Received: 11 April 2023 | Revised: 27 July 2023 | Accepted: 18 September 2023

DOI: 10.1002/ecy.4197

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Investigating tritrophic interactions using bioenergetic demographic models

Gioele Passoni[1,2] | **Tim Coulson**[1] | **Francesca Cagnacci**[2] | **Peter Hudson**[3] | **Daniel R. Stahler**[4] | **Douglas W. Smith**[4] | **Shelly Lachish**[5]

[1]Department of Biology, University of Oxford, Oxford, UK

[2]Animal Ecology Unit, Research and Innovation Centre (CRI), Fondazione Edmund Mach, San Michele all'Adige, Italy

[3]The Huck Institutes, Penn State University, State College, Pennsylvania, USA

[4]Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA

[5]Commonwealth Scientific Industrial Research Organisation (CSIRO) Environment Unit, Dutton Park, Queensland, Australia

Correspondence
Gioele Passoni
Email: passonigioele@live.it

Funding information
Natural Environment Research Council, Grant/Award Number: NE/L002612/1; U. S. National Science Foundation, Grant/Award Numbers: DEB-0613730, DEB-1245373

Handling Editor: Madan K. Oli

Abstract

A central debate in ecology has been the long-running discussion on the role of apex predators in affecting the abundance and dynamics of their prey. In terrestrial systems, research has primarily relied on correlational approaches, due to the challenge of implementing robust experiments with replication and appropriate controls. A consequence of this is that we largely suffer from a lack of mechanistic understanding of the population dynamics of interacting species, which can be surprisingly complex. Mechanistic models offer an opportunity to examine the causes and consequences of some of this complexity. We present a bioenergetic mechanistic model of a tritrophic system where the primary vegetation resource follows a seasonal growth function, and the herbivore and carnivore species are modeled using two integral projection models (IPMs) with body mass as the phenotypic trait. Within each IPM, the demographic functions are structured according to bioenergetic principles, describing how animals acquire and transform resources into body mass, energy reserves, and breeding potential. We parameterize this model to reproduce the population dynamics of grass, elk, and wolves in northern Yellowstone National Park (USA) and investigate the impact of wolf reintroduction on the system. Our model generated predictions that closely matched the observed population sizes of elk and wolf in Yellowstone prior to and following wolf reintroduction. The introduction of wolves into our basal grass–elk bioenergetic model resulted in a population of 99 wolves and a reduction in elk numbers by 61% (from 14,948 to 5823) at equilibrium. In turn, vegetation biomass increased by approximately 25% in the growing season and more than threefold in the nongrowing season. The addition of wolves to the model caused the elk population to switch from being food-limited to being predator-limited and had a stabilizing effect on elk numbers across different years. Wolf predation also led to a shift in the phenotypic composition of the elk population via a small increase in elk average body mass. Our model represents a novel approach to the study of predator–prey interactions, and demonstrates that explicitly considering and linking bioenergetics, population demography and body mass phenotypes can provide novel insights into the mechanisms behind complex ecosystem processes.

KEYWORDS
bioenergetics, body-size, demography, elk, integral projection models, population dynamics, predator–prey, trophic cascades, wolf, Yellowstone

INTRODUCTION

A central debate in ecology focuses on the role of apex predators in affecting the dynamics of their prey and ecosystem. Predator-induced mortality ranges from additive to compensatory (Williams et al., 2002) and is often highly selective, removing sick and weak individuals (Hudson et al., 1992; Packer et al., 2003). In addition, predators can affect their prey nonconsumptively by altering their behavior (e.g., movement, foraging, escape response) (Gaynor et al., 2019). In some cases, nonconsumptive effects can be equal to or even exceed those of direct predation (Peckarsky et al., 2008). At the same time, prey affect and are affected by the food resources they depend on, such that the challenge is to understand the complex interactions and feedbacks between primary resources, herbivores and predators. Understanding these processes will improve our ability to assess the ecosystem effects of global changes in predator abundance (Chapron et al., 2014; Ripple et al., 2014) and to predict population performance under environmental change (Lachish et al., 2020). It will also help inform landscape management decisions such as species reintroductions (Nilsen et al., 2007) and enhance our knowledge of complex natural systems.

Empirical evidence to address these issues has come primarily from freshwater systems where community structure can be manipulated through mesocosms, allowing for an evaluation of the effects of predation and competition for food. In terrestrial systems, several experimental and modeling approaches have focused on testing the impacts of resources and predation in the context of rodent and hare population cycles (Krebs et al., 1995, 2001; Oli, 2019; Prevedello et al., 2013; Sinclair & Krebs, 2002). However, such studies reveal issues with scale and do not necessarily extrapolate to systems where the food web is dominated by apex carnivores such as lions or wolves that range over large areas. In part, this is because it is difficult to implement robust experimental approaches that involve adequate replication and appropriate controls at a landscape scale. Most observational studies in extensive terrestrial systems thus have weak inferential strength (Ford & Goheen, 2015; Peterson et al., 2014; but see Ford et al., 2015). Mathematical modeling of ecosystem dynamics offers an alternative approach to understanding species interactions at landscape scales and capturing the key elements of the ecosystems. These models can be fitted to long-term data to assess the effects of vegetation dynamics and predator addition and removal on herbivore populations.

However, to date, most models have lacked a mechanistic underpinning of the biological interactions, limiting the accuracy of inferences (Ford, 2015; Ford & Goheen, 2015). These interactions can both affect and be affected by the phenotypic traits of individuals within populations (e.g., body mass) and can potentially generate unexpected feedbacks among different trophic levels (DeLong et al., 2015; Lachish et al., 2020; Ozgul et al., 2010). These issues can be addressed through the mechanistic modeling of bioenergetics, which can capture the intake of food by herbivores, their growth and reproduction, and the flow of this energy into the predator population.

Structured population models, such as integral projection models (IPMs), can be used to describe population dynamics by linking demographic rates to phenotypic traits (Coulson, 2012). IPMs have already been used to model consumer–resource dynamics between two trophic levels (Lachish et al., 2020; Smallegange et al., 2017). These models were used to obtain the demographic functions (i.e., survival, growth, reproduction, and inheritance) within a modeling framework based on bioenergetic principles, which define how animals acquire and transform resources into body mass, energy reserves, and breeding potential (Lachish et al., 2020). In this study, we extended this approach to embrace a third trophic level and so provide a deeper understanding of how tritrophic interactions are affected by resources and predation.

We developed a bioenergetic mechanistic model of a tritrophic system where the primary vegetation resource follows a simple seasonal growth function and the herbivore and carnivore species are modeled using two IPMs with body mass as the phenotypic trait. Within each IPM, the demographic functions are bioenergetic in form (Lachish et al., 2020), describing how animals acquire and transform resources into body mass, energy reserves, and breeding potential. Adapting and extending the model developed in Lachish et al. (2020), we parameterized this model to reproduce the population dynamics of grass, elk, and wolves in the northern part of Yellowstone National Park and the adjoining areas of Montana (hereafter, "Northern Yellowstone"; MacNulty et al., 2016).

We chose this study system for several reasons. First, we have sufficient data available on the demography, vital rates, and energetics of each species to allow model parameterization (Lachish et al., 2020). Second, since the wolf reintroduction, ecosystem changes have been observed, including a rapid decline in the population of elk, heterogeneous resurgence in aspen and willow, and increases in biodiversity (MacNulty et al., 2016, 2020; Peterson et al., 2020; Smith, Daniel, & MacNulty, 2020). These changes have been attributed to the return of the wolf (Ripple et al., 2001), although other ecological factors have been documented, including the role of other predators (i.e., cougars, bears), droughts, severe winters, and hunting (MacNulty et al., 2016). For this reason, the role of the wolf has been frequently debated, and the causality between wolf reintroduction and the observed ecosystem changes has not been proven (Ford & Goheen, 2015; MacNulty et al., 2020; Peterson et al., 2014; Vucetich et al., 2005). As such, a mechanistic analysis of the system dynamics should improve our understanding of this causality beyond the available evidence based on correlational approaches. In addition, such an analysis has the potential to provide useful insights into the role of specific environmental and eco-evolutionary processes affecting the system like diseases, animal behavior, climate, and management practices. In this paper, we use our model to identify the key biological features shaping tritrophic dynamics and to assess the impact of wolves on the elk–grass system in Northern Yellowstone. We also use our model to test the hypothesis that, after wolf reintroduction, Northern Yellowstone elk switched from being food-limited (bottom-up regulation) to being predator-limited (top-down regulation).

METHODS

Modeling overview

To investigate population dynamics and body mass in a tritrophic system, we developed a mechanistic, bioenergetic model extending and advancing the approach described by Lachish et al. (2020). The model is built to simulate the ecology and the population dynamics of a herbivore and a carnivore population and comprises three trophic levels: the vegetation base, a herbivore feeding on the vegetation, and a predator feeding on the herbivore. While the model is iterated monthly, the three components have an annual life history that can be determined by seasonal variation in the weather. The base of the model is the vegetation. Vegetation growth follows a simple growth function based on environmental conditions and herbivore consumption. Each month, the herbivores feed on the vegetation, and if they survive, they transform the acquired energy into body mass. Here, we define total body mass (Z) as the sum of a structural body mass (Z_S), which is made of bones and essential organs and cannot decrease over time, and a reserve mass (Z_R), which is made of muscle and fat and can fluctuate over time. In the model, herbivores partition the energy acquired through food between structural and reserve mass according to certain parameters. Then, depending on these masses, they have different probabilities of surviving, growing, and, in 1 month per year, reproducing by allocating a proportion of their stored reserves to their offspring. Herbivores' survival is also dependent on predation, which is a function of the number of predators. The predator component works in a very similar way, by feeding on the herbivores, and growing and reproducing analogously. The herbivore and the carnivore populations are modeled using two distinct IPMs that model the demographic outcomes as functions of the distribution of individual body masses (Z). Although the model is generalizable, we parameterized it using existing knowledge about vegetation, elk, and wolves in Northern Yellowstone.

We start by describing the dynamics of the vegetation. We then outline the generic structure of the two IPMs, illustrate the survival, growth, reproduction, and investment in offspring functions, and explain how they were parameterized.

Dynamics of vegetation and herbivore consumption

The model describing vegetation dynamics is formulated to capture the dynamics of grassy vegetation in a seasonal environment (grasses constitute more than 75% of elk winter diet in Northern Yellowstone; Christianson & Creel, 2007). The model structure follows that described in Lachish et al. (2020).

