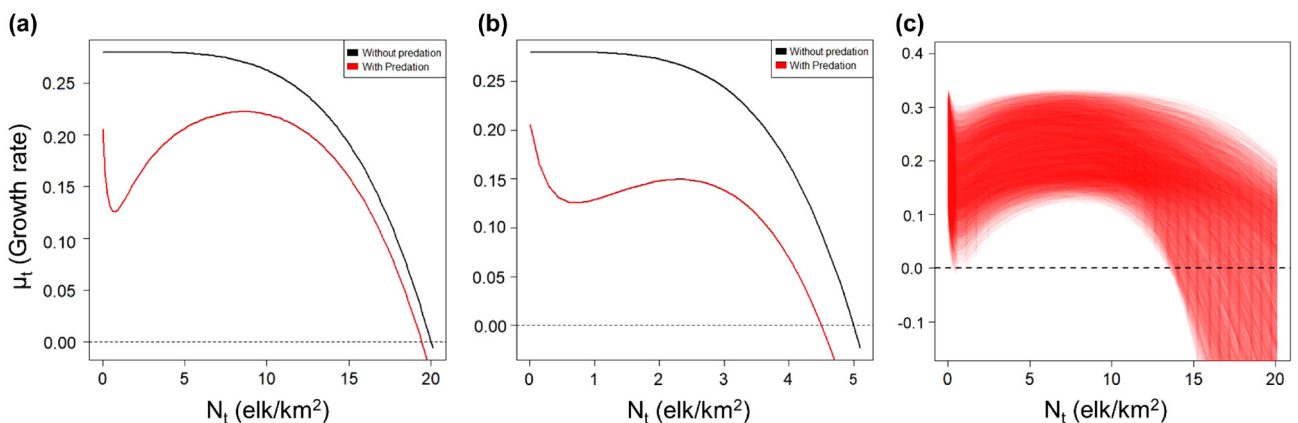


Figure 2. Growth rate,  $\mu$ , per density for (a), high carrying capacity ( $K=20$ ) (b), low carrying capacity ( $K=5$ ) deterministic models of wolf *Canis lupus* predation on elk *Cervus canadensis* and (c), bifurcation analysis in deterministic predator-prey models. Parameter values in (c) were obtained from 10 000 random draws of uniform distributions from  $-30$  to  $+30\%$  of each original parameter value (Table 1). Black and red solid lines represent Eq. 3 without and with predation ( $P/A$ ), respectively. All wolf-elk predator-prey scenarios (a–b) resulted in one equilibrium near  $K$  where the growth rate curves cross the dashed black line (growth rate of zero), and thus no predator pit occurs. 1.04% of simulations in the bifurcation analysis (c) resulted in two equilibria, and thus a predator pit.

