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Predator foraging mode controls the effect of antipredator behavior in a tritrophic model

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Abstract

Antipredator behavior is known to have a strong effect on prey population dynamics. While there have been many studies of antipredator behavior in population dynamic models, none have examined how antipredator behavior interacts with predator foraging mode. To examine this process, we incorporated predator and prey velocities into a simple tritrophic food chain. In this model, antipredator behavior allows prey to respond to predators by slowing their velocity in response to predator density. Prey can slow their velocity to hide from predators, but this in turn reduces their ability to consume resources, creating a trade-off between hiding and foraging. We examined the effects of both fast-moving "mobile" predators and slow-moving "sit-and-wait" predators on equilibrium prey density and amplitude of predator-prey cycles. We found that antipredator behavior was ineffective against mobile predators, but it was very effective against sit-and-wait predators. Antipredator responses to sit-and-wait predators reduced top-down control and allowed prey density to increase with increased carrying capacity. Furthermore, antipredator responses to sit-and-wait predators eliminated population cycles within the community, whereas antipredator behavior had no effect on population cycles within mobile predator communities. Therefore, our model demonstrates predator foraging mode must be taken into account when examining predator-prey cycles. We discuss the potential implications of this model for invasive species and for trophic cascades.

Keywords Behavior · Antipredator · Cycles · Naïveté · Top-down · Bottom-up

Introduction

Predators are known to have strong consumptive and nonconsumptive effects on their prey (Werner and Peacor 2003; Preisser et al. 2005; Peckarsky et al. 2008). Often nonconsumptive effects are mediated through changes in prey behavior that lead to changes in prey foraging (Lima and Dill 1990; Berger 2010). By adjusting behavior in response to predators, prey can compensate for mortality risk by changing their foraging intensity (Trussell et al. 2002), patch use (Orrock et al. 2008; Bishop and Byers 2015; Davidson et al. 2015), or landscape use (Matassa and Trussell 2011). These decisions create trade-offs such that prey will increase their antipredator behavior (e.g., hiding) and decrease their foraging or reproductive behavior (Brown et al. 1999).

Variation in the degree of expression of antipredator behavior could come about through predator foraging strategy (Peckarsky et al. 2008; Schmitz 2008; Reynolds and Bruno 2013). Prey exhibit differential responses to alternative foraging modes in systems as diverse as insects (Schmitz and Suttle 2001), marine amphipods (Reynolds and Bruno 2013), lizards (Sherbrooke 2008), and birds (Billings et al. 2017). It may be difficult for prey to predict the presence of mobile predators based on the chemical (e.g., scat, urine) or physical (e.g., burrows, markings) trace evidence they leave behind (Schmitz and Suttle 2001; Preisser et al. 2007; Kauffman et al. 2010), whereas slow-moving predators that wait for prey to come near (sit-and-wait predators) may leave higher density of trace evidence that could be more reliable indicators of predator activity.

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Even though antipredator behavior has been the subject of numerous studies (e.g., Ives and Dobson 1987; Sih 1987; Abrams 1992), there has been comparatively little research into the theoretical importance of predator foraging mode. Models that allow migration between risky habitat and predator-free refuges are typically conceptualized with one predator foraging strategy (e.g., Sih 1992). Models that incorporate a basal resource trophic level (Ramos-Jiliberto 2003) or varying antipredator effectiveness or cost (Ives and Dobson 1987; Ramos-Jiliberto et al. 2008) demonstrate that the costs and benefits associated with the antipredator responses influence both community stability and equilibrium population densities but do not consider multiple predator types. Models of the relative value of mobile and sit-and-wait predator foraging mode indicate that the success of each foraging mode depends on the relative speeds of predators and prey (Werner and Anholt 1993; Scharf et al. 2006). However, only two papers have linked foraging mode to analytical studies of population dynamics. One used an individual based models and found that prey exhibit little behavioral response when predators are hard to predict (i.e., mobile predators; Luttbeg and Trussell 2013). The other (Calcagno et al. 2011) phenomenologically modeled foraging mode by removing all antipredator response to mobile predators and found that sit-and-wait predators promoted coexistence among basal resource species. No study has looked at the role of predator foraging mode in determining community cyclicity, and no study has used a mechanistic framework for representing predator foraging mode in an analytical model.

Studies of population dynamics also indicate that predator foraging mode may be an important determinant of population cycles. Analyses of the Global Population Dynamics Database indicate that 17 to 29% of these populations undergo cycles (Kendall et al. 1998; Louca and Doebeli 2015). Over half of the approximately 400 cyclical populations in Louca and Doebeli (2015) conservative analysis are aphid populations with the remainder being plankton, insect, bird, fish, and mammal populations. The aphid cycles are likely induced by cyclical weather patterns or by highly mobile predators such as parasitoid wasps or lady beetles (Leslie et al. 2009). Of the remaining 200 cyclical populations, 26.5% of them are either a hare or a lynx species and 25% were mobile mammalian predators (foxes, mustelids, or coyotes) (Louca and Doebeli 2015). While these population cycles could have many potential mechanisms besides predator-prey forcing (e.g., demographic stochasticity), there were no sit-and-wait predators in the list of species with cyclical dynamics, which suggests that sit-and-wait predators may dampen or eliminate predator-prey cycles.

We incorporated predator foraging mode and antipredator behavior into a theoretical model in order to examine this knowledge gap and to determine if it could explain the lack of sit-and-wait predators in empirical patterns of cyclicity. Using the same logic behind Dell et al. (2014) and Scharf et al. (2006), we assigned small predator velocities to sit-and wait predators and large predator velocities to mobile predators. We analyzed how a specific method of antipredator response (hiding behavior) could influence community dynamics. We model prey hiding behavior by explicitly describing the prey's mean movement rate and utilize a sensitivity parameter that controls the degree of prey response to predator density (i.e., the degree of naïveté). Using this model we investigate (1) how antipredator response modifies cyclical dynamics in mobile predator– or sit-and-wait predator–dominated communities and (2) whether antipredator responses to sit-and-wait predators lead to higher prey densities relative to responses to mobile predators. Our model clearly shows that even in the simplest cases, predator foraging mode has an outsize effect on community dynamics. We discuss the implications of these results on predator-prey dynamics and invasion ecology.