Over a 6-month growing season, and in the absence of herbivores, vegetation (V) grows according to the following equation:

$$V_{t+1} = (1 - a_t)V_{\max} + a_t V_t, \tag{1}$$

where $0 < a < 1$. Thus, in each month of the growing season, the biomass of vegetation increases asymptotically toward $V_{\max}$. During the remaining 6 months of the year, vegetation does not grow ($a = 1$) and can be covered by snow. The biomass of vegetation is reduced via herbivore consumption, which is modeled according to bioenergetics principles, as described in Lachish et al. (2020). Consumption follows a Type II functional response with vegetation biomass (Owen-Smith, 2002), and the maximum ingestion rate is proportional to the structural mass$^{2/3}$ (${Z_S}^{2/3}$; Illius & O'Connor, 2000; Lachish et al., 2020;

van der Meer, 2006). Consumption is limited by a sigmoid function of reserve mass and total mass, such that consumption decreases asymptotically to zero as the ratio of reserve mass to total mass increases toward a target value (f_e) (De Roos et al., 2009). Thus, the maximum vegetation consumed by a herbivore each month is defined by

$$C_{\max,e}(Z_{S,e}) = \left(c_e Z_{S,e}^{\frac{2}{3}}\right)\left(\frac{V_t}{\theta_e + V_t}\right)\left(\frac{1}{1+e^{-\eta_e(f_e Z_e - Z_{R,e})}}\right), \tag{2}$$

where c_e is the slope of the power function, θ_e represents the value at which half of the maximum consumption rate is reached (i.e., the half saturation constant), η_e determines the steepness in satiation scaling of the consumption rate, and f_e is the target energy reserve mass ($Z_{R,e}$) as a fraction of total body mass (Z_e). We note that a high value of η_e can increase the steepness of the curve in Equation (2) to a point that leads to model simplification, whereby only herbivores below a certain $Z_{R,e}/Z$ ratio eat, while herbivores above this threshold do not eat at all.

The total maximum consumption for all herbivores is described as $\int H_{S,e}(Z_{S,e},t)C_{\max,e}(Z_{S,e})dZ_{S,e}$, where $H_{S,e}(Z_{S,e},t)$ represents the distribution of structural mass, $Z_{S,e}$, in the herbivore population (details follow).

The vegetation cannot be consumed to full depletion. The value $V_{\min}$ represents the minimum quantity to which the resource can be consumed and reflects the minimum height of the vegetation that herbivores can graze. To ensure that the vegetation never goes below $V_{\min}$, we scaled resource consumption by a constant, p, defined as follows:

$$p = \begin{cases} 0 \text{ if } (V_t \le V_{\min}) \\ 1 \text{ if } \left(V_t - \int N_e(Z_{S,e},t)C_{\max,e}(Z_{S,e})dZ_{S,e} > V_{\min}\right) \\ \dfrac{V_t - V_{\min}}{\int H_{S,e}(Z_{S,e},t)C_{\max,e}(Z_{S,e})dZ_{S,e}} \\ \text{if } V_t - \int H_{S,e}(Z_{S,e},t)C_{\max,e}(Z_{S,e})dZ_{S,e} < V_{\min}. \end{cases} \tag{3}$$

Finally, in winter months, snow can cover the resource, which reduces the vegetation available to herbivores by a constant proportion, ς. The whole dynamic of the resource is therefore defined by

$$\begin{aligned} V_{t+1} = {} & (1-a)V_{\max} + aV_t \\ & - \varsigma p \int H_{S,e}(Z_{S,e},t)C_{\max,e}(Z_{S,e})dZ_{S,e}, \end{aligned} \tag{4}$$

where $\varsigma = 0.5$ when snow falls, and $\varsigma = 1$ otherwise.

Generic IPM structure

The overall model is composed of two distinct but interacting single-sex bioenergetic IPMs for two populations of female herbivores and carnivores, respectively. Although they are two distinct models, their structure is analogous and based on a single-species model published by Lachish et al. (2020). The dynamics of each population are defined by an IPM that models the demographic outcomes as functions of the distribution of individual body masses. For both herbivores and predators, we assume an annual life history, iterated forward on a monthly time step. For each month, the IPM calculates the distribution of body masses (Z) from time $t, H(Z,t)$ to time $t+1, H(Z',t+1)$ using the following equation:

$$H(Z',t+1) = \int_{\Omega}[D(Z'|Z,t)R(Z,t) + G(Z'|Z,t)S(Z,t)]H(Z,t)dZ, \tag{5}$$

where the survival function $S(Z,t)$ is the probability that individuals of mass Z will survive and the growth function $G(Z'|Z,t)$ is the probability that individuals of mass Z at time t, if they survive, will grow to mass Z' at time $t+1$. The reproduction function $R(Z,t)$ calculates the number of offspring produced by an individual of mass Z between time t and $t+1$. Finally, the investment in offspring function $D(Z'|Z,t)$ gives the probability that the offspring of an individual of mass Z will have mass Z' at time $t+1$. As explained earlier, Z is defined as the sum of a structural component (Z_S) and a reserve component (Z_R). The equations in our model can depend on Z, Z_S, and/or Z_R. While the survival functions of herbivores and predators differ, the reproduction, growth, and investment in offspring functions are analogous—that is, they have the same structure but different parameters. To simplify readability, when equations are analogous, we report one single equation in its generic form for both herbivores and predators. The subscripts "*e*," for elk, and "*w*," for wolf, will be added only when needed for clarity. For example, Z represents the total mass in its generic form (and valid for either elk or wolf), Z_e is the total mass of elk only, and Z_w is the total mass of wolf only.

Survival

Herbivore survival function

Bigger, older elk have higher survival rates than smaller, younger elk in Northern Yellowstone, while individuals in poorer conditions (those with less body fat) experience higher mortality rates (Wright et al., 2004). Thus, we modeled mortality as a function of total body mass using a logit function, with a survival threshold determined by the ratio of reserve mass to body mass. We also made survival a function of predation. Survival is thus described as

$$S_e(Z_e,t)=\begin{cases} 0 \text{ if } \left(\frac{Z_{R,e}}{Z_e}<b_e\right), \\ \frac{1}{1+e^{-\left(\beta_{0,e}+\beta_{1,e}Z_{R,e}-\xi W_t\right)}} \text{ otherwise,} \end{cases} \quad (6)$$

where b_e is the starvation ratio, W_t is the total wolf biomass, and ξ regulates the extent to which the total wolf biomass impacts elk survival.

Predator survival function

Similarly to elk, we modeled wolf survival as a function of body mass and condition, such that bigger individuals survive at higher rates than smaller individuals, while those with insufficient reserve mass die. We also included a density-dependent term to account for the negative effect of intraspecific aggression on wolf survival (Cubaynes et al., 2014). Survival is thus described as

$$S_w(Z_w,t)=\begin{cases} 0 \text{ if } \left(\frac{Z_{R,w}}{Z_w}<b_w\right), \\ \frac{1}{1+e^{-\left(\beta_{0,w}+\beta_{1,w}Z_{R,w}-\varrho W_t\right)}} \text{ otherwise,} \end{cases} \quad (7)$$

where b_w is the starvation ration, W_t is the total wolf biomass at time t, and ϱ represents the strength of intraspecific aggression.

Herbivores as a resource and predator consumption

To survive, grow, and reproduce, predators are able to hunt and feed on herbivores. The total elk biomass (P_t) that predators can eat at time t is

$$P_t=\int(1-S_e(Z_e,t))\,H_e(Z_e,\mathrm{t})dZ_e. \quad (8)$$

This includes all the dead elk, regardless of whether the wolf killed them. This is because wolf in Yellowstone have shown themselves to be effective scavengers, gaining up to around 10% of their energetic requirement from scavenged carcasses (Metz et al., 2012). We note, however, that through the parameter l in Equation (12) we limit the quantity of P_t available to the wolves due to scavenging by other species.

The maximum ingestion rate of wolves was modeled proportionally to structural mass$^{2/3}$, with consumption of elk described by a Type II functional response (Becker et al., 2008; Hebblewhite, 2013; Zimmermann et al., 2015) and a check on overconsumption (as described above for vegetation consumption by elk):

$$C_{\max,w}(Z_{S,w})=\left(c_w Z_{S,w}^{\frac{2}{3}}\right)\left(\frac{P_t}{\theta_w+P_t}\right)\left(\frac{1}{1+e^{-\eta_w(f_w Z_w-Z_{R,w})}}\right), \quad (9)$$

where c_w is the slope of the power function, θ_w represents the half-saturation constant, η_w determines the steepness of the curve toward satiation, and f_w is the target proportion of energy reserve mass and total mass. We note that by Equations (8) and (9), the amount of elk eaten by wolves could theoretically exceed the amount of dead elk available. This does not occur in our model, as shown in Appendix S1: Figure S1.

Growth

The growth functions describe the way in which consumed resources are converted into energy and allocated to the individual structural and reserve mass. For herbivores, as described in the preceding equations, the maximum quantity of resources consumed by each individual corresponds to $pC_{\max,e}(Z_{S,e})$. The energy assimilated by a herbivore from these resources is, thus, $j_e pC_{\max,e}(Z_{S,e})$, where j_e is the energy content of the resource.

Predators assimilate energy in a similar way; however, wolves do not consume elk carcasses in their entirety (as parts of the carcass are inedible) and moreover often lose a portion of their kills to other carnivores and scavengers in the ecosystem (Metz et al., 2012; Wilmers et al., 2003). Hence, the expected total resource consumed by any individual predator will be given by $d(1-l)C_{\max,\mathrm{w}}(Y_{\mathrm{S}})$, where d is the edible proportion of elk biomass and 1 is the proportion of dead elk biomass scavenged by other species. The expected amount of assimilated energy is then $j_w d(1-l)C_{\max,\mathrm{w}}(Z_{\mathrm{S,w}})$, where j_w is the energy content of prey meat.

