Habitat preference can contribute to the stability of a multi-predator-prey system

Brian J. Smith
November 21, 2019
Ph.D. Student
Department of Wildland Resources, Ecology Center
Utah State University
bjsmith@aggiemail.usu.edu
BIOL 6270 – Theoretical Ecology

Abstract

Predator-prey interactions are among the most iconic and studied interspecific relationships in ecology. Most prey species in nature have multiple predators, but experimental and theoretical work in the past has mostly focused a single predator and a single prey. Recent empirical work, such as that on the elk-wolf-cougar system in Yellowstone National Park, highlights the importance of considering the effects of multiple predators on a prey species. Multiple mechanisms can potentially stabilize these systems, including space-use behavior by the prey. In this paper, I developed a theoretical model to test the extent to which habitat preferences by a mobile prey species can stabilize a multi-predator-prey system. After model development, I tested 10 scenarios with different amounts of habitat preference in the face of two predators with different attack rates. While habitat preference on its own was not enough to stabilize the system, habitat preference was able to stabilize situations where there were large differences in predator attack rates. The scenarios also displayed three examples of the paradox of enrichment, in which the "worse" habitat was stable, but the "better" habitat was not. Future empirical work should carefully consider the confounding effects of multiple predators when looking at habitat selection.

Introduction

Predator-prey interactions are among the most iconic and studied interspecific relationships in ecology, capable of shaping entire food webs. Although most prey species in natural systems are affected by multiple predators, experimental and theoretical work in the past has mostly focused a single predator and a single prey (Sih et al. 1998). The dynamics of these two-species systems can be captured by a simple Lotka-Volterra model, but a second predator makes modeling the system more challenging. For example, a simple three-species Lotka-Volterra model always results in extinction for one of the species (Korobeinikov and Wake 1999), contradicting observations from natural systems. There are multiple possible mechanisms that can allow for coexistence, and spatial heterogeneity in predator and prey populations is one of them (Lampert and Hastings 2016).

Empirically, specific space-use behaviors have been shown to be an important factor mediating predator-prey coexistence. Often, the prey species adopts behaviors to deal with predation, such as altering habitat selection (Mao et al. 2005), altering daily movement patterns (Kohl et al. 2018), or a combination of both (Kohl et al. 2019). A clear theoretical framework can help with understanding when space-use can stabilize multi-predator-prey interactions in natural systems.

This theoretical approach is motivated by empirical work from Yellowstone National Park, USA. Yellowstone protects an iconic ecosystem with multiple species of large carnivores and large ungulates forming the most conspicuous part of the food web. A quarter century ago, wolves (*Canis lupus*) were reintroduced into northern Yellowstone, and the relationship between wolves and their primary prey, elk (*Cervus canadensis*), has been closely studied ever since. This system has resulted in many insights into predator-prey ecology, but we should also recognize that wolves and elk are only part of the picture. There are other major predators of elk in this system, namely cougars (*Puma concolor*), black and grizzly bears (*Ursus americanus* and *U. arctos*), and even humans (Vucetich et al. 2005). A recent study showed that to deal with both wolves and cougars simultaneously, elk adopt a movement strategy between habitats that allows them to reduce the effect of both predators (Kohl et al. 2019).

I developed a theoretical model to test hypotheses about these multi-predator systems. I (1) developed a discrete-time theoretical modeling framework focused on a single prey species (Fig. 1), (2) tested the behavior of this model under different combinations of parameter values, and (3) generalized the cases in which the model shows stability.

Methods

Model Structure

For clarity, parameters referring specifically to the prey will use Latin symbols, while parameters referring to the predator will use Greek symbols (Table 1). The model assumes there are two habitat types in this system, specifically denoted A and B, but which I will refer to collectively with H (*i.e.*, $H \in \{A, B\}$). The prey can move between the two habitats, but each habitat has a unique predator that does not move between habitats. This is similar to the elk-wolf-cougar system in Yellowstone, where wolves hunt mostly in open habitats, cougars hunt mostly in forested habitats, and elk move in between the two. The prey species abundance in each habitat

at a given time, t, will be denoted by $N_{H,t}$. Similarly, the predator abundance in each habitat at a given time will be denoted by $\rho_{H,t}$. Each habitat has a carrying capacity for the prey species denoted by K_H and a carrying capacity for the predator denoted by κ_H. The predator carrying capacity implies there is a factor besides prey abundance – *e.g.*, intraspecific competition, territoriality – that limits predator populations.

In each time step, three events occur simultaneously (Fig. 1). First, the prey will transition from habitat H to habitat H' with probability, $T_{HH'}$, or remain with probability $1 - T_{HH'}$. Second, the prey will be killed by predators according to the density of predators ($\rho_{H,t}$) in that time and the attack rate of that predator (α_H), with number of individuals dying given by:

$$d_{H,t} = \alpha_H \rho_{H,t} N_{H,t}$$

Third, the populations of prey and predators will grow, according to the discrete time logistic growth equation. The growth of prey in each habitat is:

$$G_{H,t} = r N_{H,t} \left(1 - \frac{N_{H,t}}{K_H} \right)$$

with r representing the intrinsic growth rate. The predator population in each habitat will grow depending on their consumption of prey and their own density:

$$\Gamma_{H,t} = \epsilon_H \alpha_H \rho_{H,t} N_{H,t} \left(1 - \frac{\rho_{H,t}}{\kappa_H} \right)$$

where ϵ_H is the conversion efficiency. Independent of prey, predators will have survival rate ϕ_H. Thus, the full set of difference equations for prey and predators is:

$$\begin{cases} N_{H,t+1} = \left[N_{H,t}(1 - T_{HH'}) + N_{H',t} T_{H'H} \right] + \left[-\left(\alpha_H \rho_{H,t} N_{H,t} \right) \right] + \left[r N_{H,t} \left(1 - \frac{N_{H,t}}{K_H} \right) \right] \\ \\ \rho_{H,t+1} = \phi_H \rho_{H,t} + \epsilon_H \alpha_H \rho_{H,t} N_{H,t} \left(1 - \frac{\rho_{H,t}}{\kappa_H} \right) \end{cases}$$