Model

We model a linear tritrophic system with moving predators (P) attacking moving consumers (C) and with consumers foraging on continuously growing and stationary basal resource (R) such as a plant. We refer to consumers as "prey" when describing predator-prey dynamics in the text. All species are expressed in terms of species density (species abundance per unit area). We chose to use a traditional Rosenzweig-MacArthur model structure (Rosenzweig and MacArthur 1963) for our analysis as this model structure is known for its variety of oscillatory (stable limit cycles) and chaotic dynamics (Hastings and Powell 1991; McCann and Yodzis 1994):

$$\begin{aligned}
\frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right)-\frac{\alpha_C(P)R}{(1+\alpha_C(P)\beta_C R)}C \\
\frac{dC}{dt} &= \frac{\alpha_C(P)R}{(1+\alpha_C(P)\beta_C R)}s_C C-\frac{\alpha_P(P)C}{(1+\alpha_P(P)\beta_P C)}P-m_C C \\
\frac{dP}{dt} &= \frac{\alpha_P(P)C}{(1+\alpha_P(P)\beta_P C)}s_P P-m_P P
\end{aligned} \tag{1}$$

In this model, r is the intrinsic growth rate of the resource, K is the carrying capacity of the resource, s_i represents the conversion factor of consumed biomass into biomass of species i, and m_i represents the density-independent mortality rate of species i. Both predators and consumers have Holling (1959) type II functional response such that $\alpha_i(P)$ represents the predator-dependent encounter rate of species i with its food source, and β_i is the handling time of species i on its food source. Dimensions for all parameters are given in Table 1 (for

Table 1 Parameter definitions used for investigating how predator and prey velocity influence equilibrium densities

Description	Parameter	Value	Units
Intrinsic rate of growth	r	2.5	Time^{-1}
Carrying capacity	K	4	R density × length^{-2}
Prey detection diameter	D_C	0.5	Length
Predator detection diameter	D_P	0.25	Length
Handling time of prey on resource	β_C	0.1	Time × R density^{-1}
Handling time of predator on prey	β_P	0.5	Time × C density^{-1}
Density-independent mortality of prey	m_C	0.1	Time^{-1}
Density-independent mortality of predator	m_P	0.1	Time^{-1}
Prey density conversion factor	s_c	0.2	R density^{-1}
Predator density conversion factor	s_P	0.2	C density^{-1}
Prey movement velocity	γ	0–5	Length × time^{-1}
Predator movement velocity	w	0–5	Length × time^{-1}
Antipredator sensitivity	θ	0, 0.69, 5	P density^{-1} × length^{2}
Predator density	P	Dynamic	P abundance × area^{-1}
Prey density	C	Dynamic	C abundance × area^{-1}
Resource density	R	Dynamic	R abundance × area^{-1}

brevity, dimensions are not included when discussing parameter values in the text). See Appendix A in the supplementary material for full discussion of model assumptions.

Recently Ross and Winterhalder (2015) developed a two-dimensional predator-prey encounter rate model with random movement of prey and predators. In our case, if predator and consumer movement velocities follow a two-dimensional Maxwell's distribution (see Skellam 1958), then the attack rate (α) can be represented by

$$\alpha_P(P) = D_P\sqrt{w^2 + v^2} \tag{2}$$

$$\alpha_C = D_C v \tag{3}$$

Equation 2 makes the attack rate of the predators (P) on the consumers (C) an explicit function of the mean predator velocity (w), the mean prey velocity (v), and the effective foraging diameter of the predator (D_P). The effective foraging diameter (D_i) represents the distance at which food items can be detected. Both Eqs. 2 and 3 assume that all food items the forager encounters within that diameter are successfully eaten. Similar models have been used to examine the relative success of mobile predator and sit-and-wait predator strategies (Werner and Anholt 1993; Scharf et al. 2006). We chose to examine the simplest case possible in which consumers cannot escape encounters with predators and in which predator attack rates increase as mean consumer velocity increases. In short, the random distribution of predators implies that running from one predator will in turn lead to an encounter with another predator. Foragers (either predators or consumers) benefit from increasing velocity by increasing their foraging rate via Eq. 2 (for predators) or Eq. 3 (for consumers). On the other hand, increasing velocity hinders consumers by simultaneously increasing their encounter rate with predators (Eq. 2).

We can incorporate antipredator behavior into this model by allowing mean consumer velocity to respond to predator density. We assume that the mean consumer velocity (v) is a decreasing function of P:

$$v(P) = \gamma e^{-\theta P} \tag{4}$$

In this case, γ represents the maximum mean foraging velocity of the consumer (the velocity that occurs in the absence of the predator) and θ is the consumer's antipredator sensitivity. Because the velocity of the consumer depends on the dynamic quantity P, γ sets the upper bound on the consumer's potential movement rates. We interpret this reduction in mean foraging velocity as an increase in consumer hiding behavior that simultaneously reduces encounter rates with predators (Eq. 2) and reduces their foraging rate on resources (Eq. 3).

Antipredator sensitivity is the key parameter in this model and represents the consumer's behavioral change to increases in predators. Generally, θ would likely be negligible or zero for naïve consumers, while θ would likely be nonzero for experienced consumers. Mathematically, θ is the negative natural log of the proportional reduction in velocity at unit P density. For example, if $\theta = -\ln(0.5) = 0.693$, then average consumer velocity is reduced by 50% when $P = 1$. Importantly, because of the dimensional assumptions of this model (Table 1), $P = 1$ signifies that there is on average one predator per unit area (e.g., km^2) and that this predator moves w units of length per unit time (e.g., km/day).

When we substitute Eqs. 2, 3, and 4 into Eq. 1, our full model becomes

$$
\begin{aligned}
\frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right)-\frac{D_C\gamma e^{-\theta P}R}{(1+D_C\gamma e^{-\theta P}\beta_C R)}C \\
\frac{dC}{dt} &= \frac{D_C\gamma e^{-\theta P}R}{(1+D_C\gamma e^{-\theta P}\beta_C R)}s_C C-\frac{D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}C}{\left(1+D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}\beta_P C\right)}P-m_C C \\
\frac{dP}{dt} &= \frac{D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}C}{\left(1+D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}\beta_P C\right)}s_P P-m_P P
\end{aligned}
\qquad (5)
$$

See Appendix B in the supplementary material for a non-dimensional version of this model.

Model analysis

Antipredator behavior influence on community dynamics

Our first analysis addressed the influence of predator foraging mode on the transition from stable point equilibria to stable limit cycles. Using a computational bifurcation analysis, we determined how predator and prey velocities modify the interaction between antipredator sensitivity (θ) and productivity metrics (K or r). To examine the effect of these factors on community stability, we used the differential equation solver *lsoda* from the R package deSolve (Soetaert et al. 2010).

We present two different community modes, one in which predators are much slower than prey ($w = 0.71$, $\gamma = 3.5$) similar to a sit-and-wait predator and one in which predators are marginally faster than prey ($w = 1.79$, $\gamma = 1.75$) similar to a mobile predator. Note that we are simultaneously changing both predator and prey velocities in these simulations; therefore, these simulations do not show causality. To illustrate that predator velocity is the casual factor in this model, we conducted a third simulation that uses the predator velocity from the sit-and-wait predator community (w = 0.71) with the consumer velocity from the mobile predator community ($\gamma = 1.75$; see Appendix C in the supplementary material). The values chosen for presentation in the main text exemplify the differences between foraging modes and hold the predator-prey encounter rate constant across simulations when prey have no antipredator behavior ($\alpha_P = 0.625$ for both simulations, Eq. 2). Each mode was simulated along a gradient of increasing K ranging from 0.1 to 10.0 (see Appendix D in the supplementary material for r simulations).