For both herbivores and predators, part of the assimilated energy is spent on maintenance costs, while the rest is allocated to growth and reproduction. According to Kleiber's law, we assume that daily metabolic costs scale to a three-quarters power law with body mass (Van Savage et al., 2004). Monthly maintenance costs for both herbivores and predators are calculated by multiplying daily metabolic costs by the number of days in a month:

$$M(Z) = 30 \times \delta Z^{\frac{3}{4}}. \tag{10}$$

The amount of energy available for growth and reproduction in herbivores and predators is thus calculated by subtracting maintenance costs from the total energy consumed:

$$\Delta E_e(Z_e) = j_e p C_{\max,e}(Z_{S,e}) - M_e(Z_e), \tag{11}$$

$$\Delta E_w(Z_w) = j_w d(1-l) C_{\max,w}(Z_{S,w}) - M_w(Z_w). \tag{12}$$

This energy is added to an individual's stored resources,

$$Z_R^o = Z_R + m^{-1}\Delta E(Z), \tag{13}$$

where the metabolic coefficient m defines the conversion between assimilated energy and energy reserves. This coefficient varies between anabolic conditions, when $\Delta E(Z)$ is positive, and catabolic conditions, when $\Delta E(Z)$ is negative.

Smaller (younger) individuals can grow their structural mass (Z_S) up to a certain threshold k. Individuals below this threshold turn a proportion ψ of their stored resources into structural mass with a constant efficiency ε_1, while the remaining stored resources are added to their reserve mass. Once k is reached, the individual's structural mass stops growing, and in nonbreeding months, all stored resources are allocated to the reserve mass. Structural and reserve mass at time $t+1$ are thus calculated as follows:

$$Z'_S = \begin{cases} Z_S + \psi\varepsilon_1 Z_R^o \text{ if } (Z_S \le k), \\ Z_S \text{ if } (Z_S > k), \end{cases} \tag{14}$$

$$Z'_R = \begin{cases} (1-\psi) Z_R^o \text{ if } (Z_S \le k), \\ Z_R^o \text{ if } (Z_S > k). \end{cases} \tag{15}$$

For 1 month per year, those individuals that are fully grown ($Z_S > K$) can reproduce, provided that the proportion of stored energy to total mass (Z_R^o/Z) is above a certain threshold g. We call the individuals who satisfy these two conditions potential breeders. In the breeding month, potential breeders allocate a proportion τ of their stored resources to reproduction (see dedicated section below). The change in reserve mass after the breeding period is thus defined by

$$Z'_R = \begin{cases} (1-\psi) Z_R^o \text{ if } (Z_S \le k), \\ Z_R^o \text{ if } \left(Z_S < k \text{ and } Z_R^o : Z \le g\right), \\ (1-\tau) Z_R^o \text{ if } \left(Z_S > k \text{ and } Z_R^o : Z > g\right). \end{cases} \tag{16}$$

In our model, we then assume that the distribution of phenotypic values at time $t+1$ for any given value at time t is Gaussian. Growth for Z_S or Z_R is then described as

$$G(X'|X,t) = N\left(\mu_{X'} \sigma_X^2\right) = \frac{1}{\sqrt{2\pi\sigma_X^2}} e^{\frac{-(X'-\mu_X)^2}{2\sigma_X^2}}, \tag{17}$$

where X is either Z_S or Z_R, N is a normal distribution, and μ and σ^2 are its mean and variance, respectively. The mean is obtained from Equation (10), (11), or (12), while the variance is assumed to be phenotype-dependent defined as

$$\sigma_{X'}^2 = \vartheta - e^{-\gamma X}, \tag{18}$$

where X is either Z_S or Z_R, and ϑ and γ represent the intercept and slope of the function.

Reproduction

Reproduction occurs once every year. As described earlier, to reproduce, an individual must reach a threshold structural mass k and have a sufficient ratio g between reserve mass and total body mass. In our model, we assumed litter size to be 1 and accounted for a fixed proportion of neonates (ω) experiencing immediate mortality. Reproduction is described by

$$R(Z,t) = \begin{cases} 0 \text{ if } (Z_S \le k) \text{ or } \left(Z_S > k \text{ and } Z_R^o : Z \le g\right), \\ 1-\omega \text{ if } \left(Z_S > k \text{ and } Z_R^o : Z > g\right). \end{cases} \tag{19}$$

Investment in offspring

The investment in offspring function describes how the phenotypes are passed on from the parents to the offspring. From the preceding growth equations, we see that potential breeders allocate a proportion of their stored resources (τ) to reproduction. Of these, a proportion υ is allocated to the offspring structural mass, while the remainder forms the offspring reserve mass. The parent-stored resources are converted into the offspring structural and reserve mass with efficiency ε_2 and ε_3, respectively:

$$Z'_{S,\text{offspring}} = \begin{cases} 0 \text{ if } (Z_S \leq k) \text{ or } \left(Z_S > k \text{ and } Z_R^o : Z \leq g\right), \\ \upsilon \times \varepsilon_2 \times \tau \times Z_R^o \text{ otherwise;} \end{cases} \tag{20}$$

$$Z'_{R,\text{offspring}} = \begin{cases} 0 \text{ if } (Z_S \leq k) \text{ or } \left(Z_S > k \text{ and } Z_R^o : Z \leq g\right), \\ (1-\upsilon) \times \varepsilon_3 \times \tau \times Z_R^o \text{ otherwise.} \end{cases} \tag{21}$$

The distribution of Z_S and Z_R in the offspring for any given value in the parents is then described by an equation that is analogous to Equation (17) for growth. Hence,

$$D(X'|X,t) = N\left(\mu_{X'}\sigma_X^2\right) = \frac{1}{\sqrt{2\pi\sigma_X^2}} e^{\frac{-(x'-\mu_X)^2}{2\sigma_X^2}}, \tag{22}$$

where X is either Z_S or Z_R. As for the growth functions, the variance σ^2 of the normal distribution N is phenotype-dependent and calculated using the equation

$$\sigma_{X'}^2 = \lambda - e^{-\varsigma X}, \tag{23}$$

where λ and ς are the intercept and slope of the function, respectively.

Model parameterization

Although the model is generalizable, we parameterized it for vegetation, elk, and wolves in Northern Yellowstone. Grasslands and shrublands mainly composed of sagebrush represent the main habitat for grazing ungulates such as elk, bison, mule deer, and pronghorn and bighorn sheep (Garroutte et al., 2016). Among these species, the elk is one of the most abundant, despite a recent population decline and increasing bison numbers (Metz, Hebblewhite, et al., 2020; Ripple & Beschta, 2012). Elk is also the wolf's main prey, representing ~88% of all ungulates killed by wolf (Metz et al., 2012; Metz, Hebblewhite, et al., 2020; Tallian et al., 2017). For these reasons, we only consider grassy vegetation, wolves, and elk, without explicitly modeling other species. Given the complexity of elk migration dynamics and the nonspatial nature of our model, we do not model elk movement outside of the northern range, although this movement can be significant in the winter.

All parameters were obtained from the available literature and are shown in Appendix S1: Table S1, together with their values and references. Parameters for the vegetation and elk closely follow those detailed in Lachish et al. (2020), while wolf parameters are described below. While our model is based on the elk-only model published by Lachish et al. (2020), it is important to note that, unlike Lachish et al. (2020), we do not incorporate stochasticity in the dynamics of vegetation growth, instead modeling the abiotic environment as seasonal within years but constant across different years. For this reason, the results presented in this study can differ slightly from those of Lachish et al. (2020). The model was run for 1500 months (125 years) to make sure it would reach population values at equilibrium.

Wolf parameters

Adult female wolves in Yellowstone weigh around 41 kg on average (MacNulty et al., 2009). Of these, 21%–30% can be catabolized before all internal energy reserves are exhausted (Mech & Boitani, 2003). We created a vector of 25 values between 0.1 and 43 kg for structural mass (Z_S) and a vector of 25 values from 0.1 to 27 for reserve mass (Z_R). We combined these two vectors as we did in the elk, obtaining a vector of 625 possible total body masses (Z) ranging from 0.2 to 70 kg. Our starting values were limited to the observed weight range (0.1 to 37 for Z_S, 0.1 to 21 for Z_R). Wolf survival was modeled using estimates from the field and included a coefficient to consider density-dependent intraspecific aggression (Cubaynes et al., 2014). In particular, adult survival ranged from an average of around 0.85 with 30 wolves/1000 km^2 to less than 0.6 with 90 wolves/1000 km^2 (Cubaynes et al., 2014).

Wolf population dynamics are complicated by their sociality. In this model, we do not include wolf pack dynamics explicitly. In a typical pack, only the alpha female is able to breed (Mech & Boitani, 2003), and in Yellowstone, females give birth to a litter of around five pups on average (Stahler et al., 2013). We do not model this social complexity and instead make the simplifying assumption that each individual wolf can give birth to one pup. This generated mean reproductive rates that were similar to those observed across the whole population (Smith, Stahler, et al., 2020). Incorporating pack structures and more realistic social group interactions among predators is the focus of ongoing work.

We parameterized the model to reflect food intake by wild wolves and the known impact of wolf predation on elk. Food consumption rates for an average adult wolf based on kill rates in Yellowstone ranged between 5.7 and 17.1 kg of prey per wolf per day (Mech et al., 2001; Stahler et al., 2006). These quantities were calculated based on the live weights of killed prey and do not take into consideration inedible parts (e.g., large bones) and scavenging by other species. The edible elk biomass was measured as 68% of the elk live weight (Wilmers et al., 2003), while the proportion of scavenged prey biomass was estimated at around 25% (Wilmers et al., 2003). The impact of wolf predation on elk survival was modeled based on survival rates measured before and after the wolf reintroduction (Barber-Meyer et al., 2008; Evans et al., 2006).

Sensitivity analysis

We performed a sensitivity analysis to assess how model predictions varied by altering parameters values and to quantify the effect of each parameter on the final model outcome. We varied the value of each individual parameter by −5%, −2.5%, +2.5%, and +5%, running a separate model each time and recording the amount of vegetation, elk, and wolves after the model reached equilibrium (after 1500 months).

Population perturbations

To explore the relative importance of each trophic level and test the hypothesis that the elk becomes predator-limited when the wolf is added to the system, we ran the model three times, each time reducing the abundance of each trophic level by 25%. In particular, in the case of the elk and wolf components, we reduced their population by 25% at a given month while keeping the same population structure. For the vegetation, we reduced the maximum biomass ($V_{\max}$) by 25% for 12 months. These perturbations were applied in March to both systems with and without wolves. To quantify the effect of each perturbation, we measured the extent to which the abundance of each component varied before returning at equilibrium. We chose to perturb the system in March because it is the month before the wolf and the elk reproduce (in April and May, respectively). These perturbations can yield important insights on the system because they could mimic the impact of diseases, such as canine distemper and sarcoptic mange in wolves and chronic wasting disease in elk (Brandell et al., 2021, 2022).