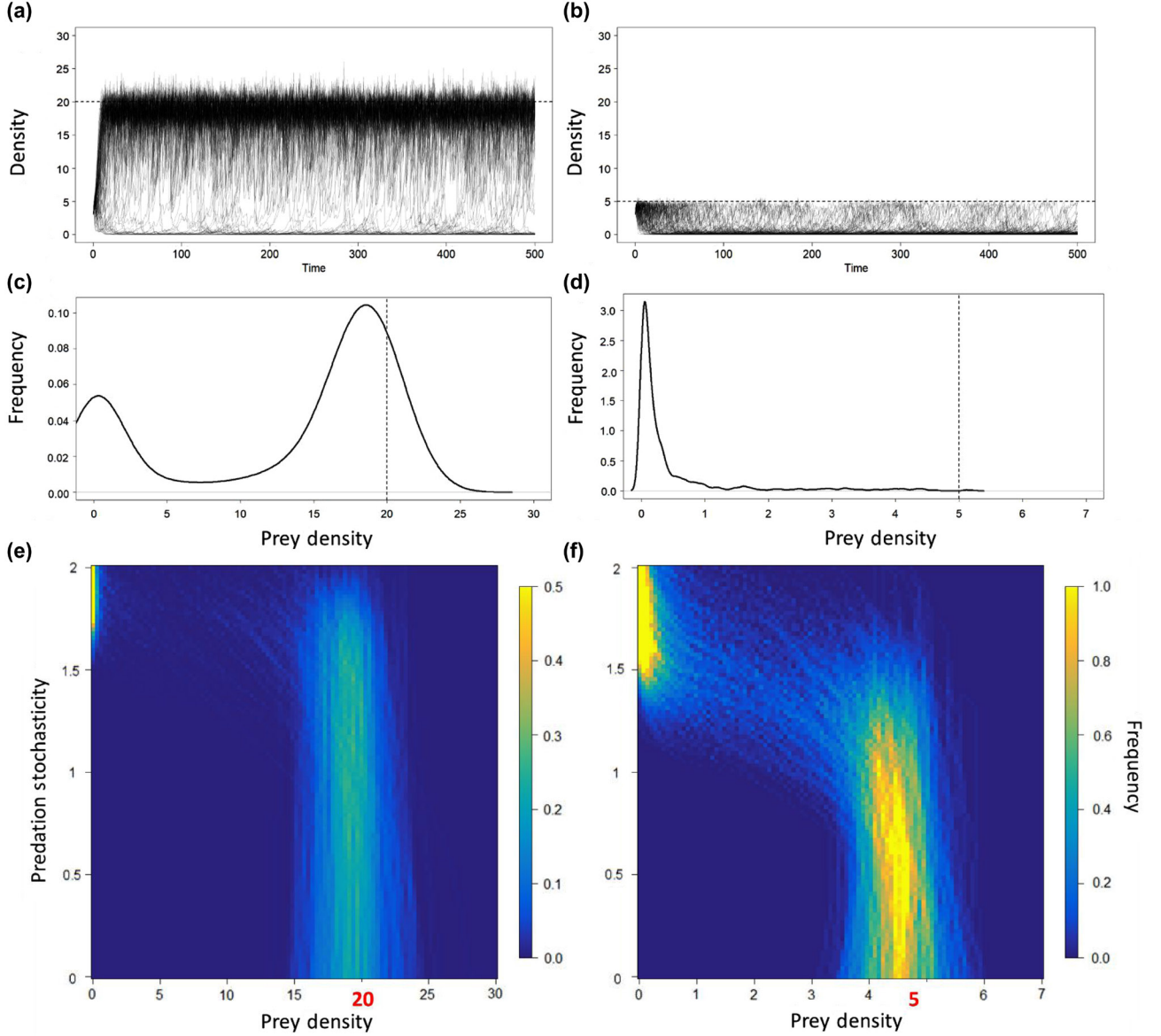


Figure 3. Population growth under predation stochasticity with high ( $K=20$ ) and low carrying capacity ( $K=5$ ). (a and b) Represent 1000 simulations of population growth (Eq. 8) with high predation stochasticity ( $\tau^2 = 1.75$ ) under high (a) and low (b) carrying capacity. (c and d) Show frequency plots of the stationary distribution of densities (a) and (b) at  $t=500$ . Dashed lines represent carrying capacity. (e and f) Show a heatmap of the change in the distribution of prey densities at  $t=500$  across varying levels of predation stochasticity ( $\tau^2$ ). Red numbers in the ‘prey density’ axis indicate carrying capacity.

states has been studied extensively (e.g. stochasticity perturbs dynamics into a different stable state) (Ives et al. 2008, Scheffer et al. 2009, Hastings et al. 2018), the effects of stochasticity have been poorly investigated within higher-trophic levels, especially with data-driven systems. Moreover, these noise-induced transitions to new dynamical behaviors are seldom investigated in predator-prey theory and the larger ecological literature but are quite common in physics (Ridolfi et al. 2011). We suggest that the pedagogy of ecological theory rooted in deterministic basins of attraction has led to some phenomenon, such as alternative stable states and predator pits, to be thought unlikely to occur in systems or

only by complex mechanisms. In fact an evaluation of deterministic models led Messier (1994) to conclude that the parameter space necessary for predator pits is so small that they should be rare in nature. In light of our results, we echo Dennis et al. (2016) statement that: ‘the deterministic modeling tradition obscures emergent dynamic behavior caused by stochasticity’. As such, we suggest that the consideration of stochasticity is necessary to understand animal population dynamics and alternative stable states in ecological systems.