We determined equilibrium dynamics by allowing each simulation to run for 70,000 time steps with the last 20,000 time steps examined for stable point equilibria. Each velocity simulation was run with θ set to either 0, 0.69, or 5. These sensitivity values correspond to average prey velocities of 0%, 49.8%, or 99.3% less than γ, when $P = 1$. The coarse grain of θ levels is sufficient for this analysis because as will be shown below, there is no optimal value of θ. Other parameters were set according to Table 1. The values of m_i, s_i, and β_C were chosen to fall within the range of biologically estimated parameters (see McCann and Yodzis 1994 for density-independent mortality; Trussell et al. 2011 for energetic efficiency; and Johnson and Amarasekare 2015 for handling time). However, the parameters within this range were chosen arbitrarily to illustrate the potential dynamics of this system. We chose values of β_P that are near the maximum of handling times observed (Johnson and Amarasekare 2015) but are large enough to induce cyclical dynamics. A small β_P eliminated cyclical dynamics but did not alter the patterns of consumer density (not shown). We chose values of r, D_P, D_C, w, and γ that allowed all species to persist indefinitely in this parameter space when antipredator behavior is absent. We constructed bifurcation plots by plotting the stable equilibria or stable limit cycle range for each K value.

Fine-scale analysis of antipredator sensitivity

Our second analysis used a fine gradient of antipredator sensitivity to examine where the Hopf bifurcation occurs along the gradient of carrying capacity. Again we compared whether these effects differ between sit-and-wait predators ($w = 0.71$, $\gamma = 3.5$) and mobile predators (w = 1.79, γ = 1.75). We estimated model equilibrium along a gradient of K (from 0 to 10) and θ (from 0 to 5) using the multiroot function in the R package rootSolve (Soetaert 2009; Soetaert and Herman 2009; R Core Team 2017), all other parameters were set to Table 1. This function uses the Newton-Raphson method to calculate equilibrium values given the system of equations. After numerically calculating an equilibrium, we then determined if each equilibrium was stable or unstable by calculating the leading eigenvalue of the Jacobian matrix (see Appendix E in the supplementary material) using the eigen function in R. We considered parameter combinations with negative leading eigenvalues (point equilibria) to be stable and all others to be unstable. A large proportion of our eigenvalues had nonzero imaginary parts, but we considered these eigenvalues to be stable as long as the real part of the leading eigenvalue was negative. These criteria mean that both chaotic dynamics and stable limit cycles are considered to be "unstable." By using a fine gradient of θ, we could better determine if there are any nonlinearities where the Hopf bifurcation occurred along the K gradient. We considered increasing values of θ to be stabilizing (destabilizing) by determining whether an increase in θ led to greater (fewer) stable equilibria along the K gradient.

The effect of predator and prey velocity on prey density

Based on the model structure, we expected that without antipredator behavior, both predator and prey velocities would have equal influence on final equilibrium prey densities. Any increase in predator or prey velocity should increase prey mortality and reduce equilibrium prey density. However, by incorporating antipredator behavior, the relative importance of each velocity parameter could be skewed. To determine how predator foraging mode influenced this model, we calculated expected equilibrium values across a fine gradient of predator and prey velocities using the multiroot function.

We varied predator velocities and prey maximum velocities from 0 to 5 for both species and set θ to 0, 0.69, or 5. These parameter values were chosen to examine the full range of effects of antipredator behavior on model dynamics. Other parameters were set according to Table 1. Like in analysis 2, we numerically estimated each equilibrium and determined if they were stable or unstable using the leading eigenvalue of the Jacobian matrix. As above, we considered equilibria to be stable if the leading eigenvalue was negative. Thus, our focus was only on point equilibria rather than stable limit cycles.

Model results

Antipredator behavior influence on community dynamics

For all velocity simulations using either sessile ($w = 0$, not shown) or sit-and-wait predators (e.g., $w = 0.71$, Fig. 1), antipredator sensitivity had strong effects on both community stability and relationship between prey density and resource growth rates. As antipredator sensitivity increased to moderately high levels (Fig. 1b, e, h), stable limit cycles collapsed into stable equilibria over the examined parameter range (e.g., Fig. 1a vs. Fig. 1b). In communities with sit-and-wait predators, a nonzero antipredator sensitivity allowed prey densities to increase with increasing K (compare Fig. 1d with Fig. 1e, f) or r (Appendix D in the supplementary material). Thus, adding antipredator behavior to a sit-and-wait predator community effectively releases prey from top-down control and allows prey to capture increases in resource productivity. In contrast, when there was no antipredator behavior or when the community was dominated by mobile predators, predators were able to capture all of the increases in productivity.

Model simulations with mobile predators exhibited stable limit cycles throughout the analysis, even when antipredator behavior was present (Fig. 2). Fast moving predators alone were sufficient to induce cycles because in these cases, even if prey were moving faster than predators, predator attack rates (and thus predator population growth rates) remain large no matter the behavioral adjustment. Additionally, when predators move faster than consumers ($w > \gamma$), the relationship between resource productivity and consumer density becomes a horizontal line with all increases in productivity (compare Fig. 2d with Fig. 2e, f) captured by the predator, consistent with top-down control.

We attribute the positive effect of K on prey equilibrium density to the relationship between per-predator predation rates and antipredator sensitivity. Because of this model, when we solve for the equilibrium per-predator predation rate (i.e., functional response) in Eq. 5, we find that it is always set to m_P/s_P, giving us

$$\frac{D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}\,C}{\left(1+D_P\sqrt{w^2+\gamma^2 e^{-2\theta P}}\,\beta_P C\right)}=\frac{m_P}{s_P} \tag{6}$$

We can use this equation to solve for consumer density (C) at equilibrium and to determine how consumer density is related to both predator density and antipredator sensitivity:

$$C=\frac{m_P}{D_P(s_P-m_P\beta_P)\sqrt{w^2+\gamma^2 e^{-2\theta P}}} \tag{7}$$

which has an inflection point at

$$P=\frac{\ln\left(\frac{\gamma^2}{2w^2}\right)}{2\theta} \tag{8}$$

From Eq. 6, we find that equilibrium consumer densities will increase if equilibrium predator density (P) or antipredator sensitivity (θ) increases or if predator velocity (w) decreases. Given that larger values of K will lead to larger equilibrium predator densities, the equilibrium consumer density will increase with K only if antipredator sensitivity is nonzero. If predator velocity (w) is less than $\frac{\gamma}{\sqrt{2}}$, then the inflection point occurs at positive values of predator density, which allows consumers to increase with K until predator densities reach the inflection point (e.g., Fig. 3b). However, if $w > \frac{\gamma}{\sqrt{2}}$, then an increase in K will only have marginal effects on consumer densities (Fig. 3d). Figure 3 illustrates how Eq. 6 predicts the results of the two simulations in the bifurcation analysis. Ultimately, when $w > \frac{\gamma}{\sqrt{2}}$, we expect that the community will behave as a mobile predator–dominated community, with strong top-down control and little to no relationship between prey density and carrying capacity (compare Fig. 3a, b with Fig. 3c, d). To emphasize this point, when predator velocity is below the $\frac{\gamma}{\sqrt{2}}$ threshold, consumers can capture a portion of any increase in productivity and the community is partially dominated by bottom-up forcing. This effect disappears once the predator velocity increases above the $\frac{\gamma}{\sqrt{2}}$ threshold.