RESULTS

Population estimates

We ran the model with and without wolves until equilibrium (Figure 1). In the model without wolves, the elk population at equilibrium oscillated between 14,938 and 25,289 (mean = 19,944) individuals

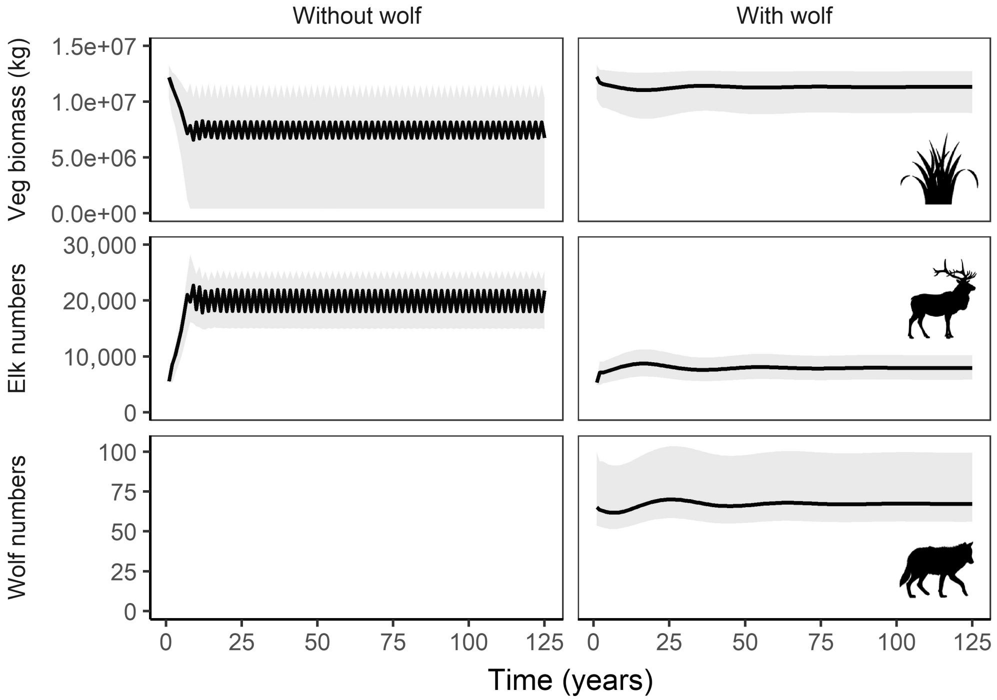

FIGURE 1 Population trends for vegetation, elk, and wolf (top to bottom) modeled in absence (left) and presence (right) of wolves. Black line: mean model projections per year; gray shadings: minimum and maximum in every year (oscillations within years are due to reproduction and mortality).

throughout the year. These model projections reflect the Northern Yellowstone elk counts before the reintroduction of wolves (19,045 individuals in January 1994, just before wolf reintroduction; MacNulty et al., 2016) and are similar to those obtained by Lachish et al. (2020). Our results do not match exactly those in Lachish et al. (2020) since we do not consider environmental stochasticity across different years (see *Methods* section). Other than the expected monthly fluctuation in elk numbers due to breeding and seasonality, the elk population showed a biennial cycle. This cyclical fluctuation occurs because, due to the increase in elk numbers in the absence of predation, vegetation periodically reaches its minimum biomass (V_{min}), causing the elk to starve and temporarily decline in numbers (Lachish et al., 2020).

When we add wolves to the model, the elk population fluctuates between 5805 and 10,280 (mean = 7911) individuals, and wolf numbers vary between 56 and 100 (mean = 67). In this case, no cycles are observed beyond those typical of breeding and seasonality, and across the 1500 months, the vegetation never reaches its minimum value. The values from the model for the elk and wolf populations are consistent with estimates obtained in Northern Yellowstone after wolf reintroduction (5800 elk in March 2018; Loveless et al., 2019; MacNulty et al., 2016; 55 wolves in December 2019; Smith, Stahler, et al., 2020).

Elk and wolf body mass distributions

In our model, the elk average body mass in March was 210 kg in the absence of wolves and 214 kg with wolves. These weights broadly are consistent with those observed in the field in the same season (189–275 kg, Cook et al., 2004) (Figure 2). Wolf predation changed the elk body mass distributions, because wolves selected prey with smaller structural and reserve mass (Figure 2). In wolves, the average body mass in March was 44 kg (Figure 3), which also matches the observed range for female adults in Yellowstone (ca. 30–52 kg; MacNulty et al., 2009).

Sensitivity analysis

Perturbing each model parameter from −5% to +5% showed that different parameters could have different effects on the final model projections and that these effects could vary for the three trophic levels (Appendix S1: Figure S2).

Overall, the elk was the most affected trophic level in the sensitivity analysis. The parameters causing the largest changes in elk population projections were the wolf satiation threshold (f_w, that is, the ratio of energy reserve mass above which wolf food consumption decreases); the reserve allocation to offspring in wolves (υ_w, that is, the proportion of parent reserve mass converted into

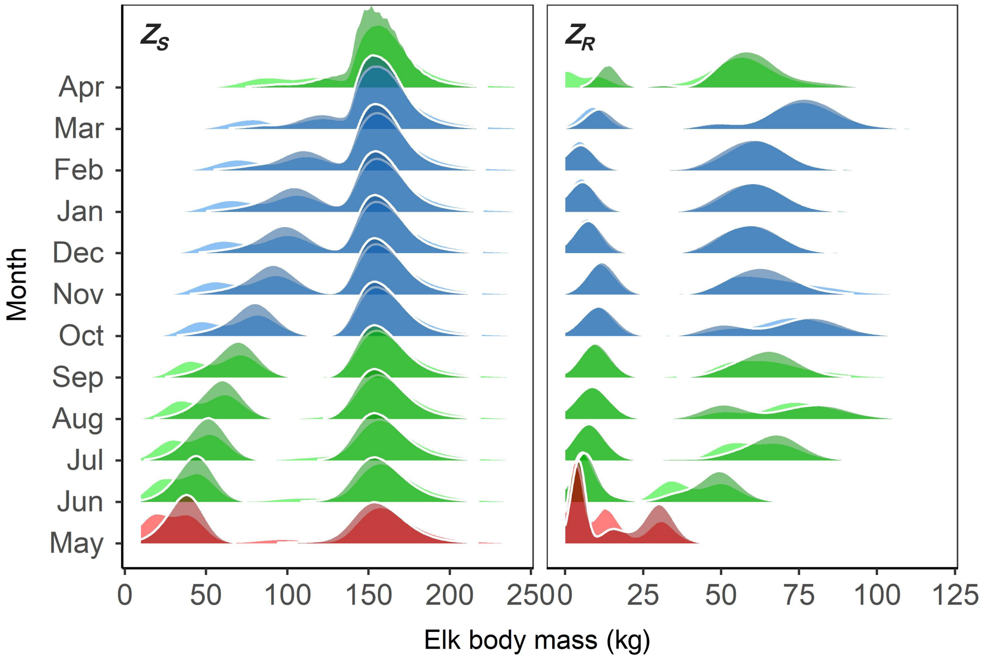

FIGURE 2 Elk body mass distributions for structural (Z_s) and reserve mass (Z_r). Lighter distributions refer to elk population in model without wolves; darker distributions refer to elk population in presence of wolves. Months in which vegetation grows are in green, nongrowing months in blue, and breeding month in red.

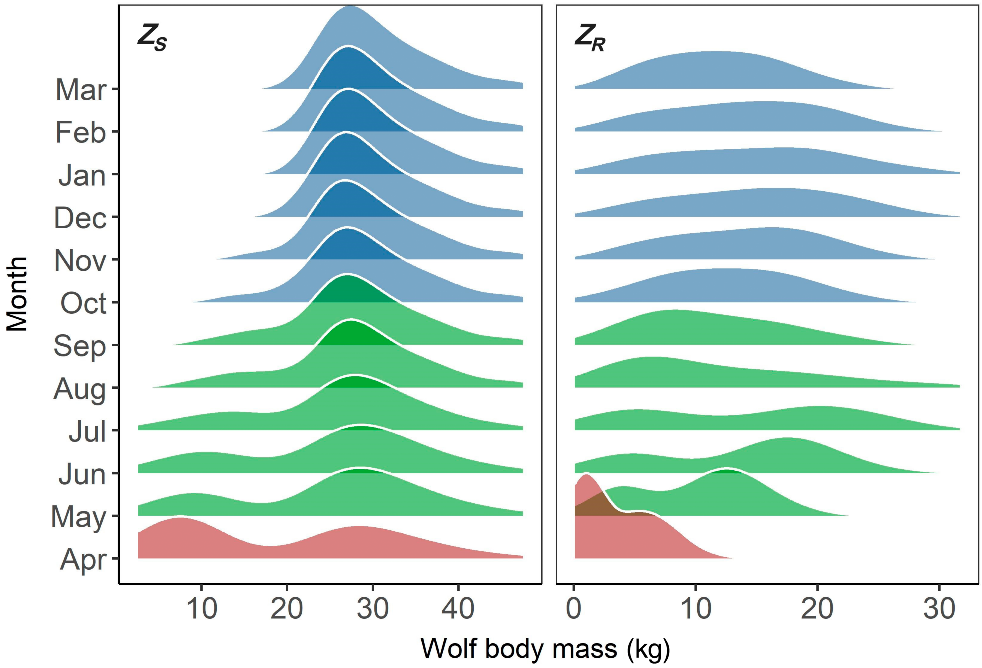

FIGURE 3 Wolf body mass distributions for structural (Z_s) and reserve mass (Z_r). Months in which vegetation grows are in green, nongrowing months in blue, and breeding month in red.

offspring structural mass in wolves); the wolf survival intercept ($\beta_{0,w}$, that is, the intercept of the logit function describing wolf survival); the wolf metabolic costs (δ_w, that is, a scalar constant of wolf daily metabolic costs); the wolf metabolic conversion rate (m_w, that is, the coefficient for catabolic conversion between assimilated energy and energy reserves in wolves); the elk survival intercept ($\beta_{0,e}$, that is, the intercept of the logit function describing elk survival); the vegetation energy content (j, that is, the energy content of the vegetation); and elk ingestion rate (c_e, that is, a scalar content for ingestion rate for elk).