This model allows prey and predator populations to take on any positive real value, *i.e.*, fractions of individuals are possible. This resulted in the unexpected behavior that populations would almost never go "extinct", but instead the modeled population could decline to a very small positive number, *e.g.*, $\approx 1.0 \times 10^{-28}$. To deal with this model artifact, I added a rule to the simulations that anytime one of the populations fell below 0.5 individuals, I would set it to exactly 0.

Model Behavior

After developing the model, I tested its behavior under different parameter combinations. I coded all simulations in R v 3.6.1 (R Core Team 2019), and all R code used in these analyses can be found on GitHub (https://github.com/bsmity13/theo_eco_proj). Before examining aspects of spatial heterogeneity, I tested that the model performed as expected under simplified conditions

(Supporting Information). After confirming expected model performance, I began to vary parameters that controlled the degree of spatial heterogeneity between the habitats. I began with a base scenario which was the starting point for all further variation. The values of the parameters under the base scenario (scenario 1) are presented in Table 2. Under the base scenario, I defined habitat A to be lower quality than habitat B. I reflected this in the model by setting the carrying capacity for both the predators and the prey in habitat A to be half of what it was in habitat B. I assumed that intrinsic growth rates (prey) and survival rates (predators) did not vary, but rather that carrying capacities alone reflected habitat quality. However, the predator that lives in habitat B (the "better" habitat) is more lethal to the prey species, representing a trade-off. Under the base scenario, the prey cannot move between habitats.

Beginning with the base model, I varied the model parameters to test situations where (i) the prey shows no, weak, or strong habitat preferences; (ii) the predators have varying attack rates; and (3) combinations of both. I kept all other model parameters constant throughout these simulations. All scenarios and their parameters are summarized in Table 2.

Habitat Preference Scenarios

Habitat selection is defined as occurring when an animal uses a habitat in a greater proportion than it is available on the landscape (Manly et al. 2002). A similar, but not equivalent, term is habitat preference. Preference usually refers to choices measured in the laboratory under conditions where the alternatives are equally available. Because habitats in nature are not often equally available, habitat selection is the preferred term to describe the space-use choices in free-living animals. However, for the purposes of this model, we will treat the two habitats as equally available, and thus we will characterize preference as opposed to selection.

I varied the prey species' habitat preferences by altering the transition parameters, *i.e.*, the $T_{HH'}$ parameters. Under the *base* scenario (scenario 1), $T_{AB} = T_{BA} = 0$, meaning the prey cannot move at all between habitats, effectively removing habitat selection from consideration. Under the *no preference* scenario (scenario 2), $T_{AB} = T_{BA} = 0.5$, *i.e.*, there is an equal chance that an individual would switch habitats or not, regardless of the habitat where it is currently. Under the *weak preference* scenario (scenario 3), $T_{AB} = 0.6$ and $T_{BA} = 0.4$, *i.e.*, there is a slightly higher chance that an individual will choose habitat B in the next time step, regardless of the habitat where it is currently ($T_{AB} = 1 - T_{BA} = 0.6$). Under the *strong proportional preference* scenario (scenario 4), $T_{AB} = 0.1$ and $T_{BA} = 0.9$, *i.e.*, there is a much higher chance that an individual will choose habitat B in the next time step, regardless of where it is currently. Under the *strong inverse preference* scenario (scenario 5), $T_{AB} = 0.9$ and $T_{BA} = 0.1$, the reverse of the probabilities in the previous scenario. Under this scenario, individuals strongly prefer the lower quality habitat.

Attack Rate Scenarios

I varied the predator attack rates by altering the α_H parameters. All other parameters remain the same as in the base scenario, in particular, there is no movement between habitats. Under the *base* scenario, $\alpha_A = 0.01$. and $\alpha_B = 0.02$. In this case, we can think of the base scenario as a *low proportional attack difference* scenario (scenario 1), where the "better" habitat has the "better" predator. Under *low inverse attack difference* scenario (scenario 6), $\alpha_A = 0.02$ and $\alpha_B = 0.01$, *i.e.*, the "worse" habitat has the "better" predator. Under the *high proportional attack difference*

scenario (scenario 7), $\alpha_A = 0.005$ and $\alpha_B = 0.03$. Under the *high inverse attack difference* scenario (scenario 8), $\alpha_A = 0.03$ and $\alpha_B = 0.005$.

Combination Scenarios

After testing the parameter differences separately, I then moved to scenarios where both habitat selection and attack rate parameters varied. I combined the scenarios of strong preference and high attack difference to try to see if the combinations would stabilize them. Under the *strong proportional preference & high proportional attack difference* scenario (scenario 9), $T_{AB} = 0.1, T_{BA} = 0.9, \alpha_A = 0.005$ and $\alpha_B = 0.03$. Thus, in this scenario, the "better" habitat (B) is both highly preferred and has a much more effective predator (attack rate 6 times higher). Under the *strong inverse preference & high inverse attack difference* scenario (scenario 10), $T_{AB} = 0.9, T_{BA} = 0.1, \alpha_A = 0.03$ and $\alpha_B = 0.005$. Thus, it is the converse of scenario 9, where the "worse" habitat (A) is both highly preferred and has a much more effective predator.