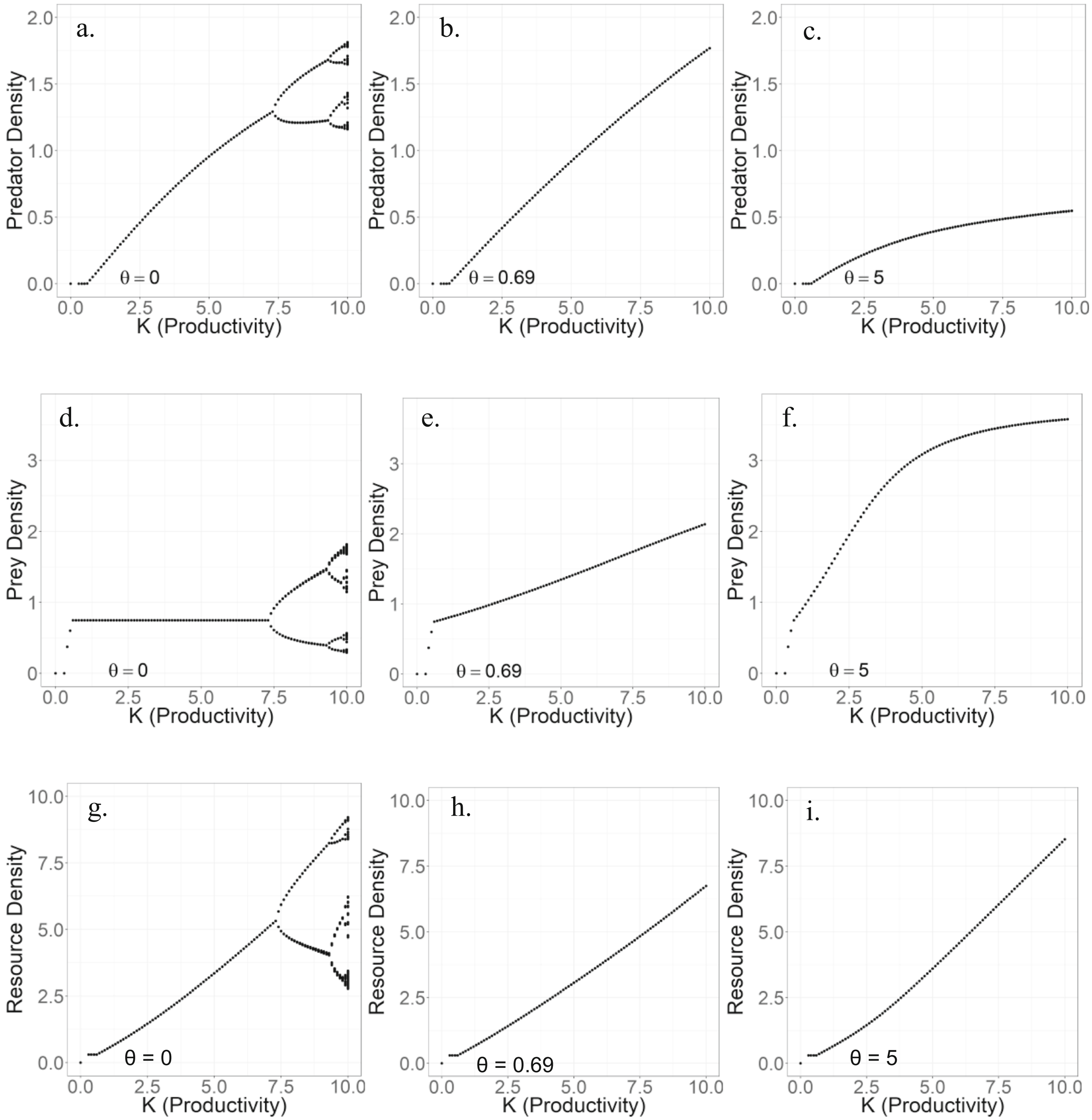

Fig. 1 Bifurcation plots showing equilibria when communities are dominated by sit-and-wait predators ($w = 0.71$, $\gamma = 3.5$), θ is as shown (either 0, 0.69, or 5), and all other variables are set to Table 1. When predator velocity is small, increases in carrying capacity (K) lead to increases in prey density (panels **d**–**f**) when antipredator sensitivity (θ) is nonzero. Predator density (panels **a**–**c**) declines with increasing θ. At moderate θ values ($\theta = 0.69$), predator density remains high, but prey density (panels **d**-**f**) exhibits weakened top-down control (panels **e** and **f**). Resources continually increased with K (panels **g**–**i**), but the rate of increase depended on θ. Small θ led to resource densities that were slightly smaller than the $\theta = 0$ case, while large θ led to densities slightly larger. Overall the effect of θ on resources seemed minor

Unlike changes in consumer density, antipredator sensitivity did not modify the effect of increasing K on predators (P) or resources (R). Generally, allowing prey to respond to predators has a negative effect on predators but a positive effect on resources. However, antipredator sensitivity has a relatively weak effect on resource density. In both the sit-and-wait predator case (Fig. 1g–i) and mobile predator case (Fig. 2g–i), increases in antipredator sensitivity lead to only marginal increases in resources (compare panel g with h and i in Figs. 1 and 2). This may partially be explained by the fact that when antipredator sensitivity is large, consumers have relatively small consumption rates of resources at equilibrium.