These parameters were the same for the vegetation, although in a slightly different order. Perturbing the wolf satiation threshold (f_w) from −5% to +5% caused the largest change in the overall model, having a positive effect on vegetation biomass (+381%) and wolf numbers (+842%) and a negative effect on elk numbers (−72%). Varying parameter values always had opposing effects on vegetation and elk. As such, varying parameters in favor of the elk population would increase herbivory, leading to a reduction in vegetation biomass and vice versa. For example, perturbing the wolf survival intercept ($\beta_{0,w}$) from −5% to +5% caused a change of +308% in vegetation biomass and −71% in elk numbers. In comparison, perturbing the elk survival intercept ($\beta_{0,e}$) generated a change of −52% in vegetation biomass and +140% in elk numbers.

For wolves, the parameters that, when perturbed, had the greatest impact on population size were the wolf satiation threshold (f_w, that is, the ratio of energy reserve mass above which wolf food consumption decreases); the reserve allocation to offspring in wolves (υ_w, that is, the proportion of reserve mass converted to offspring structural mass in wolves); the vegetation energy content (j, that is, the energy content of the vegetation); the elk ingestion rate (c_e, that is, a scalar content for ingestion rate for elk); the elk survival intercept ($\beta_{0,e}$, that is, the intercept of the logit function describing elk survival); the elk metabolic costs (δ_e, that is, a scalar constant of elk daily metabolic costs); the elk satiation threshold (f_e, that is, the ratio of energy reserve mass above which elk food consumption decreases); and the wolf metabolic conversion rate (m_w, that is, the coefficient for catabolic conversion between assimilated energy and energy reserves in wolves). It is interesting to note that some vegetation-related and elk-related parameters are relatively more important for wolves than they are for the vegetation and elk populations themselves. For example, the energy content of the vegetation (j) is the sixth and seventh most important parameters for the vegetation and the elk, respectively; however, it is the third most important parameter for the wolf. On the other hand, the wolf survival intercept ($\beta_{0,w}$) is the second and third most important parameter for the vegetation and the elk, but only the tenth for the wolf.

An interesting parameter is the wolf hunting efficiency (ξ), which regulates the extent to which wolves kill elk. Increasing the value of this parameter caused the wolf to kill more elk and reduce future prey availability, eventually leading to a reduced wolf population (Figure 4). Finally, some parameters showed some nonlinear responses to the sensitivity analysis (e.g., the wolf satiation threshold—f_w; see Appendix S1: Figure S2). Varying all other parameters had small effects on model predictions.

Population perturbations

Perturbation in the system without wolves

The system without wolves shows cyclical biennial fluctuations. Perturbation of the vegetation caused the vegetation itself to initially decrease from 8M kg to 5.7M kg (28.6%). This reduced the numbers of elk from 23,807 to 4781 (−80%) in 2 years, leading to reduced grazing and, therefore, an increase in vegetation up to 12.9M kg (+126%) (Figure 5A).

Perturbation of the elk had a much smaller impact, with elk numbers decreasing from 23,806 to 18,967 (−20%) and bouncing back to 27,195 (+43%) in 2 years, before starting a return to equilibrium. The impact on grass was even more limited, with vegetation biomass varying from 8M kg to 8.6M kg (+8%), before rapidly returning to equilibrium.

Perturbations in the system with wolves

The addition of the wolf to the model stabilized the overall system, as shown by the lack of cyclical fluctuation in Figure 5B compared to Figure 5A. Reducing the maximum vegetation biomass in the system (Figure 5B) caused the vegetation to oscillate between 11.4M kg and 9.1M kg (−20%) before settling close to equilibrium in 3 years. The elk and wolf were only marginally affected with variations being smaller than 0.1%.

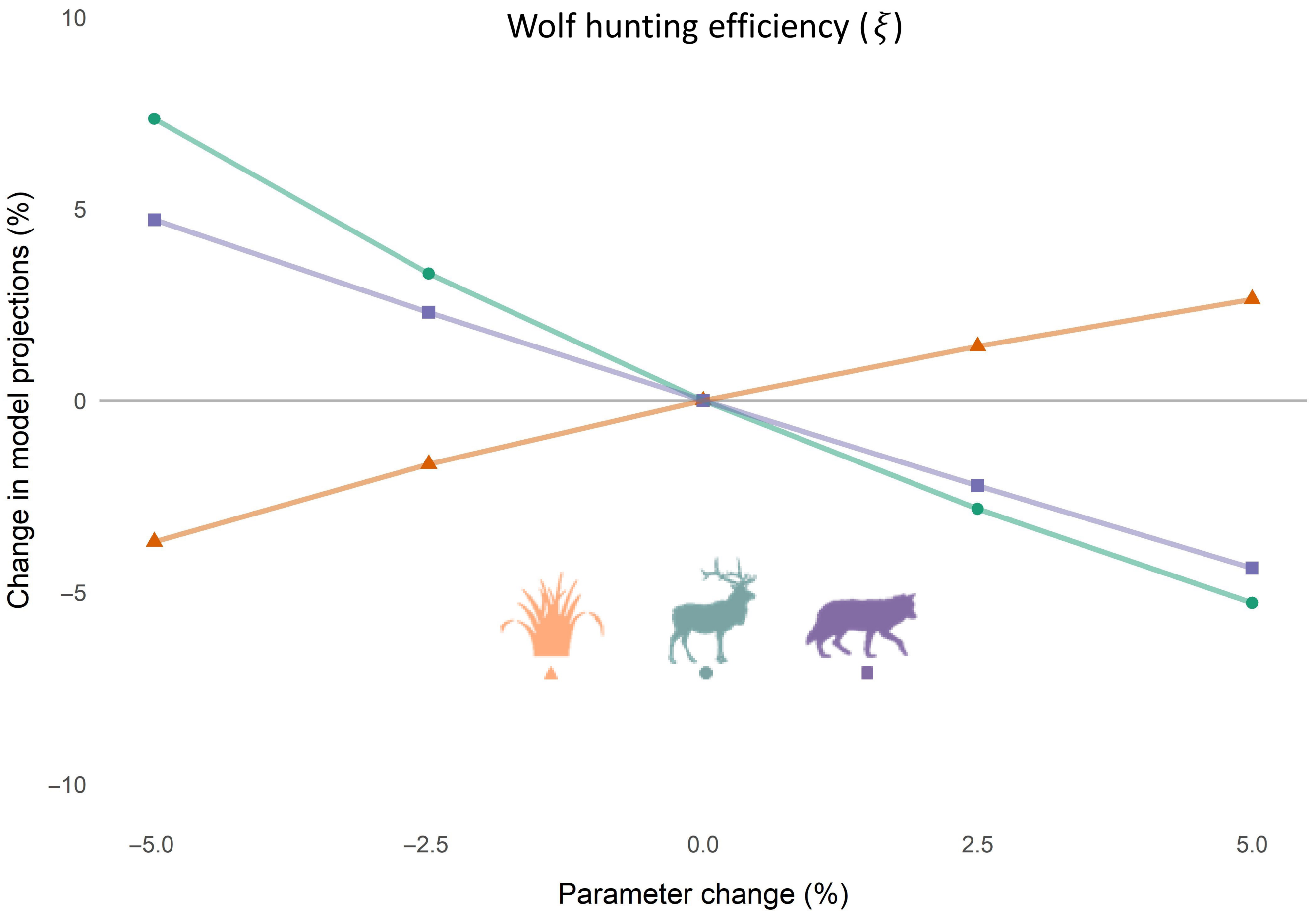

FIGURE 4 Effect that changing the wolf hunting efficiency (ξ—that is, coefficient regulating effect of predation on elk) from −5% to +5% has on model projections (in March). Change in model projections is quantified as relative changes compared to the model with unchanged parameters.

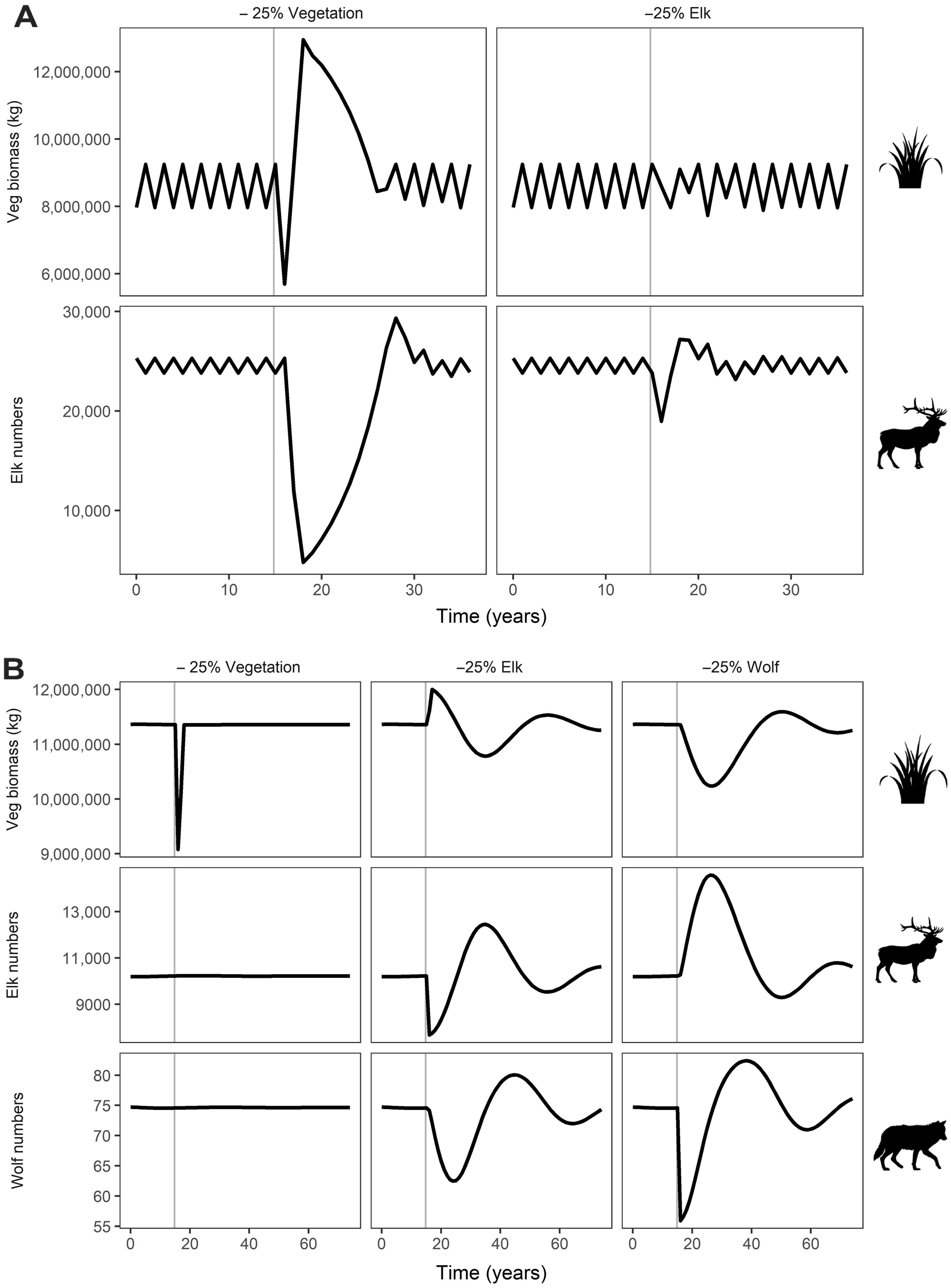

FIGURE 5 Population perturbations in system without wolves (A) and with wolves (B) in March. Columns show effects of perturbations applied to vegetation, elk, and wolf populations. Rows show effects of those perturbations on vegetation, elk, and wolf. Gray lines represent time when perturbations were applied.