Our study suggests that predator pits might be more common than deterministic models suggest, therefore, we hope this spurs future research to conduct rigorous tests of

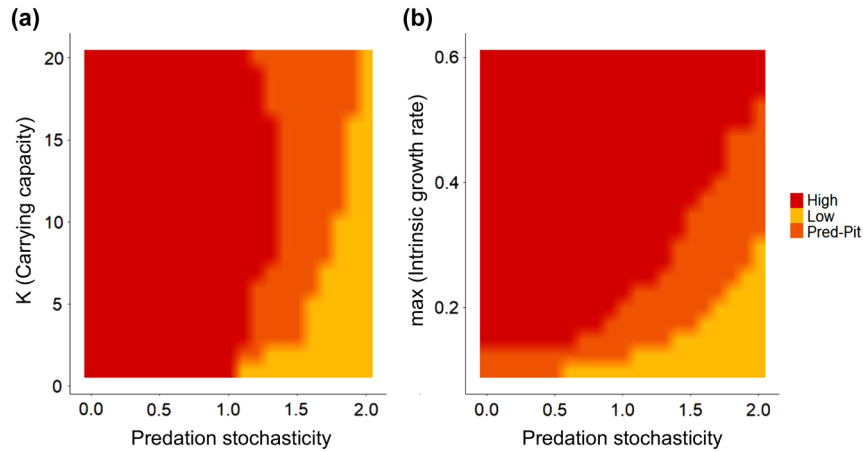


Figure 4. Equilibria of population growth in stochastic predator–prey models. P-bifurcation plots show the qualitative changes in the stationary distributions of 1000 simulations of prey population growth with stochastic predation (Eq. 8) as a function of predation stochasticity ( $\tau^2$ ) and (a)  $K$  (carrying capacity) or (b)  $r_{\max}$  (intrinsic growth rate of prey). ‘High’ shows that one stable equilibrium near  $K$  is found; ‘Low’ shows that one stable equilibrium near or at 0 is found; and ‘Pred-Pit’ shows two stable equilibria separated by one unstable equilibrium are found in the corresponding parameter space. Stationary distributions were recorded at  $t = 500$ .

their prevalence in natural systems. However, to do so, one must conduct an experiment called a ‘test for non-recovery’ (Schröder et al. 2005), where a perturbation (predator control) is used to prompt a discontinuous transition between stable states (May 1977, Scheffer et al. 2001), thereby testing the existence of alternative stable states (predator pit). Yet most cases of alternative stable states in predator–prey systems using predator control are equivocal (however, Schmitz 2004) because of three rigorous, necessary evidentiary criteria. First, a perturbation experiment (complete predator control/removal) must disrupt the ecosystem structure long enough to cause a dramatic change (‘catastrophic shift’; Scheffer et al. 2001) to another stable state (low to high prey density) (May 1977, Connell and Sousa 1983). Second, the control must be reversed (predator reintroduction, immigration, etc.) and demonstrate that the original stable state (low prey density) cannot be recovered, which is known as hysteresis (Connell and Sousa 1983, Scheffer et al. 2001, Schröder et al. 2005). Lastly, both alternative stable states (low and high prey densities) must be shown to persist under identical abiotic conditions for at least one turnover of all individuals in the system (e.g. ungulates  $\approx 10$ –20 years) (Connell and Sousa 1983).