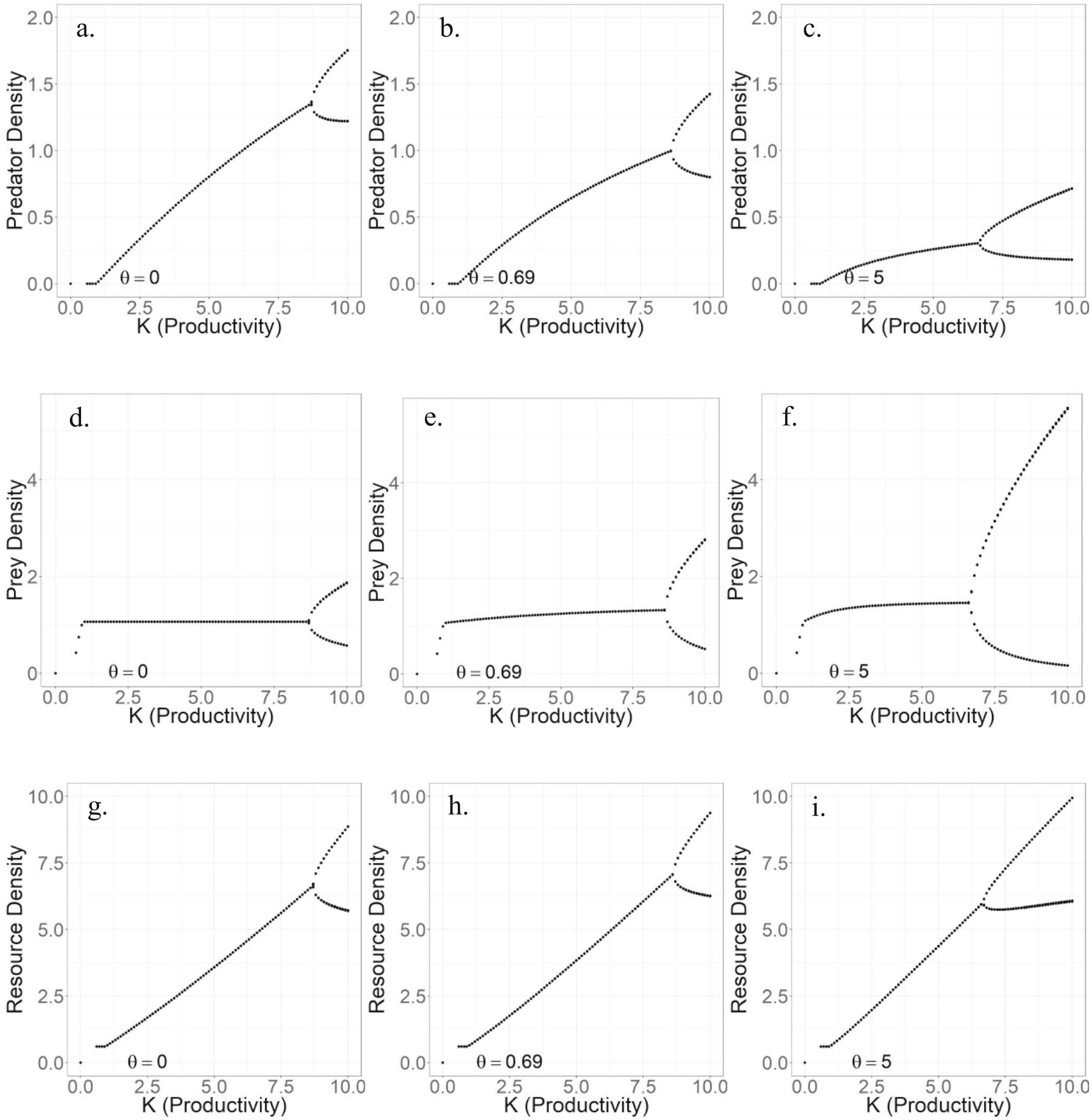

Fig. 2 Bifurcation plots showing equilibria when predators are mobile ($w = 1.79$, $\gamma = 1.75$), θ is as shown (either 0, 0.69, or 5), and all other variables are set to Table 1. Unlike Fig. 1, prey (panels **d**–**f**) exhibit only slight evidence for reduced top-down control. However, even though top-down control is strong, predators (panels **a**–**c**) have the reduced equilibrium densities, indicating that antipredator behavior continues to have a negative effect on predators. As in Fig. 1, resource density (panels **g**–**i**) increased marginally with θ but to a lesser extent than that in the sit-and-wait predator case, again supporting top-down control

Fine-scale analysis of antipredator sensitivity

The location of the Hopf bifurcation along the K and θ gradients depended on predator foraging mode. In the sit-and-wait predator community, increased antipredator behavior rapidly eliminated stable limit cycles in the community and there was no indication of cycles at high sensitivity ($\theta > 3$) values (Fig. 4a). However, in the mobile predator community, the effect of antipredator behavior did not always eliminate cycles (see Fig. 4b). Generally, antipredator behavior caused the Hopf bifurcation to occur at larger K values until a critical sensitivity value was reached ($\theta \approx 0.6$), after which further increases in θ shifted this