Reduction of the elk population by 25% (from 10,228 to 7675) caused an increase in vegetation 11.4M kg to 12M kg (+6%) in 2 years and a reduction in wolf numbers from 75 to 62 (−17%) over a 9-year period. This fall in predator numbers created a feedback in the elk population, which increased from 7675 to 12,452 (+62%) individuals over 19 years before trending back toward equilibrium. The wolf and vegetation followed this rise in prey numbers. In particular, the wolf population peaked at 80 individuals over a 21-year period from their minimum of 62 (+29%) (Figure 5B).

Perturbation of the wolf had the biggest impact on the system. Reducing the wolf population by 25% (from 75 to 56 individuals) caused a sudden increase in elk numbers by 43% (from 10,228 to 14,579) over an 11-year period. This led to a reduction in vegetation biomass (−10% in 12 years) and a subsequent increase in wolf numbers by 46% (from 56 to 82) over 22 years. The elk then decreased from 14,579 to 9299 (−36% in 24 years), before the system started moving toward equilibrium again (Figure 5B).

DISCUSSION

We developed a bioenergetic mechanistic model to describe population dynamics in tritrophic systems, explicitly considering population sizes and body masses. We applied our model to wolves, elk, and grassy vegetation in Northern Yellowstone and showed that the reintroduction of the wolf was expected to cause a significant decline in elk numbers, which would translate into higher vegetation growth. Our model showed that wolves had a stabilizing effect on resource variability and a relatively large impact on the ecosystem, helping to shed light on the potential role that wolves play in ecosystem dynamics in Yellowstone. Wolf predation also led to a shift in the phenotypic composition of the elk population, via a small increase in elk average body mass. Our sensitivity analysis showed that our general results were robust over a wide range of parameter values, although the exact quantification of effects remained a challenge. Changing parameter values affected trophic levels in different ways, and the most important parameters were not the same for all levels. Moreover, the sensitivity analysis highlighted interesting feedbacks in the system, which sometimes led to counterintuitive model outcomes.

Introducing the wolf into our model led to a population of 99 individuals (including pups in the breeding month) at equilibrium and a 61% reduction in elk numbers (from 14,948 to 5823), consistent with observed trends in elk population size following wolf reintroduction into Yellowstone (MacNulty et al., 2016). In turn, vegetation biomass, on average, increased by approximately 23% in the growing season and more than threefold (328%) in the nongrowing season. In winter, when we excluded wolves from the model, vegetation biomass reached its minimum value ($V_{\min}$), suggesting that in the absence of wolves, the elk is largely food-limited and the entire system is controlled by primary production (bottom-up regulation). When wolves were added to the model, vegetation biomass at equilibrium increased across all seasons because of reduced herbivory, suggesting that the elk population became predator-limited while the wolf population became food-limited (top-down regulation). The addition of the wolf also had a stabilizing effect on elk numbers, whose population at equilibrium became constant across years, rather than exhibiting biannual cyclic fluctuations (Figure 1). This stabilizing effect of predation on prey fluctuations is consistent with what has been observed in other systems (Letnic & Crowther, 2013; Pople et al., 2000; Wilmers et al., 2006).

The population perturbations confirmed these processes and yielded further insights. In the absence of wolves, the elk was food-limited, and the system was regulated by bottom-up processes. However, when we added the wolf to the model, perturbation of vegetation biomass had no significant effects on the overall system, whereas changing wolf numbers had the biggest impact, exerting top-down regulation (Hairston et al., 1960; Ripple et al., 2001). Moreover, the fact that perturbing vegetation biomass did not have a significant effect when wolves were added to the model also confirmed that wolves could act as buffers against fluctuations in resource variability (Wilmers & Getz, 2005). Perturbing the elk population had a limited impact when wolves were absent but became much more important when wolves were added to the system. As shown here, elk can have significant impacts on ecosystems and is often considered a keystone species (Frank et al., 2016; Ripple et al., 2015; Starns et al., 2015).

Overall, our bioenergetic ecosystem model revealed subtle nuances in the mechanisms underlying tritrophic interactions between vegetation, elk, and wolves. Nevertheless, it did not produce precise predictions on broader ecosystem processes. Such processes may well arise with the contribution of other interacting factors that we did not consider in our analysis (Peterson et al., 2014). For example, increases in vegetation biomass following predator introductions that are predicted by our model may be less evident in the field (Brice et al., 2022) because the vegetation may become available to other herbivores. This effect was experimentally demonstrated in Kenya, where wild dog recolonization reduced dik-dik numbers by 33% but did not translate into reduced overall herbivory and vegetation recovery (Ford et al., 2015). Our model did not include herbivory by bison within Northern Yellowstone because wolves do not heavily prey upon them (Tallian et al., 2017). However, bison compete with elk for resources while being less vulnerable to wolf predation (Tallian et al., 2017). As such, the increase in vegetation predicted by our model could be one of the causes of the observed increase in bison numbers (from ~500 in 1995 to ~4000 in 2018 and 6000 in 2022; Beschta et al., 2020; National Park Service [unpublished data]). Additionally, our model did not include potential offsets to wolf predation rate on elk related to the bison biomass acquisition by wolves. Over the last decade, bison biomass acquired by wolves has increased significantly in Yellowstone, primarily through winter scavenging of bison dying from other causes, thereby offsetting predation on elk (Metz et al., 2020).

Research has demonstrated that the observed decline in the Yellowstone elk population is not directly, or solely, due to the reintroduction of wolves but rather a consequence of broader ecosystem changes, including more frequent droughts and fires, increases in human harvesting, and increased predation by other carnivores besides wolves (MacNulty et al., 2020; Metz, Hebblewhite, et al., 2020; Peterson et al., 2014; Vucetich et al., 2005). While models show that reductions in resource availability due to greater environmental variation can have substantial impacts on elk population size (Lachish et al., 2020), this impact should decrease when predators are added to the system and the elk becomes predator-limited, as shown by the population perturbations in this study (Letnic & Crowther, 2013; Wallach et al., 2015; Wilmers et al., 2006). Other carnivores, such as grizzly bears, black bears, and cougars, have also increased in numbers over the same period as the wolf reintroduction and recovery (Hamlin et al., 2009; Ruth et al., 2019). Despite the paucity of analyses critically evaluating these other carnivores' impacts on elk, it has been argued that their effect on elk can match or even exceed that of wolves (Metz, Smith, et al., 2020; Peterson et al., 2014; Stahler et al., 2020).

Including the wolf in the model also altered the elk body mass distribution. While wolf predation caused only a 2% reduction in elk average body mass (from 214 to 210 kg), the distribution of body masses (Figure 2) shows that wolves selectively removed individuals with a low structural mass (i.e., younger individuals) consistently across all months of the year and those with a lower reserve mass in the breeding month and during the growing season (i.e., females with lower reproductive values). This finding supports the healthy herd hypothesis, whereby predators remove weaker (sick, starving, or injured) individuals from a population, giving a selective advantage to bigger individuals with better body condition (Hudson et al., 1992; Packer et al., 2003). The body mass distributions predicted by our model were broadly similar to those observed in Yellowstone (189–275 kg; Cook et al., 2004). In wolves, the average body mass predicted by our model in March was 44 kg (Figure 3), which also fell within the observed range for female adults in Yellowstone (ca. 30–52 kg; MacNulty et al., 2009).

The sensitivity analysis showed that our results were relatively stable across a wide range of parameter values, although varying the most influential parameters caused substantial declines in model projections of up to 72%. Some interesting patterns in wolf–elk dynamics also arose. For example, increasing the wolf hunting efficiency (ξ) led to a reduction in wolf numbers, a seemingly counterintuitive finding. However, increased predation causes a decline in prey numbers, ultimately resulting in lower available resources for predators. Other parameters showed some nonlinear responses in the sensitivity analysis. An example of this is the wolf satiation threshold (f_w). Reducing this threshold from 0 to −2.5 led to a reduction in wolf numbers because wolves did not eat enough. However, increasing the same parameter from 0% to +2.5% also caused a very small decline in the wolf population, perhaps because wolves could then overeat elk, causing their own resources to decrease, as explained earlier. The observed patterns in these two examples demonstrate the complexity of trophic interactions and wider ecosystem processes. Nonetheless, they could also partly derive from the way in which we constructed our model. Model parameterization was one of the biggest challenges in our work. Some parameters were relatively easy to find and were measured in the field in our study area (e.g., those about elk and wolf survival, the proportion of elk edible biomass, proportion of elk scavenged). Others came from other systems, and in one particular case, it was not specific to our study species but to mammals in general (e.g., the coefficient for anabolic/catabolic conversion between assimilated energy and energy reserves; Blaxter, 1989). Finally, some parameters, such as the intercept and slope of the variance equation in the growth function, were simply assumed. Our sensitivity analysis showed that our results were insensitive to variations in these parameters (Appendix S1: Table S2). Nonetheless, given all of these findings, interpretation of the extent of the effects of individual parameters should be undertaken with caution.