Results

Model Testing

Test scenarios behaved as expected under the model, and the detailed results are available in the Supplemental Information. In short, predator-free scenarios show growth as expected under the logistic growth model, and the addition of movement between habitats had the effect of moderating the realized carrying capacity of each habitat, such that the populations are closer in size under equilibrium than they were without movement. The models with low baseline levels of predation show damped oscillations before reaching a stable equilibrium with the prey far below their respective K.

Model Behavior

Under the *base* scenario (scenario 1), the predators strongly suppress the prey populations far below their carrying capacities (Fig. 2). In the "better" habitat (B), the initial predator population grows extremely rapidly in response to the high numbers of prey, then immediately depletes the prey population. This sharp swing results in the prey going extinct, followed by the predator population "starving" to extinction (*i.e.*, declining due to ϕ with no recruitment until the population hits 0). In the "worse" habitat, however, the initial oscillations are less extreme, allowing the predator and prey to stabilize at approximately $N_A \approx 38, \rho_A \approx 8$.

Habitat Preference Scenarios

Under the *no preference* scenario (scenario 2), the initial transient dynamics are much less strong than under the base scenario. Nonetheless, one of the predators still goes extinct, this time the predator in habitat A (Fig. 3a). Under the *weak preference* scenario (scenario 3), both predators go extinct, completely releasing the prey to grow to their carrying capacities (but due to movement, those equilibrium populations are not equal to the K in each habitat; Fig. 3b). Under the *strong proportional preference* scenario (scenario 4), transient dynamics are again strong, and this time the predator in B goes extinct. However, due to strong movement between habitats, the remaining predator in A is able to stabilize the prey population in both habitats, and neither one blows up to carrying capacity (Fig. 3c). Under the *strong inverse preference* scenario (scenario 5), initial transient dynamics are extreme, and in less than 50 years all three species go extinct. Thus, all four habitat preference scenarios result in one or more extinctions.

Again, the *base* scenario can also be framed as a *low proportional attack difference* scenario, where the "better" habitat has the "better" predator. As presented above, this scenario results in the extinction of the predator in habitat B. Under *low inverse attack difference* scenario (scenario 6), the prey and both predators are able to survive, and the system undergoes damped oscillations, eventually evolving to a stable equilibrium (Fig. 4a). Under the *high proportional attack difference* scenario (scenario 7), the predator in habitat B is able to almost immediately eradicate the prey population, and because there is no movement in this scenario, that predator goes extinct, leaving just the predator and prey in habitat A (Fig. 4b). Under the *high inverse attack difference* scenario (scenario 8), the transient dynamics are less extreme, but the predator in A eventually goes extinct, allowing the prey in A to grow to their carrying capacity (Fig. 4c). Thus, only scenario 6 is stable, and the other two result in at least one extinction.

Combination Scenarios

Under the *strong proportional preference & high proportional attack difference* scenario (scenario 9), the initial transient dynamics are strong, but no populations go extinct, and they are able to recover to a stable equilibrium with the populations in habitat A greater than those in B (despite the higher carrying capacities in B; Fig. 5a). Under the *strong inverse preference & high inverse attack difference* scenario (scenario 10), the transient dynamics are again strong, but the oscillations again settle down and persistence is possible, with the populations in habitat B greater than those in habitat A (Fig. 5b). However, while these populations were all able to persist for the 200-year window over which I simulated, this is not a stable system. The predators in habitat A were still slowly declining and would have eventually gone extinct.

Discussion

In this paper, I have shown that habitat selection is a mechanism that can allow for coexistence in a predator-prey system with multiple predators. While habitat selection alone does not prevent extinction, strong habitat selection can help overcome differential attack rates by predators in different habitats, as seen in the combination scenarios (scenarios 9 and 10; Fig. 5). This is similar to a finding by Reeve (1990), who investigated the effects of spatial dynamics in a theoretical host-parasitoid system.

This model was able to reproduce several effects that were expected, and several that may have initially seemed counterintuitive. The easiest effects to predict were those in the absence of predators (Supplemental Information). Another effect that I expected was the strong transient dynamics under strong habitat preferences. I did not, however, expect the results that I observed from the scenarios in which habitat A showed stability and habitat B experienced extinction, *i.e.*, where the "worse" habitat was stable and the "better" habitat was not (scenarios 1, 4, and 7). This seems counterintuitive that the "better" habitat should fare worse, but this is an example of Rosenzweig's "Paradox of Enrichment" (Rosenzweig 1972). The higher carrying capacity in B allowed for larger oscillations, which were ultimately destabilizing.

This model could be extended in several ways. First, adding both environmental and demographic stochasticity would add a realistic dimension to the model. Environmental stochasticity could, for example, be modeled by allowing random fluctuations in the carrying

capacity parameters (K_H, κ_H) or the growth rate/survival parameters (r, ϕ_H) by sampling them from a normal distribution. Demographic stochasticity could be modeled by randomly drawing the new recruits from a Poisson distribution with mean intensity given by the growth parameters (G_H, Γ_H). Another way to extend this model would be by allowing the habitats to be composed of many discrete patches. This could be done in a spatially implicit way by tracking a number of subpopulations with a constant transition probability between all cells, or a spatially explicit way by tracking the location of patches on a raster grid and allowing transition probabilities to vary as a function of the distance between patches, *sensu* a cellular automata model.