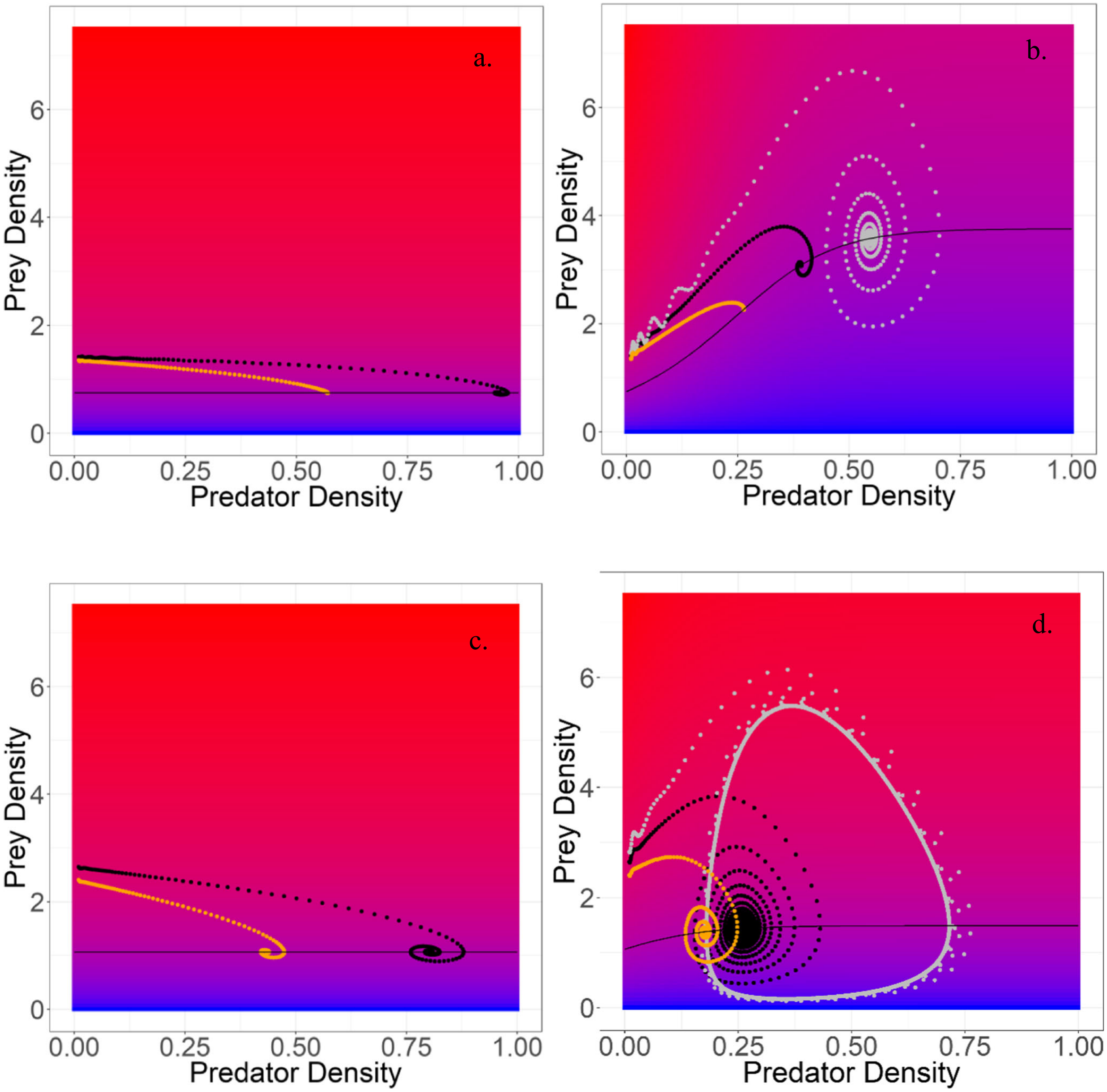

Fig. 3 Per-predator predation rate on the prey as a function of predator and prey density. Panels **a** and **b** represent a relatively slow, sit-and-wait predator ($w = 0.71$, $\gamma = 3.5$), and panels **c** and **d** represent a relatively mobile predator ($w = 1.79$, $\gamma = 1.75$). Panels **a** and **c** are the no behavior case, in which per-predator predation depends only on the static parameters; therefore, Eq. 7 (black line) is horizontal; changes in P (caused by changes in K) lead to no change in C. The orange dots are the trajectory of the model in the predator-prey space when $K = 3$, and the black dots represent the trajectory when $K = 5$. The larger K values shift the final equilibrium to larger predator densities. Panels **b** and **d** contrast this with strong antipredator behavior by setting $\theta = 5$. Equation 7 is now nonlinear and dependent on P as well as the static parameters; thus, C increases when P increases. Here, we have added the extreme value of $K = 10$ (gray dots) to further illustrate how increasing K shifts the final equilibrium along Eq. 7. Panels **a** and **b** show a large nonlinear shift in the Eq. 7 curve (and thus a large increase in prey density) whereas panels **c** and **d** show only a minor shift in the Eq. 7 curve (and thus a minor increase in prey density). In all graphs, warmer colors represent greater per-predator predation rates (left-hand side of Eq. 6). All other parameters besides K are set to Table 1

transition point to smaller and smaller K values. In other words, above the critical sensitivity value, further increases in antipredator sensitivity make the community more likely to exhibit cyclical dynamics. This result was largely explained by the fact that at high sensitivities, very small changes in predator density led to large changes in prey velocity. See Appendix B in the supplementary material for further analysis of this question using the nondimensional version of the model.

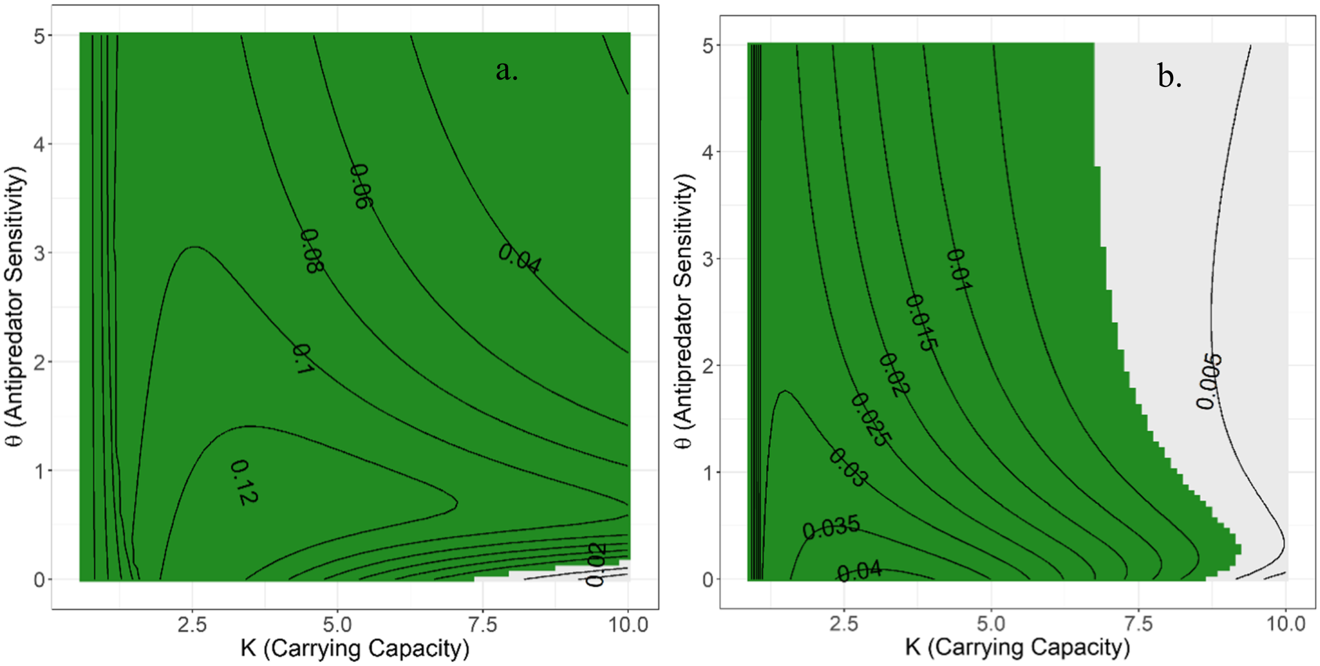

Fig. 4 Regions of stability for **a** sit-and-wait predators ($w = 0.71$, $\gamma = 3.5$) and **b** mobile predators ($w = 1.79$, $\gamma = 1.75$) and all other parameters are set to Table 1. Contour lines are the resilience value of the Jacobian matrix, the absolute value of the maximum real eigenvalue. Green shading indicates where the leading eigenvalue is negative (point equilibria), and gray shading indicates where the leading eigenvalue is positive (stable limit cycles or chaotic fluctuations). The boundary between the green and gray shading represents where the Hopf bifurcation occurs. In the mobile predator case, increasing θ shifts the Hopf bifurcation to large values of K until about $\theta = 0.6$, at which larger values of θ shift the bifurcation point to smaller values of K

The effect of predator and prey velocity on prey density

When $\theta = 0$ (i.e., no antipredator behavior), both predator and prey velocities had equal influence on equilibrium prey density (see Fig. 5a). By increasing antipredator sensitivity, we increase the effect of predator velocity and reduce the effect of prey velocity. When antipredator sensitivity is large (Fig. 5c), the chosen value of prey velocity (γ) becomes unimportant since prey are moving slowly and velocities close to γ rarely occur. Regardless of antipredator sensitivity, the highest prey densities occurred when both prey and predator average velocity was low, when the predator attack rate would be the smallest (the bottom left corner of each panel in Fig. 5). Importantly, nonzero antipredator sensitivities allowed prey densities to remain high through a range of prey velocities (Fig. 5b, c).

As expected from our previous results, cyclicity was also influenced by antipredator sensitivity. After a brief decline at small prey velocities, the relationship between point equilibria and prey velocity shifts from unimodal (Fig. 5a) to monotonic (Fig. 5c) as antipredator sensitivity increases. However, the overall number of stable point equilibria in the parameter space only marginally decreased (compare the area of plotted values in Fig. 5a to Fig. 5c). Interestingly, these responses appear to be directly related to the weakening of the relative influence of prey velocity on prey density noted above.

