



Theoretical impacts of habitat loss and generalist predation on predator–prey cycles



Kelsey Vitense^{a,*}, Aaron J. Wirsing^b, Rebecca C. Tyson^c, James J. Anderson^d

^a Quantitative Ecology and Resource Management, University of Washington, Box 352182, Seattle, WA 98195, USA

^b School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA

^c Mathematics & Statistics, University of British Columbia Okanagan, IKBSAS BLDG SCI, 1177 Research Road, Kelowna, BC V1V 1V7, Canada

^d School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98105, USA

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ABSTRACT

Certain herbivores and their predators undergo high amplitude periodic fluctuations in abundance in northern latitudes but exhibit damped cyclic dynamics in their respective southern ranges. Generalist predators and habitat disturbance have been identified as two features of southern habitats that may contribute to the attenuation of cycles in southern latitudes. Using the snowshoe hare and Canada lynx as model species, we employed a reaction–diffusion–advection framework with reaction terms taken from the May and Rosenzweig–MacArthur models to study the relative and joint damping impacts of generalist predation and habitat loss on predator–prey cycles. We found that generalist predation has consistently strong stabilizing effects and may represent a threat to the persistence of specialized predators. Habitat loss also ultimately results in the loss of cycles, but cycle amplitude and animal densities may not always decrease monotonically with habitat loss. The joint damping impacts of generalists and habitat loss can be severe, consistent with observations of low cycle amplitude, high predation rates, and significant habitat loss in the southern ranges of cyclic species. Elevated generalist predation rates at patch edges and in the surrounding matrix hasten cycle attenuation in situations that lead to increased prey exposure to generalists, including small patch sizes, higher movement rates into the matrix, and increased prey density at patch edges. The dominant driver of cycle attenuation, as well as cycle response to habitat disturbance, may vary between regions and systems. Field data that help clarify the relationships between habitat loss and fragmentation, generalist density and behavior, and cyclic activity would be invaluable in informing future modeling and conservation efforts.

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1. Introduction

The multiannual population cycles of certain mammals and their predators in northern latitudes have been studied extensively over the last century (Howell, 1923; Elton and Nicholson, 1942; Keith, 1990; Akçakaya, 1992; King and Schaffer, 2001; Korpimäki et al., 2004; Krebs, 2011). The importance of cyclic herbivores, such as snowshoe hares (*Lepus americanus*) and brown lemmings (*Lemmus trimucronatus*), to boreal and tundra ecosystems lies at the heart of this interest in oscillatory population dynamics (Krebs, 2011). These species are major food resources for many predators in addition to being consumers of large amounts of plant material. Much

research has been devoted to the cause of population cycles, and predation is now widely accepted as the key driver of cyclic fluctuations (Akçakaya, 1992; Turchin, 2003; Korpimäki et al., 2004; Krebs, 2011). However, less attention has been given to the cause of the observed reductions in amplitude and densities of cyclic species in their respective southern ranges (Akçakaya, 1992), and it is this phenomenon to which this study is devoted. The snowshoe hare and its specialist predator, the Canada lynx (*Lynx canadensis*), will serve as a case study due to the pair's use as a classic example of oscillatory predator–prey dynamics and because population parameter estimates are readily available. However, this study provides insight into the processes behind the damped cycles in the southern ranges of other cyclic predator–prey systems in the Northern Hemisphere.

Hare populations in northern boreal forests are famous for their dramatic cyclic fluctuations in abundance, characterized by a period of eight to 11 years and amplitudes that are often 10- to 25-fold (Hodges, 2000). In contrast to populations in the north,

* Corresponding author. Present address: Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, St. Paul, MN 55108, USA. Tel.: +1 3192135357.

E-mail address: viten003@umn.edu (K. Vitense).

the oscillatory dynamics of hare and lynx populations at southern latitudes are much attenuated (Keith, 1990), with hare cycle amplitudes usually on the lower end of the 2- to 25-fold observed range (Hodges, 2000). Two factors that may contribute to the damped dynamics of snowshoe hares and other species in their respective southern latitudes are landscape fragmentation and generalist predation. Suitable prey habitat in southern latitudes is naturally patchier or more fragmented due to human influences (Wolff, 1980; Keith et al., 1993; Agee, 2000), and this reduction in reproductive habitat may not allow for the rates of population increase necessary to produce high amplitude cycles. The density and diversity of numerically stable generalist predators is also higher in the south, and prey are therefore consistently removed by predators that do not cycle along with them (Hanski et al., 1991; Erlinge et al., 1992; Klemola et al., 2002). Moreover, with increased landscape disturbance, generalist predators are able to use areas occupied by specialists that were previously inaccessible, so fragmentation and increased abundance of generalists are expected to occur simultaneously (Buskirk, 2000).