A great deal of work throughout the history of ecology has been dedicated to predator-prey interactions, but we have unfortunately devoted little of this effort to systems with multiple predators. This work represents a small step toward filling this gap, and it can guide the interpretation of empirical work. Field measurements of habitat selection should consider the effects that predators can have on prey density, especially in light of Rosenzweig's Paradox of Enrichment.

Acknowledgements

Literature Cited

Kohl, M. T., T. K. Ruth, M. C. Metz, D. R. Stahler, D. W. Smith, P. J. White, and D. R. MacNulty. 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat? Ecology Letters 22:1724–1733.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Korobeinikov, A., and G. C. Wake. 1999. Global properties of three-dimensional predator-prey Lotka-Volterra systems. Journal of Applied Mathematics & Decision Sciences 3:155–162.

Lampert, A., and A. Hastings. 2016. Stability and distribution of predator-prey systems: Local and regional mechanisms and patterns. Ecology Letters 19:279–288.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals. Springer Netherlands, Dordrecht, The Netherlands.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat Selection By Elk Before and After Wolf Reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reeve, J. D. 1990. Stability, Variability, and Persistence in Host-Parasitoid Systems. Ecology 71:422–426.

Rosenzweig, M. L. 1972. Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time. Science 171:385–387.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350–355.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos 111:259–270.

Tables and Figures

Table 1. Summary of model parameters and their interpretations.

Parameter	Description
$N_{H,1}$	Prey population size in habitat H at time $t = 1$
K_H	Prey carrying capacity in habitat H
$T_{HH'}$	Probability of transitioning from habitat H to habitat H'
r	Prey intrinsic growth rate
$\rho_{H,1}$	Predator population size in habitat H at time $t = 1$
ϕ_H	Base predator survival rate in habitat H
κ_H	Predator carrying capacity in habitat H
α_H	Attack rate of the predator in habitat H
ϵ_H	Assimilation efficiency of the predator in habitat H

Table 2. Description of scenarios and corresponding parameter values. The values in **bold** differ from the base scenario.

|	Base	Habitat Selection				Attack Rates			Combination	
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6	Scenario 7	Scenario 8	Scenario 9	Scenario 10
	Base	*No preference*	*Weak preference*	*Strong proportional preference*	*Strong inverse preference*	*Low inverse attack difference*	*High proportional attack difference*	*High inverse attack difference*	*Strong prop pref & high prop attack*	*Strong inv pref & high inv attack*
$N_{H,1}$	250, 250	250, 250	250, 250	250, 250	250, 250	250, 250	250, 250	250, 250	250, 250	250, 250
K_H	250, 500	250, 500	250, 500	250, 500	250, 500	250, 500	250, 500	250, 500	250, 500	250, 500
$T_{HH'}$	0, 0	**0.5, 0.5**	**0.6, 0.4**	**0.1, 0.9**	**0.9, 0.1**	0, 0	0, 0	0, 0	**0.1, 0.9**	**0.9, 0.1**
r	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
$\rho_{H,1}$	25, 25	25, 25	25, 25	25, 25	25, 25	25, 25	25, 25	25, 25	25, 25	25, 25
ϕ_H	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9	0.9, 0.9
κ_H	25, 50	25, 50	25, 50	25, 50	25, 50	25, 50	25, 50	25, 50	25, 50	25, 50
α_H	0.01, 0.02	0.01, 0.02	0.01, 0.02	0.01, 0.02	0.01, 0.02	**0.02, 0.01**	**0.005, 0.025**	**0.025, 0.005**	**0.005, 0.025**	**0.025, 0.005**
ϵ_H	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4	0.4, 0.4
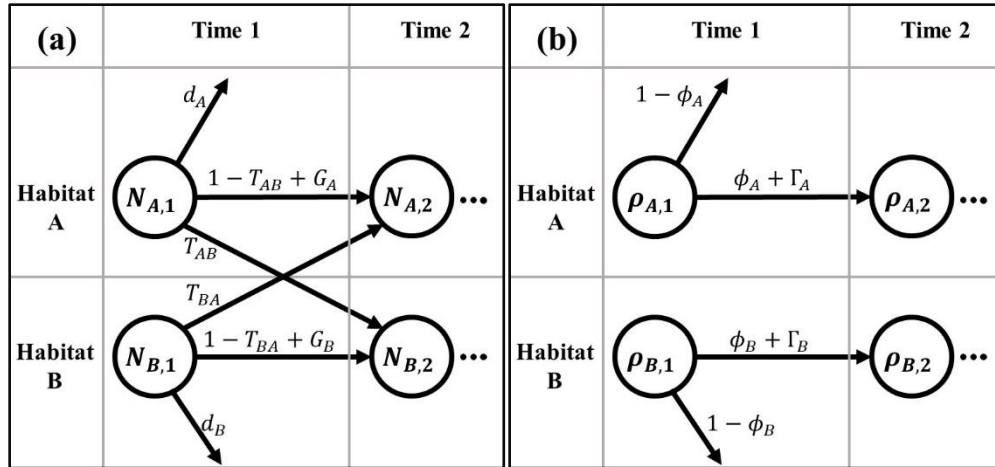
Figure 1. Diagram showing prey population change (a) and predator population change (b). See the main text for a detailed description of each component of population change.
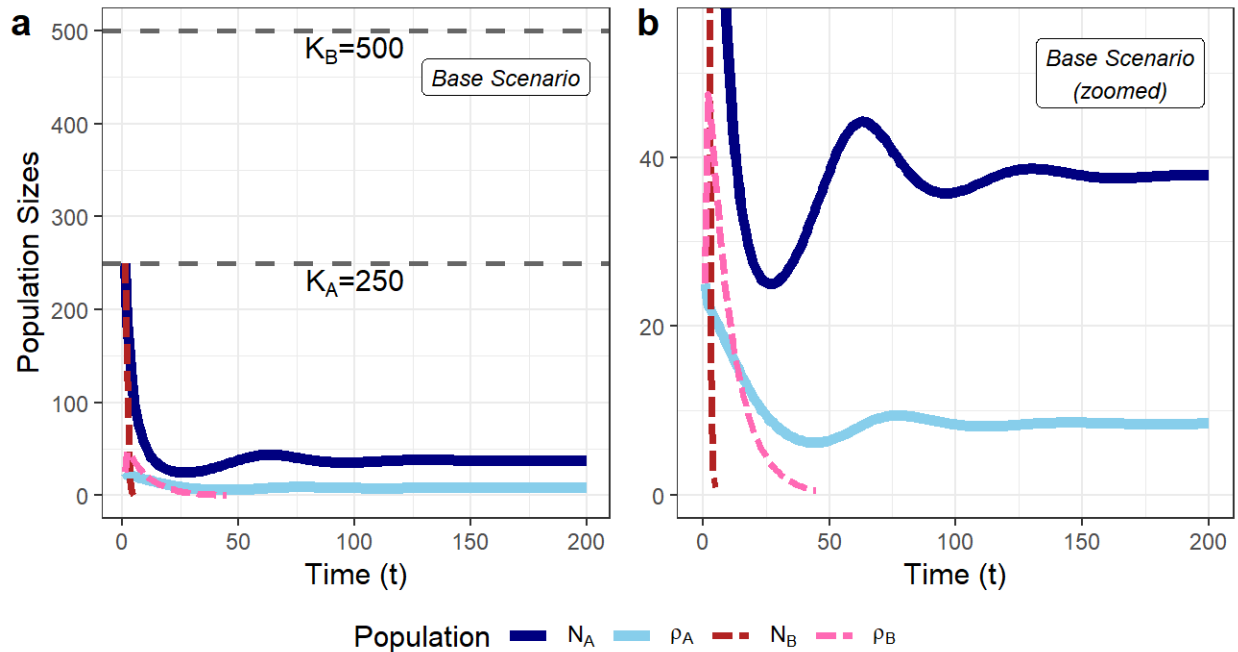