Our model is based on three major assumptions. First, because our model is not spatially explicit and the migration patterns of Northern Yellowstone elk are complex with significant heterogeneity in migration distance and direction (White et al., 2010), we treated our study area as a closed system, with no animal movement from and to adjacent areas (Lachish et al., 2020). Second, we did not consider wolf sociality and pack dynamics (Brandell et al., 2021). Given the complexity of our model, we made the simplifying assumption that all adult female wolves that reached a threshold of structural mass ($K_w = 24$ kg) could reproduce, giving birth to one offspring annually. We checked the appropriateness of this assumption by ensuring that the reproductive rates in the model (45 wolf pups with a population size of 56 wolves at equilibrium) were similar to those expected in a real population (42 pups for 52 wolves in Yellowstone National Park in 2019; Smith, Stahler, et al., 2020). Nonetheless, we acknowledge that this is an important aspect of wolf biology (Mech & Boitani, 2003), and inclusion of these components in the model is the focus of ongoing work. Finally, we considered energetics alone and did not consider the role of individual heterogeneity or macronutrients that could potentially constrain food webs (e.g., carbon, nitrogen, phosphorus, proteins). We believe these additions will be important for future work but go beyond the objectives of this study.

Our model represents a novel approach to the study of predator–prey interactions and trophic cascades. While we focused on describing the model and applying it to a well-studied system, our framework holds great potential when it comes to exploring unanswered eco-evolutionary questions. Explicitly considering and linking bioenergetics, population sizes, and body masses can provide novel insights into the mechanisms behind complex ecosystem processes. By tweaking the number and variety of equations and parameters available, our modeling framework can be analyzed, adapted, and expanded to explore the role of environmental and eco-evolutionary processes, including diseases, animal behavior, interactions with other species, climate change, and landscape and wildlife management practices.

ACKNOWLEDGMENTS

This work was funded by the UK Natural Environment Research Council through the Environmental Research Doctoral Training Partnership at the University of Oxford (Grant NE/L002612/1). The Yellowstone Wolf Project (YWP) was supported by funding from the U.S. National Science Foundation DEB-0613730 and DEB-1245373, Yellowstone Forever, the Beagle Foundation, and key donors, especially Annie and Bob Graham and Valerie Gates. Francesca Cagnacci contributed to this work partly under the Institut de recherche pour le developpement (IRD) Fellowship at Fondation IMéRA, Institute for Advanced Studies at Aix-Marseille University in Marseille, France.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Passoni et al., 2023) is available in Figshare at https://doi.org/10.6084/m9.figshare.24238966.

ORCID

Gioele Passoni https://orcid.org/0000-0002-9652-0128
Tim Coulson https://orcid.org/0000-0001-9371-9003
Francesca Cagnacci https://orcid.org/0000-0002-4954-9980
Peter Hudson https://orcid.org/0000-0003-0468-3403
Daniel R. Stahler https://orcid.org/0000-0002-8740-6075
Douglas W. Smith https://orcid.org/0000-0002-8080-0571
Shelly Lachish https://orcid.org/0000-0003-1886-6454

REFERENCES

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. “Elk Calf Survival and Mortality Following Wolf Restoration to Yellowstone National Park.” *Wildlife Monographs* 169: 1–30.

Becker, M. S., R. A. Garrott, P. J. White, R. Jaffe, J. J. Borkowski, C. N. Gower, and E. J. Bergman. 2008. “Chapter 17 Wolf Kill Rates.” In *The Ecology of Large Mammals in Central Yellowstone—Sixteen Years of Integrated Field Studies* 339–369. Burlington, MA, and San Diego, CA: Academic Press.

Beschta, R. L., W. J. Ripple, J. Boone Kauffman, and L. E. Painter. 2020. “Bison Limit Ecosystem Recovery in Northern Yellowstone.” *Food Webs* 23: e00142. https://doi.org/10.1016/j.fooweb.2020.e00142.

Blaxter, K. 1989. *Energy Metabolism in Animals and Man*. Burlington, MA, and San Diego, CA: Academic Press.

Brandell, E. E., P. C. Cross, D. W. Smith, W. Rogers, N. L. Galloway, D. R. MacNulty, D. R. Stahler, J. Treanor, and P. J. Hudson. 2022. “Examination of the Interaction between Age-Specific Predation and Chronic Disease in the Greater Yellowstone Ecosystem.” *Journal of Animal Ecology* 91(7): 1373–84.

Brandell, E. E., A. P. Dobson, P. J. Hudson, P. C. Cross, and D. W. Smith. 2021. “A Metapopulation Model of Social Group Dynamics and Disease Applied to Yellowstone Wolves.” *Proceedings of the National Academy of Sciences of the United States of America* 118(10): e2020023118. https://doi.org/10.1073/pnas.2020023118.

Brice, E. M., E. J. Larsen, and D. R. MacNulty. 2022. “Sampling Bias Exaggerates a Textbook Example of a Trophic Cascade.” *Ecology Letters* 25(1): 177–188.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, et al. 2014. “Recovery of Large Carnivores in Europe’s Modern Human-Dominated Landscapes.” *Science* 346: 1517–19. https://doi.org/10.1126/science.1257553.

Christianson, D. A., and S. Creel. 2007. “A Review of Environmental Factors Affecting Elk Winter Diets.” *Journal of Wildlife Management* 71(1): 164–176. https://doi.org/10.2193/2005-575.

Cook, R. C., J. G. Cook, and L. David Mech. 2004. “Nutritional Condition of Nothern Yellowstone Elk.” *Journal of Mammalogy* 85(4): 714–722.

Coulson, T. 2012. “Integral Projections Models, Their Construction and Use in Posing Hypotheses in Ecology.” *Oikos* 121(9): 1337–50. https://doi.org/10.1111/j.1600-0706.2012.00035.x.

Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. “Density-Dependent Intraspecific Aggression Regulates Survival in Northern Yellowstone Wolves (*Canis lupus*).” *The Journal of Animal Ecology* 83(6): 1344–56. https://doi.org/10.1111/1365-2656.12238.

De Roos, A. M., N. Galic, and H. Heesterbeek. 2009. “How Resource Competition Shapes Individual Life History for Nonplastic Growth: Ungulates in Seasonal Food Environments.” *Ecology* 90(4): 945–960.

DeLong, J. P., B. Gilbert, J. B. Shurin, V. M. Savage, B. T. Barton, C. F. Clements, A. I. Dell, et al. 2015. “The Body Size Dependence of Trophic Cascades.” *The American Naturalist* 185(3): 354–366. https://doi.org/10.1086/679735.

Evans, S. B., L. D. Mech, and G. A. Sargeant. 2006. “Survival of Adult Female Elk in Yellowstone Following Wolf Restoration.” *Journal of Wildlife Management* 70: 1372–78.

Ford, A. T. 2015. “The Mechanistic Pathways of Trophic Interactions in Human-Occupied Landscapes.” *Science* 350(6265): 1175–76.

Ford, A. T., and J. R. Goheen. 2015. “Trophic Cascades by Large Carnivores: A Case for Strong Inference and Mechanism.” *Trends in Ecology & Evolution* 30(12): 725–735. https://doi.org/10.1016/j.tree.2015.09.012.

Ford, A. T., J. R. Goheen, D. J. Augustine, M. F. Kinnaird, T. G. O’Brien, T. M. Palmer, R. M. Pringle, and R. Woodroffe. 2015. “Recovery of African Wild Dogs Suppresses Prey but Does Not Trigger a Trophic Cascade.” *Ecology* 96(10): 2705–14.

Frank, D. A., R. L. Wallen, and P. J. White. 2016. “Ungulate Control of Grassland Production: Grazing Intensityand Ungulate Species Composition in Yellowstone Park.” *Ecosphere* 7: e01603.

Garroutte, E., A. Hansen, and R. Lawrence. 2016. “Using NDVI and EVI to Map Spatiotemporal Variation in the Biomass and Quality of Forage for Migratory Elk in the Greater Yellowstone Ecosystem.” *Remote Sensing* 8(5): 404. https://doi.org/10.3390/rs8050404.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. “Landscapes of Fear: Spatial Patterns of Risk Perception and Response.” *Trends in Ecology & Evolution* 34(4): 355–368.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. “Community Structure, Population Control, and Competition.” *American Naturalist* 94: 421–25.

Hamlin, K. L., J. A. Cunningham, and K. Alt. 2009. *Monitoring and Assessment of Wolf-Ungulate Interactions and Population Trends within the Greater Yellowstone Area, Southwestern Montana Statewide, and Montana Statewide*. In Rocky Mountain Wolf Recovery Annual Reports. Cambridge, UK: Cambridge University Press.

Hebblewhite, M. 2013. “Consequences of Ratio-Dependent Predation by Wolves for Elk Population Dynamics.” *Population Ecology* 55(4): 511–522. https://doi.org/10.1007/s10144-013-0384-3.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1992. “Do Parasites Make Prey Vulnerable to Predation? Red Grouse and Parasites.” *Journal of Animal Ecology* 61(3): 681–692.

Illius, A. W., and T. G. O’Connor. 2000. “Resource Heterogeneity and Ungulate Population Dynamics.” *Oikos* 89(2): 283–294.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. Sinclair, J. M. S. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. “Impact of Food and Predation on the Snowshoe Hare Cycle.” *Science* 269: 1112–15.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001. *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. New York: Oxford University Press.

Lachish, S., E. E. Brandell, M. E. Craft, A. P. Dobson, P. J. Hudson, D. R. MacNulty, and T. Coulson. 2020. “Investigating the Dynamics of Elk Population Size and Body Mass in a Seasonal Environment Using a Mechanistic Integral Projection Model.” *American Naturalist* 196(2): E23–E45. https://doi.org/10.1086/708723.

Letnic, M., and M. S. Crowther. 2013. “Patterns in the Abundance of Kangaroo Populations in Arid Australia Are Consistent with the Exploitation Ecosystems Hypothesis.” *Oikos* 122(5): 761–69. https://doi.org/10.1111/j.1600-0706.2012.20425.x.

Loveless, K., D. Smith, and J. Hemenway. 2019. “2019 Late Winter Survey of Northern Yellowstone Elk.” https://www.nps.gov/yell/learn/news/2019-late-winter-survey-of-northern-yellowstone-elk.htm.

MacNulty, D. R., D. W. Smith, L. D. Mech, and L. E. Eberly. 2009. “Body Size and Predatory Performance in Wolves: Is Bigger Better?” *The Journal of Animal Ecology* 78(3): 532–39. https://doi.org/10.1111/j.1365-2656.2008.01517.x.

MacNulty, D. R., D. R. Stahler, C. T. Wyman, J. Ruprecht, and D. W. Smith. 2016. “The Challenge of Understanding Northern Yellowstone Elk Dynamics after Wolf Reintroduction.” *Yellowstone Science* 24(1): 25–33.