Generalist predators benefit from fragmented landscapes through increased visibility and mobility in disturbed areas, access to a broad range of food sources, and exploitation of edge habitats (Andrews, 1990; Harrison and Bruna, 1999; Buskirk, 2000; Gehring and Swihart, 2003). Indeed, Andrén et al. (1985) observed that the density of generalist corvids was higher south of the boreal zone in Sweden where cycles of tetraonid birds disappear, and was positively correlated with dummy nest predation rate and degree of forest fragmentation. Further, Andrén and Angelstam (1988) found that dummy nest predation rates in Sweden were highest in farmland habitat, with an increase in predation extending 200–500 m into neighboring forest habitat. Additionally, Wilcove (1985) observed elevated nest predation rates on very small forest fragments and on patches closer to suburban areas. Accordingly, some snowshoe hare studies have found increased predation in open areas with reduced cover (Dolbeer, 1975; Sievert and Keith, 1985; Griffin and Mills, 2009), while others have found predation to be very high on small patches of habitat in highly fragmented landscapes (Keith et al., 1993; Wirsing et al., 2002). These observations of spatial heterogeneity in predation rates suggest that there is strong potential for generalist predators to interact with forest fragmentation to influence cycles, but these effects and the impacts on threatened species such as the lynx are currently unknown (McKelvey et al., 2000).

Prior analyses have made use of the wealth of data provided by the Hudson's Bay Company's well-known records of hare and lynx fur returns (Elton and Nicholson, 1942; MacLulich, 1957) and intensive field studies in Rochester, Alberta (Keith, 1990) and Kluane Lake, Yukon (Krebs et al., 2001a) to propose and parameterize mechanistic models for northern hare–lynx cycles (Akçakaya, 1992; Ives and Murray, 1997; King and Schaffer, 2001; Tyson et al., 2010). In contrast, no southern field studies have exceeded four years in duration, and studies have occurred over such a wide variety of habitats and climates that generalizations are difficult to make (Murray, 2000). Though data are lacking in the south, theoreticians explore conditions that disrupt cycles by taking models similar to those fit to northern data and perturbing the cycles according to environmental and predation parameters suspected to be different in the south. For instance, Hanski et al. (1991) used differential equations to show that generalist predation has a strong damping impact on predator–prey cycles characteristic of small rodents and mustelids in Fennoscandia. Taylor et al. (2013) used the same model to show that a shortened breeding season in southern latitudes results in shorter cycle period. Strohm and Tyson (2009) demonstrated that habitat loss decreases the amplitude of hare–lynx cycles for four different mechanistic models. While some theoretical work has been done to investigate how habitat

fragmentation and generalist predation work in concert to affect predator–prey dynamics (Schneider, 2001; Swihart et al., 2001), these studies have not addressed population cycles.

Here, we investigate the effects of generalist predation and habitat loss on predator–prey cycles using two models with different functional forms. We first explore the relative effects of generalist predation and habitat loss to establish how each works to damp cycles and to compare model responses. We then examine the joint effects by considering both spatially uniform and spatially dependent, “matrix-based” generalist predation. As noted above, generalist predators often exploit open areas and edge habitats for hunting and travel (i.e., generalists are often “matrix-based”), and our comparison in spatial predation patterns provides insight into whether and when these spatial differences in predation are important to consider for future field work, modeling, and management efforts.

2. Methods

2.1. Models

Following Strohm and Tyson (2009), we used reaction–diffusion–advection models of the following form to describe population dynamics and dispersal:

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + \frac{\partial[V(x)n]}{\partial x} + f(n, x), \quad (1)$$

where $n = n(x, t)$ is population density at location x at time t , D is a spatially uniform diffusion coefficient, $V(x)$ is spatially varying velocity, and $f(n, x)$ is the reaction term describing changes in population density due to births and deaths. For simplicity, movement occurs in one spatial dimension, and similarly, population density varies in just one dimension. The reaction terms model the dynamics of a specialist predator and its prey, and these terms were taken from two different models, the May (2001) and Rosenzweig–MacArthur models (Rosenzweig and MacArthur, 1963).

The full equations for the May model with dispersal are

$$\frac{\partial H}{\partial t} = D_H \frac{\partial^2 H}{\partial x^2} + \frac{\partial[V(x)H]}{\partial x} + r(x)H \left(1 - \frac{H}{k}\right) - \frac{\alpha HL}{\beta + H} - \frac{\gamma(x)H^2}{H^2 + \eta^2}, \quad (2)$$

$$\frac{\partial L}{\partial t} = D_L \frac{\partial^2 L}{\partial x^2} + \frac{\partial[V(x)L]}{\partial x} + sL \left(1 - \frac{qL}{H}\right), \quad (3)$$

where H is prey density and L is predator density. This model includes logistic growth for both prey and predator, where the predator's carrying capacity is proportional to prey density (H/q in Eq. (3)). As prey density decreases, predator territory size increases (Turchin, 2003), consistent with observations of lynx behavior (Ward and Krebs, 1985). This form of the carrying capacity implies that predators may persist at very low prey densities, which is a common criticism of the May model (Turchin, 2003). Nonetheless, this model has been widely used in the literature on cycles (Turchin and Hanski, 1997; Strohm and Tyson, 2012; Taylor et al., 2013) and has been fit to field data from the Yukon (Tyson et al., 2010). The final piece of the May model is Holling's Type II hyperbolic functional response for the predator in Eq. (3), which is the form established for specialist predators (Holling, 1959; Turchin, 2003).

Following Turchin and Hanski (1997), a Holling Type III functional response was used to incorporate generalist predation in the prey equation (last term in Eq. (2)) (Holling, 1959). The density of generalist predators was assumed to be independent of prey density, with ample alternative prey available when the focal prey

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