Figure 2. Results from the base scenario showing (a) the full plot region and (b) a detailed view of the dynamics as the populations adjust toward equilibrium. Under this scenario, the predator and prey in habitat B go extinct, while the populations in habitat A are able to reach a stable equilibrium.
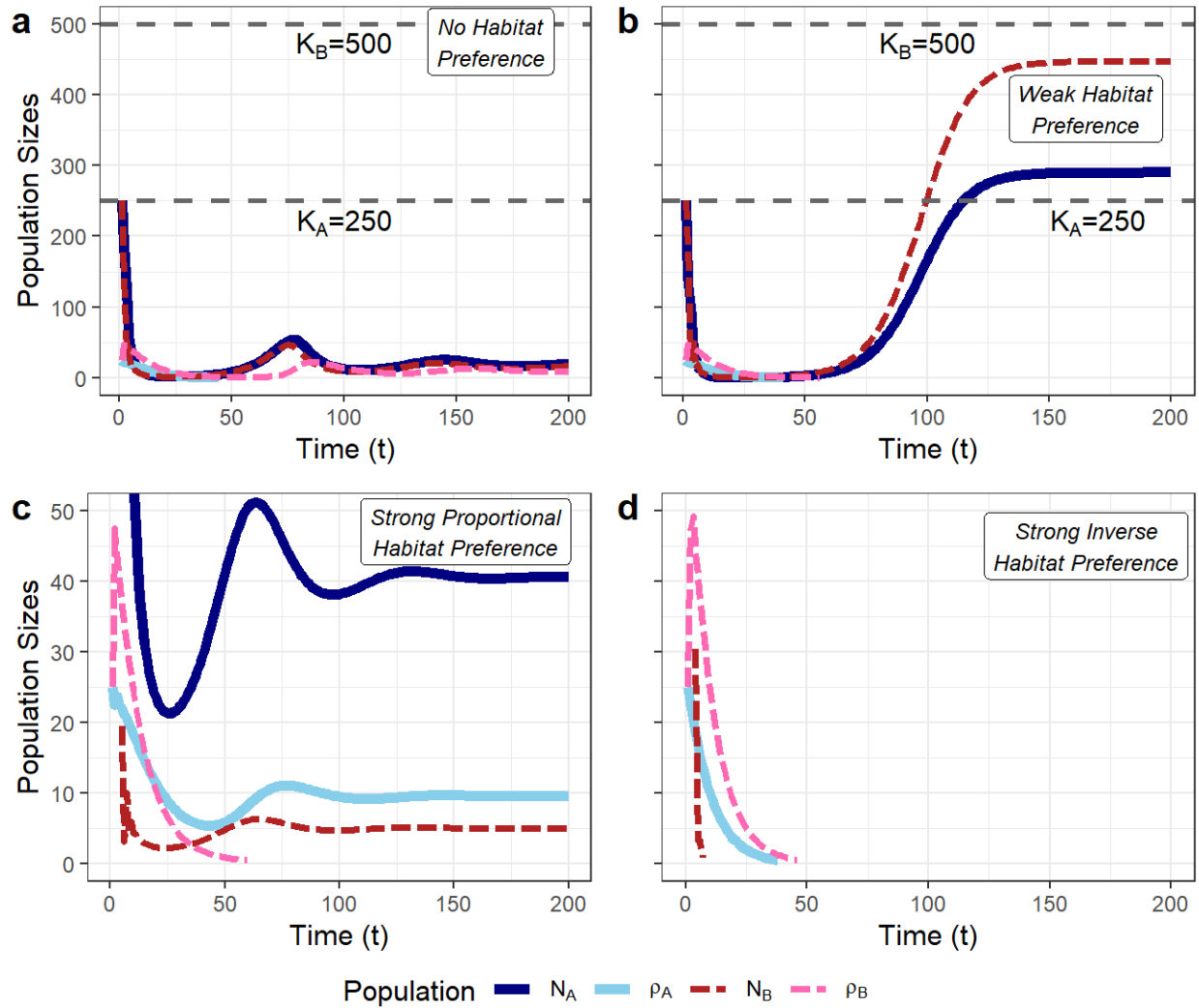
Figure 3. Results from the habitat preference scenarios showing (a) no habitat selection, (b) weak habitat selection, (c) strong proportional habitat selection, and (d) strong inverse habitat selection. In each of these scenarios, at least one species goes extinct, so none of them show full stability.
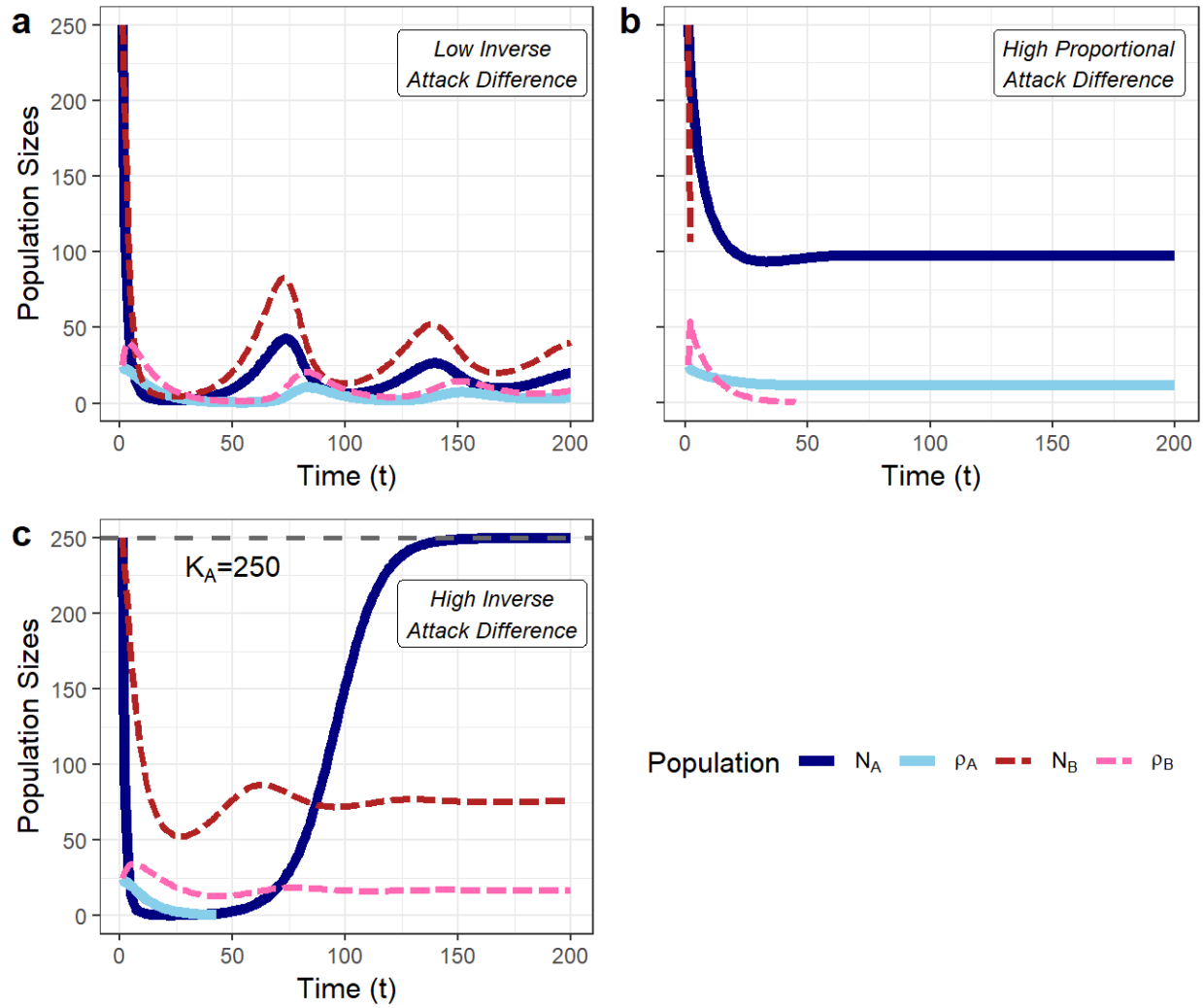