It is clear from these rigid qualifications why few robust experimental tests of predator pits have been carried out in far-ranging, large mammal predator–prey systems due to the inherent complexity, spatial and temporal scale, experimental difficulty and cost of these experiments (Schröder et al. 2005). However, statistical detection criteria developed to detect transitions between alternative stable states may help to detect predator pits. For example, statistical properties of time-series such as increasing autocorrelation, variance and nonlinearity are known to be early warning signs for abrupt transitions between stable states (Scheffer et al. 2009, Dakos et al. 2017). Moreover, approaches using quasi-potentials to analyze stable states in stochastic differential equations (Nolting and Abbott 2016, Abbott and Nolting 2017),

extended to discrete systems, could help reveal predator pit dynamics. Future research could investigate time-series from large carnivore control experiments in the 1970–1990s in Alaska, USA, which demonstrated that predator pits could occur in wolf–moose systems (Boertje et al. 1996). Another pertinent example to be investigated are predator exclusion studies in the National Bison Range, Montana, USA, which have revealed the existence of multiple stable equilibria in rangeland grasshopper populations that vary seemingly because of stochasticity between replicates (Belovsky and Joern 1995, G. Belovsky pers. comm.).

Our intention was to investigate if predator pit dynamics were possible under realistic parameter values for predator–prey systems. We chose to parameterize our models with wolves and elk because previous studies of this system provided us with estimates of many of the parameters needed in our model. Our bifurcation analyses indicate that these predator pit dynamics could extend to other predator–prey systems, which we found in systems where parameters are even far from the bifurcation point (Table 2, Fig. 4). Predator pits may even occur in prey with relatively high intrinsic rates of growth (Fig. 4b). However, alternative model structures (e.g. space, stage-structure) may lead to different, or even more complex dynamics. In some cases, we did not have information on particular processes (i.e. statistical distribution of predation stochasticity; proportion of predation additivity), so we used values that we deemed realistic for this system and sensitivity analyses to show how much expected outcomes depend on our assumptions. However, there may be some caveats to these results given the current lack of knowledge of these parameters. For example, the shape of predation stochasticity could change the emergent dynamics and likelihood of predator pits. For convenience, we chose stochastic predation to be a Gaussian process through a logit scale, however predation rate could manifest through other stochastic distributions like the beta distribution. Further research into



the shape and role of predation stochasticity in nature is therefore necessary. Uncertainty in some parameter values coupled with relatively moderate sensitivity (Supporting information) also indicates that future work is necessary to determine and constrain parameter values. For example,  $A$ , the proportion of additive mortality on the prey population, was inferred using past empirical evidence. However our sensitivity analysis indicated that  $A$  was moderately sensitive, therefore uncertainty in  $A$  could possibly influence our ability to detect dynamical behavior in these systems. Nonetheless, our simple models with feasible values for predator–prey systems coupled with our sensitivity analyses suggest that predator pits can occur under the influence of predation stochasticity.

Management and conservation of threatened, endangered or harvested prey populations necessitates consideration of the interaction between top–down (predation) and bottom–up (habitat) effects on prey population growth. This leads to two potential management scenarios of prey under stochastic predation, if predator pits are found. If habitat is poor (i.e. low carrying capacity), then low density stable states are more likely than predator pits (Fig. 3f, 4a). Therefore in this scenario, one cannot use predator control to raise prey populations to high densities, then let the predator populations regrow and expect prey to stay at high densities, as a predator pit is less likely to occur and there may be no alternative stable states. To have both high densities of predators and prey, improving the habitat is essential to move the population to a predator pit scenario. If habitat is productive or is improved from the previous scenario (i.e. high carrying capacity), then a predator pit could occur and prey populations might be held at a low density equilibrium (Fig. 1b, 3e, 4a). In this scenario, predator control may allow prey to grow to a high density equilibrium. Subsequent relaxation of predator control will then let predator populations regrow to achieve both predator and prey populations at high densities. In sum, our results illustrate a simple mechanism for predator pits, and indicate the need for robust theoretical, statistical and experimental studies in the future to elucidate the existence of predator pits.

### Data availability statement

The code needed to reproduce the analysis can be found on Github (<<https://doi.org/10.5281/zenodo.4281137>>)

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