Discussion

Our analysis is the first to show that a mechanistic change in predator foraging mode can control the effect of antipredator behavior. Recall that in our model, predators induce prey responses by reducing the average movement rate of prey through the environment. Prey reduce their encounter rate with predators (i.e., reduce their mortality), but at the same time prey reduce their foraging (i.e., reduce their growth). Therefore, for a given level of predator density, antipredator behavior has a positive direct effect on prey and an indirect positive effect on resources. In this model, predator foraging mode constrains the benefits of antipredator behavior by limiting how much control prey have on their own mortality rates.

Simulations with sit-and-wait predators had larger equilibrium prey densities (Fig. 1f) and more stable point equilibria (Fig. 1b, e, h), whereas simulations with mobile predators had smaller prey densities (Fig. 2f), more stable limit cycles, and greater likelihood of population cycles (Fig. 2b, e, h). Large antipredator sensitivity (θ) in sit-and-wait predator–dominated communities removed cyclicity from the model (Fig. 1c, f, i) whereas large θ in mobile predator–communities enhanced cyclicity and cycle amplitude (Fig. 2c, f, i).

Our analysis is also the first to link predator-prey cycles to predator foraging mode. The difference in cycles between communities with sit-and-wait predators and communities

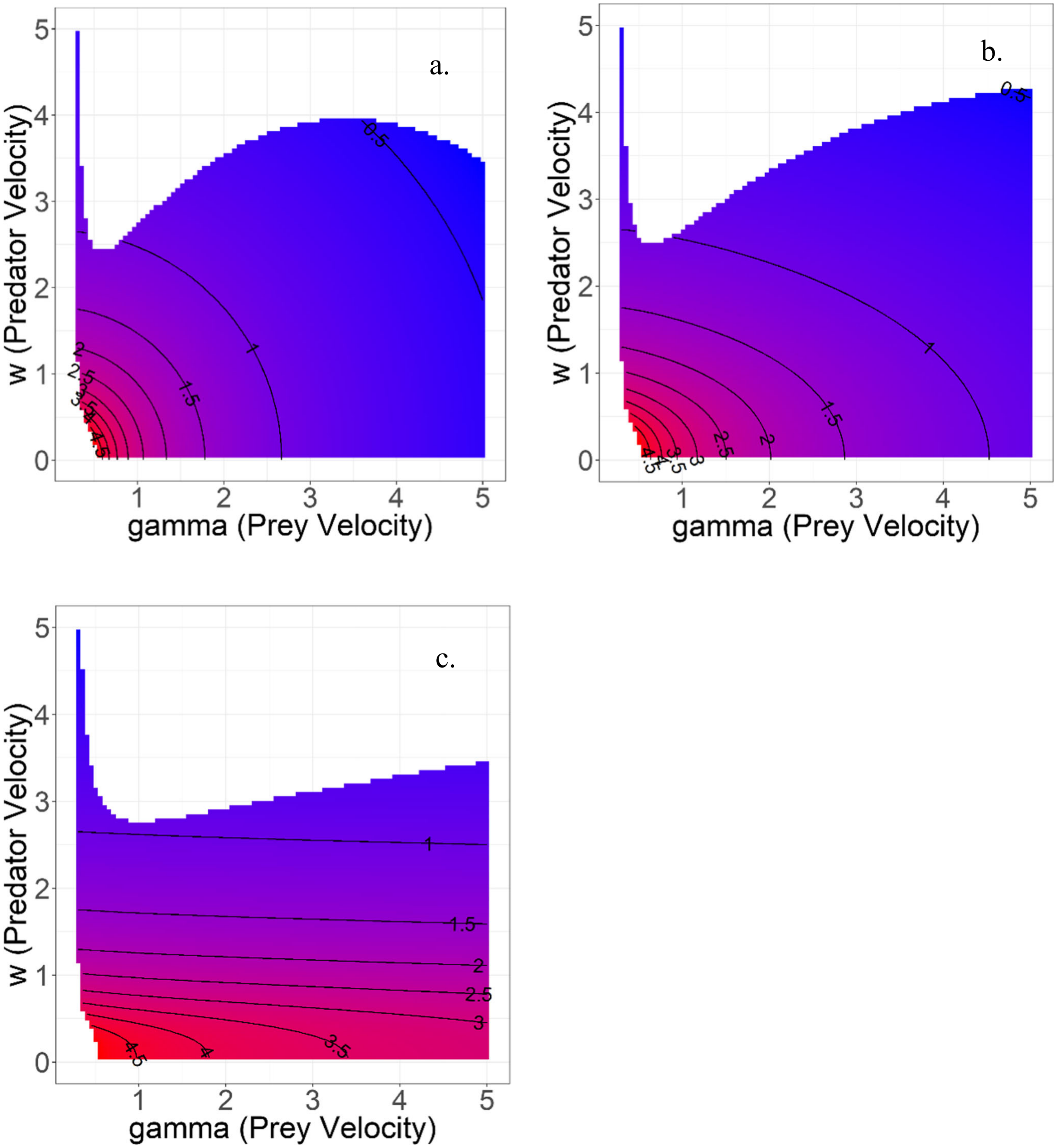

Fig. 5 Equilibrium prey density for stable solutions in the cases where **a** $\theta = 0$, **b** $\theta = 0.69$, and **c** $\theta = 5$. Isoclines are labeled by the prey density unit, and warmer colors indicate higher prey densities. Increases in θ lead to prey density isoclines that are elongated relative to the *x*-axis, thereby increasing the relative importance of *w*

with mobile predators can be explained by the population growth rates of the predators. Given the same prey, mobile predators are more successful at consuming prey, have a higher population growth rate, and are more likely to create cycles. When prey are able to respond to predator density, this lowers the predator population growth rate and can dampen or remove cycles, especially in the case of both sit-and-wait and mobile predators. Essentially, mobile predators can overcome simple changes in prey movement rates if they cover enough ground in their search patterns. A more complex model with an explicit predator avoidance or refuge habitat for prey may result in a greater reduction in cyclicity. Therefore, our model would be most appropriate in replicating communities that occur in habitats with refugia that can be penetrated by predators given enough effort, such as hawks searching for mice in a temperate grassland.

In our simulations, we found that increasing antipredator sensitivity increased cyclicity in communities dominated by mobile predators (Fig. 4b). Previous models have shown that large antipredator response can be destabilizing (Ramos-Jiliberto et al. 2008), but our study indicates that destabilization (cyclicity in our case) is linked to predator foraging behavior. Mobile predators are more likely to cause oscillations because prey are strongly responding to very small changes in predator densities. In the sit-and-wait predator case, any destabilization caused by rapid prey responses is much weaker than the stabilizing force that antipredator behavior induces, increasing θ quickly leads to regions of only point equilibria under the parameter range examined (Fig. 4a). Furthermore, while not shown in our analysis, some of our simulations found that the presence of antipredator behavior can replace chaotic dynamics with stable limit cycles in the sit-and-wait predator case.