Figure 4. Results from the attack rate scenarios showing (a) low inverse attack differences, (b) high proportional attack differences, and (c) high inverse attack differences. The base scenario (see Fig. 2) can be considered low proportional attack differences. Only the scenario in panel (a) shows stability; the other two see at least one species go extinct.
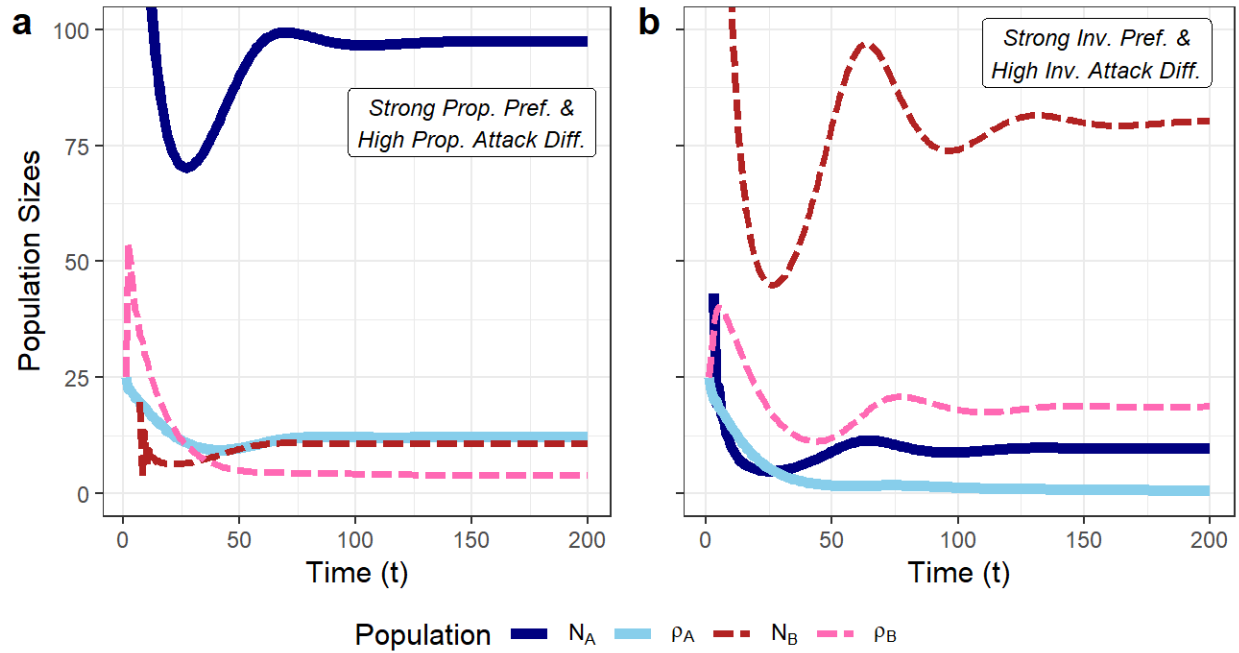
Figure 5. Results from the combined scenarios showing (a) strong proportional habitat preference & high proportional attack difference and (b) strong inverse habitat preference & high inverse attack difference. Note that in (a) the system has reached a stable equilibrium but in (b) the predator population in A (ρ_A) is still trending down and will eventually go extinct, but it does not go extinct in this 200-year time frame.