MacNulty, D. R., D. R. Stahler, T. Wyman, J. Ruprecht, L. M. Smith, M. T. Kohl, and D. W. Smith. 2020. “Population Dynamics of Northern Yellowstone Elk after Wolf Reintroduction.” In *Yellowstone Wolves: Science and Discovery in the World’s First National Park*, edited by D. W. Smith, D. R. Stahler, and D. R. MacNulty, 184–199. Chicago, IL: University of Chicago Press.

Mech, L. D., and L. Boitani. 2003. *Wolves: Behavior, Ecology, and Conservation*. Chicago, IL and London, UK: University of Chicago Press.

Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. Macnulty. 2001. “Winter Severity and Wolf Predation on a Formerly Wolf-Free Elk Herd.” *Journal of Wildlife Management* 65: 998.

Metz, M. C., M. Hebblewhite, D. W. Smith, D. R. Stahler, D. R. MacNulty, and A. Tallian. 2020. “What Wolves Eat and Why.” In *Yellowstone Wolves: Science and Discovery in the World’s First National Park*, edited by D. W. Smith, D. R. Stahler, and D. R. MacNulty, 157–168. Chicago, IL: University of Chicago Press.

Metz, M. C., D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. Hebblewhite. 2020. “Wolf Predation on Elk in a Multi-Prey Environment.” In *Yellowstone Wolves: Science and Discovery in the World’s First National Park*, edited by D. W. Smith, D. R. Stahler, and D. R. MacNulty, 169–183. Chicago: University of Chicago Press.

Metz, M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. 2012. “Seasonal Patterns of Predation for Gray Wolves in the Multi-Prey System of Yellowstone National Park.” *The Journal of Animal Ecology* 81(3): 553–563. https://doi.org/10.1111/j.1365-2656.2011.01945.x.

Nilsen, E. B., E. J. Milner-Gulland, L. Schofield, A. Mysterud, N. C. Stenseth, and T. Coulson. 2007. “Wolf Reintroduction to

Scotland: Public Attitudes and Consequences for Red Deer Management." *Proceedings of the Biological Sciences* 274(1612): 995–1002. https://doi.org/10.1098/rspb.2006.0369.

Oli, M. K. 2019. "Population Cycles in Voles and Lemmings: State of the Science and Future Directions." *Mammal Review* 49: 226–239.

Owen-Smith, N. 2002. "A Metaphysiological Modelling Approach to Stability in Herbivore–Vegetation Systems." *Ecological Modelling* 149(1-2): 153–178. https://doi.org/10.1016/S0304-3800(01)00521-X.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. "Coupled Dynamics of Body Mass and Population Growth in Response to Environmental Change." *Nature* 466(7305): 482–85. https://doi.org/10.1038/nature09210.

Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. "Keeping the Herds Healthy and Alert: Implications of Predator Control for Infectious Disease." *Ecology Letters* 6(9): 797–802. https://doi.org/10.1046/j.1461-0248.2003.00500.x.

Passoni, G., T. Coulson, and S. Lachish. 2023. "Code for Investigating Tri-Trophic Interactions Using Bio-Energetic Demographic Models." Figshare, Software. https://doi.org/10.6084/m9.figshare.24238966.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, et al. 2008. "Revisiting the Classics: Considering Nonconsumptive Effects in Textbook Examples of Predator–Prey Interactions." *Ecology* 89(9): 2416–25.

Peterson, R. O., R. L. Beschta, D. J. Cooper, N. T. Hobbs, D. B. Johnston, and E. J. Larsen. 2020. "Indirect Effects of Carnivore Restoration on Vegetation." In *Yellowstone Wolves: Science and Discovery in the World's First National Park,* edited by D. W. Smith, D. R. Stahler, and D. R. MacNulty, 204–222. Chicago, IL: University of Chicago Press.

Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. "Trophic Cascades in a Multicausal World: Isle Royale and Yellowstone." *Annual Review of Ecology, Evolution, and Systematics* 45(1): 325–345. https://doi.org/10.1146/annurev-ecolsys-120213-091634.

Pople, A. R., G. C. Grigg, S. C. Cairns, L. A. Beard, and P. Alexander. 2000. "Trends in the Numbers of Red Kangaroos and Emus on Either Side of the South Australian Dingo Fence: Evidence for Predator Regulation?" *Wildlife Research* 27(3): 269–276. https://doi.org/10.1071/WR99030.

Prevedello, J. A., C. R. Dickman, M. V. Vieira, and E. M. Vieira. 2013. "Population Responses of Small Mammals to Food Supply and Predators: A Global Meta-Analysis." *The Journal of Animal Ecology* 82: 927–936.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, et al. 2014. "Status and Ecological Effects of the World's Largest Carnivores." *Science* 343(6167): 1241484. https://doi.org/10.1126/science.1241484.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. "Trophic Cascades among Wolves, Elk and Aspen on Yellowstone National Park's Northern Range." *Biological Conservation* 102: 227–234.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everat, M. Galetti, M. W. Hayward, et al. 2015. "Collapse of the World's Largest Herbivores." *Science Advances* 1: e1400103.

Ripple, W. J., and R. L. Beschta. 2012. "Trophic Cascades in Yellowstone: The First 15 Years after Wolf Reintroduction." *Biological Conservation* 145(1): 205–213. https://doi.org/10.1016/j.biocon.2011.11.005.

Ruth, T. K., P. C. Buotte, and M. G. Hornocker. 2019. *Yellowstone Cougars: Ecology before and during Wolf Restoration*. Louisville, CO: University Press of Colorado.

Sinclair, A. R., and C. J. Krebs. 2002. "Complex Numerical Responses to Top-Down and Bottom-Up Processes in Vertebrate Populations." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 357(1425): 1221–31. https://doi.org/10.1098/rstb.2002.1123.

Smallegange, I. M., H. Caswell, M. E. M. Toorians, A. M. De Roos, and J. Metcalf. 2017. "Mechanistic Description of Population Dynamics Using Dynamic Energy Budget Theory Incorporated into Integral Projection Models." *Methods in Ecology and Evolution* 8(2): 146–154.

Smith, D. W., D. R. Stahler, K. A. Cassidy, E. Stahler, M. Metz, C. Meyer, J. Rabe, et al. 2020. *Yellowstone National Park Wolf Project Annual Report 2019*. Yellowstone National Park: National Park Service. Yellowstone Center for Resources.

Smith, D. W., D. R. Stahler, and D. R. MacNulty. 2020. *Yellowstone Wolves: Science and Discovery in the World's First National Park*. Chicago, IL: University of Chicago Press.

Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. von Holdt, and D. W. Smith. 2013. "The Adaptive Value of Morphological, Behavioural and Life-History Traits in Reproductive Female Wolves." *The Journal of Animal Ecology* 82(1): 222–234. https://doi.org/10.1111/j.1365-2656.2012.02039.x.

Stahler, D. R., D. W. Smith, and D. S. Guernsey. 2006. "Foraging and Feeding Ecology of the Gray Wolf (*Canis lupus*): Lessons from Yellowstone National Park, Wyoming, USA." *The Journal of Nutrition* 136: 1923S–1926S.

Stahler, D. R., C. C. Wilmers, A. Tallian, C. B. Anton, M. C. Metz, T. K. Ruth, D. W. Smith, K. A. Gunther, and D. R. MacNulty. 2020. "Competition and Coexistence among Yellowstone's Meat Eaters." In *Yellowstone Wolves: Science and Discovery in the World's First National Park*, edited by D. W. Smith, D. R. Stahler, and D. R. MacNulty. Chicago, IL: University of Chicago Press.

Starns, H. D., F. W. Weckerly, M. A. Ricca, and A. Duarte. 2015. "Vegetation Changes Associated with a Population Irruption by Roosevelt Elk." *Ecology and Evolution* 5: 109–120.

Tallian, A., D. W. Smith, D. R. Stahler, M. C. Metz, R. L. Wallen, C. Geremia, C. Joel Ruprecht, T. Wyman, D. R. MacNulty, and D. Costa. 2017. "Predator Foraging Response to a Resurgent Dangerous Prey." *Functional Ecology* 31(7): 1418–29. https://doi.org/10.1111/1365-2435.12866.

van der Meer, J. 2006. "Metabolic Theories in Ecology." *Trends in Ecology & Evolution* 21(3): 136–140. https://doi.org/10.1016/j.tree.2005.11.004.

Savage Van, M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. "Effects of Body Size and Temperature on Population Growth." *American Naturalist* 163(3): 429–441.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. "Influence of Harvest, Climate and Wolf Predation on Yellowstone Elk, 1995–2004." *Oikos* 111: 259–270.

Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. "Novel Trophic Cascades: Apex Predators Enable Coexistence." *Trends in Ecology & Evolution* 30(3): 146–153. https://doi.org/10.1016/j.tree.2015.01.003.

White, P. J., K. M. Proffitt, L. David Mech, S. B. Evans, J. A. Cunningham, and K. L. Hamlin. 2010. "Migration of Northern Yellowstone Elk: Implications of Spatial Structuring." *Journal of Mammalogy* 91(4): 827–837. https://doi.org/10.1644/08-mamm-a-252.1.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. San Diego, CA: Academic Press.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. "Trophic Facilitation by Introduced Top Predators: Grey Wolf Subsidies to Scavengers in Yellowstone National Park." *Journal of Animal Ecology* 72: 909–916.

Wilmers, C. C., and W. M. Getz. 2005. "Gray Wolves as Climate Change Buffers in Yellowstone." *PLoS Biology* 3: e92.

Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. "Predator Disease Out-Break Modulates Top-Down, Bottom-Up and Climatic Effects on Herbivore Population Dynamics." *Ecology Letters* 9(4): 383–89. https://doi.org/10.1111/j.1461-0248.2006.00890.x.

Wright, G. J., R. O. Peterson, D. W. Smith, and T. O. Lemke. 2004. "Selection of Northern Yellowstone Elk by Gray Wolves and Hunters." *Journal of Wildlife Management* 40(4): 1070–78.

Zimmermann, B., H. Sand, P. Wabakken, O. Liberg, and H. P. Andreassen. 2015. "Predator-Dependent Functional Response in Wolves: From Food Limitation to Surplus Killing." *The Journal of Animal Ecology* 84(1): 102–112. https://doi.org/10.1111/1365-2656.12280.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Passoni, Gioele, Tim Coulson, Francesca Cagnacci, Peter Hudson, Daniel R. Stahler, Douglas W. Smith, and Shelly Lachish. 2023. "Investigating Tritrophic Interactions Using Bioenergetic Demographic Models." *Ecology* e4197. https://doi.org/10.1002/ecy.4197