Destabilization creates a complication when trying to determine the optimal level of antipredator behavior. Recall that our equilibrium analysis (Eqs. 6 and 7) predicts that increasing θ will increase prey density, although with diminishing returns (e.g., Fig. 3). This analysis alone would indicate that prey should continue to exhibit maximal antipredator behavior until the predator goes extinct. However, the destabilization inherent to the dynamic simulations indicates that there is a limit to the effectiveness of antipredator behavior in mobile predator–dominated communities. Even if the average prey density is increasing with θ, prey become more likely to go extinct because of the high probability of low densities in large-amplitude cycles. Understanding how cyclical dynamics and average prey density interact will be an important aspect for future research into the optimal value of antipredator behavior.

Predator foraging mode and top-down control

One of the more intriguing aspects of this model is that increases in productivity (K or r) lead to changes in prey population density when prey respond to sit-and-wait predators. Previous analyses indicate that when antipredator behavior is strong, increases in prey defenses reduce per capita predation rates and increase total prey biomass (Vos et al. 2004), a similar effect occurs here (Fig. 3). Under sit-and-wait predator–dominated communities, increases in antipredator sensitivity allow prey populations to grow in a bottom-up-structured manner because predators become self-inhibiting. When θ is nonzero, increases in prey density are no longer perfectly captured by the predator because the per-predator predation rate declines with predator density. Thus, in order to maintain a constant per-predator predation rate (i.e., at equilibrium), increases in predator density require increases in prey density.

Although this model behavior has been seen in models of inducible defenses (Vos et al. 2004), it is seen in classical Rosenzweig-MacArthur models. The basic structure of the Rosenzweig-MacArthur model implies that communities are organized from the top-down, with a distinct pattern in biomass as productivity increases (Oksanen et al. 1981). Alternatively, communities could instead be regulated by bottom-up processes in which increases in productivity increase the density of all trophic levels (Polis and Strong 1996). Constitutive plant defenses are considered a potential driver of bottom-up regulation (Polis and Strong 1996), which partially explains why antipredator responses could also induce these dynamics. However, until now, there has been no indication that top-down control is more likely in mobile predator–dominated communities than in sit-and-wait predator–dominated communities. Therefore, our results show that foraging mode may be closely linked to classical trophic cascades (sensu Strong 1992).

Implications for invasive species

Changes in antipredator behavior can be induced via introduction of invasive species. Introduced predators can be more dangerous than native predators if they do not elicit proper antipredator responses in their prey (Cox and Lima 2006; Sih et al. 2010). Depending on the resident predator community, introduced predators could be completely novel to the environment (Fritts and Rodda 1998) or could be an addition to a mixed community of native and previously established introduced predators (Grosholz et al. 2000; Blumstein 2006; Ferrari et al. 2015). These alternative communities combined with the potential loss of naiveté over time (Carthey and Banks 2016) create a gradient of prey responses from complete naiveté to effective invasive predator recognition (Carthey and Blumstein 2018). Therefore, the degree of antipredator behavioral expression can be directly influenced by the degree of prey naiveté within a community.

This model provides an alternative mechanism behind the often anecdotal observation of invasive species booms and busts (Simberloff 2013). As seen in Sih et al. (2010), newly introduced invasive species may not be recognized by their prey or may not recognize their own predators. Previous theories behind boom-bust dynamics state that invasive species booms could be caused by predators not identifying the invader, thus allowing the invader to reach high densities, and that subsequent busts would be caused by predators switching to prefer the invader, thereby reducing invader density (Sih et al. 2010).

In our model, an invasive species could either be the predator or the prey. If we consider a naïve invasive prey with small antipredator sensitivity, then our model indicates this population would be more susceptible to oscillations because the population is unable to effectively respond to changes in predator density. This implies that boom-bust dynamics in invasive species need not be limited to one boom and one bust, but that as long as invaders lack effective antipredator response, oscillations in an introduced prey population could occur. Our model also predicts that these oscillatory dynamics would be more likely with active predators and at higher resource levels. An invasive predator would have much the same effect on native prey provided that native prey remain naïve and are unable to effectively alter their behavior.

Predator life history as an explanation for cyclical dynamics

There are many classic examples of cycles in predator-prey systems (e.g., Elton and Nicholson 1942; McLaren and Peterson 1994). Typically, these cycles exist when specialist predators that focus on only a few prey species exhibit delayed density dependence (Hastings 1997; Barraquand et al. 2017). Our model adds an important insight into this interaction such that specialist predators become a necessary, but not sufficient, prerequisite for population cycles. The predators in our model only have one prey; thus, they are always a specialist predator. However, in our case, when prey exhibit antipredator behavior, a specialist predator must also be highly mobile in order to see cyclical behavior.

Cyclical behavior is unlikely in sit-and-wait predator–dominated communities because these predators rely on prey movement to maintain high encounter rates. The prey responses to sit-and-wait predators create a negative feedback loop that dampens rates of predator increase and prevents predator densities from overshooting the equilibrium. Our theoretical results parallel empirical results in which cues produced by sit-and-wait predators are more reliable and more likely to induce antipredator behavior than the cues produced by mobile predators (Schmitz 2008; Reynolds and Bruno 2013). In light of our results, we hypothesize that sit-and-wait predators induce greater antipredator behavior and that the antipredator behavior they elicit is more likely to lead to a stable community.

A brief survey of the literature on population cycles supports our hypothesis. Many of the most well-known population cycles occur in populations at northern latitudes with mobile predators. The vole cycles (*Microtus* sp.) of northern Fennoscandia are thought to occur from an increase in specialist predators relative to southern populations (Klemola et al. 2002), such as the highly mobile least weasel (*Mustela nivalis*; Oksanen and Henttonen 1996). Similar cycles in the lepidopteran moth (*Epirrita autumnata*) are thought to occur from highly mobile parasitoid wasps in northern Fennoscandia (Ruohomäki et al. 2000; Klemola et al. 2002). Conversely, we found relatively few long-term studies of sit-and-wait predators (but see Packer et al. 2005) and none with predator-prey cycling. Furthermore, the analyses of the Global Population Dynamics Database found very few cyclical sit-and-wait predator populations (Kendall et al. 1998; Louca and Doebeli 2015).

It is important to note that while sit-and-wait predators may be less likely to undergo population cycles, cycles could still occur. For example, a long-term study of an African lion (*Panthera leo*) population, a known ambush predator, shows no evidence of intrinsic predator-prey cycles between lions and their ungulate prey. Though cyclical behavior does exist, it is caused by large changes to the Serengeti ecology rather than predator-prey cycles (Packer et al. 2005). It is possible that more long-term studies of sit-and-wait predators may find more evidence for cyclicity. However, our model suggests that the population cycles that sit-and-wait predator–dominated communities exhibit are more likely to be caused by environmental factors.

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