Supporting Information

Before proceeding with the scenarios that I wanted to explore (see main text), I tried simple scenarios to confirm that the model had sensible performance. I first tested two scenarios without predators by setting $\rho_A = \rho_B = 0$. The first scenario had no movement between habitats (*i.e.*, $T_{AB} = T_{BA} = 0$) and different carrying capacities for prey ($K_A = 250, K_B = 500$) as in the base scenario (see main text). As expected, both populations stabilized at exactly their carrying capacities (Fig. S1a). The second scenario had a low and equal amount of habitat preference ($T_{AB} = T_{BA} = 0.25$) and all other parameters the same. As expected, the movement between habitats effectively changed the realized carrying capacity in that habitat, with $N_A > K_A$ and $N_B < K_B$ (Fig. S1b).
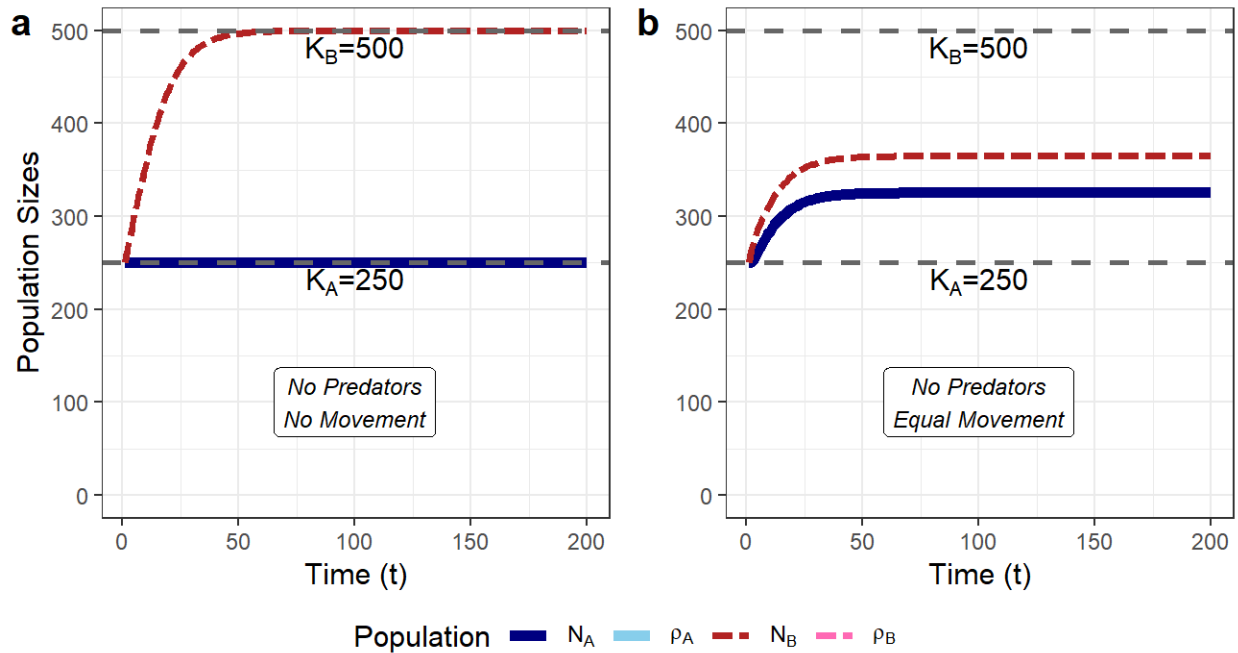

Figure S1. Test scenarios without predators ($\rho_A = \rho_B = 0$) and (a) no movement or (b) low and equal habitat selection ($T_{AB} = T_{BA} = 0.25$).

Once I confirmed that the model behaved as expected without predators, I added the predators to the model, consistent with the base scenario (see main text). Unlike in the base scenario from the main text, I set the attack rates for both predators to be equal and low enough to allow stability, *i.e.*, I set $\alpha_A = \alpha_B = 0.01$. In the first scenario, I allowed no movement by the prey (*i.e.*, $T_{AB} = T_{BA} = 0$). As expected, the populations of predators and prey in each habitat exhibited damped oscillations, and none of the populations went extinct (Fig. S2a). Oscillations and equilibrium populations were both higher in habitat B, the "better" habitat with higher carrying capacities for both prey and predator. The second scenario had a low and equal amount of habitat preference, and as expected, this served to average out the prey population fluctuations such that the oscillations were smaller for both habitats (Fig. S2b).
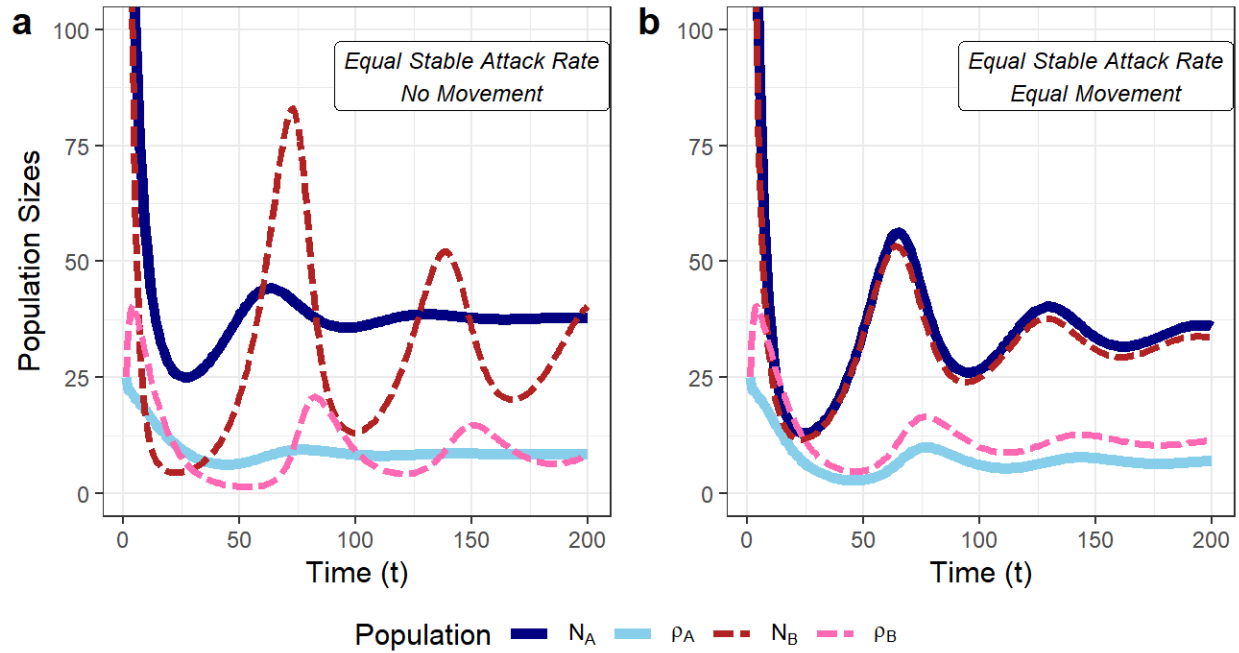
Figure S2. Test scenarios with predators and (a) no movement or (b) low and equal habitat selection ($T_{AB} = T_{BA} = 0.25$).

After confirming these expected behaviors in simple scenarios, I proceeded to the main scenarios described in the main text.