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ARTICLE

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Social learning in predators: Indirect effects let novel prey exclude familiar prey

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Abstract

Predation is a fundamental ecological process. Social learning by predators is ubiquitous. However, social learning is not incorporated into most ecological theories of predator–prey dynamics. We report how social learning changes results of classic one-predator, two-prey models. In our study, one prey (familiar) can be innately exploited by any predator. The other prey (novel) can only be exploited by predators that have learned how to consume it (i.e., informed predators). Social learning converts naïve predators into informed predators via mass action. This governs exploitation of the novel prey. Indirect effects such as apparent competition then emerge among familiar and novel prey. We find that the novel prey is a superior apparent competitor to the familiar prey because it has a refuge from naïve predators. Faster social learning helps the familiar prey coexist because it erodes this refuge. Other outcomes, such as apparent mutualism and apparent predation, occur when the system exhibits limit cycles. Social learning tends to dampen cycling relative to classic models of apparent competition, but can also exaggerate indirect effects. Our theory is applicable to biological invasions, where it predicts that social learning may determine the persistence of invaders and native species.

KEYWORDS

apparent competition, dynamical systems, indirect effects, information refuge, population cycles, social learning

INTRODUCTION

Social learning allows an animal to alter its phenotype by observing the behaviors of other individuals. Well-developed theories show how socially acquired behaviors spread through animal populations (Cavalli-Sforza & Feldman, 1981; Firth, 2019) and animals evolve to use social information (Aoki & Feldman, 2014; Borofsky & Feldman, 2022a, 2022b; Whitehead et al., 2019). Social learning is also predicted to influence ecological dynamics such as population growth and species coexistence (Cantor et al., 2021; Griffin, 2004; Kikuchi & Simon, 2023; Thorogood et al., 2018; Wooster et al., 2024). For example, the accumulation of cultural technology can change a population's carrying capacity (Lehmann & Feldman, 2009), and social learning may have allowed

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modern humans to outcompete Neanderthals (Gilpin et al., 2016; Wakano et al., 2018). Yet, our understanding of social learning remains unincorporated into most general models of ecological communities (Hämäläinen et al., 2022). Here, we develop theory for how social learning changes a simple food web where a single predator population may consume up to two species of prey. In this simple network, indirect effects can emerge. Indirect effects occur when one population influences another without directly interacting with it, but rather through interactions with other, interconnected populations (McPeek, 2022). Indirect effects are a fundamental process that structure ecological communities. It is critical to understand how realistic aspects of behavior, such as social learning, change indirect effects where prey affect one another via a shared predator.

We consider a predator species where individuals can learn from each other to consume a novel species of prey. Learning to consume new food is one of the most common types of socially transmitted information (e.g., Aplin et al., 2015; Katz & Lachlan, 2003). It has let black rats colonize Israeli pine forests by learning to feed on pine nuts (Aisner & Terkel, 1992) and may let Australian predators consume invasive cane toads (Donato & Potts, 2004; Franklin, 2005). How should we expect the spread of information among predators to affect their populations and those of their prey? A reasonable hypothesis is that novel prey might experience a population decrease when the predator begins to consume them. We can assume that predators already consume a familiar prey species because they have to eat something. If predator populations increase because novel prey provide a supplemental resource, populations of familiar prey could suffer in the long term due to elevated predation pressure. In this scenario, the two-prey species would be said to experience an indirect effect called *apparent competition* because they both feed a common enemy that negatively affects both populations (Holt, 1977; Holt & Lawton, 1994). Social learning could change the predictions of classic apparent competition models, however, because it can change patterns of food web connectivity. In most community ecology models, links in food webs are assumed to exist or not (but see, e.g., Valdovinos et al., 2016). If predators must learn from each other to exploit a novel prey, then that link in the food web will depend on social learning. Social learning acts like a switch that toggles the link from "on" to "off" and everything in between, leading to dynamics unanticipated by classic theory.

Here we analyze how social learning affects population dynamics when predators must learn about one of two possible prey species. We compare our results to those from prior apparent competition studies. Potential applications include making predictions about how native predators respond to invasive species, how invading predators incorporate new species into their diets, and how social learning impacts predator–prey dynamics in natural communities.

METHODS

We assume two species of prey, one familiar and one novel to a predator species. A biological interpretation of familiar prey is that the predator has evolved to recognize and capture them, whereas novel prey cannot be captured unless a predator learns how to do so. Prey population growth rates are given by a function $R_i(N_i)$ $(i = 1, 2)$, where N_1 and N_2 are the density of familiar and novel prey, respectively. We assume the predator species can be divided into two groups: naïve and informed. Naïve predators (P_1) can only consume familiar prey. All predators are born naïve regardless of whether their parents are naïve or informed. Once a naïve predator learns to attack novel prey, it becomes an informed predator that can attack both familiar and novel prey (P_2). Predators can only attack novel prey by learning from an informed predator or through individual discovery. The attack rate on each prey i by each class of predator j is given by a_i. The function that governs the predator's consumption rate is $E(N_i)$. In addition, sometimes we assume that predators take time h_i to handle prey i. Predators convert prey into new, naïve predators at rate b_i. Because predators are born naïve, all reproduction from P_1 and P_2 contributes to P_1.

The primary way for a naïve predator to become an informed predator is via social learning. We assume there is no age or family structure in the predator population and therefore do not distinguish vertical (parent-offspring), horizontal (within-age class), or oblique (juvenile-unrelated adult) information transmission (Cavalli-Sforza & Feldman, 1981). Instead, we assume the law of mass action governs the rate of social learning. This approach represents disease transmission in many epidemiological models (SIR-type models; Cavalli-Sforza & Feldman, 1981, Edelstein-Keshet, 2005). Arguments could be made for frequency-dependent transmission if predators strongly associate with each other (e.g., Denton et al., 2020). Thus, the choice of mass action in our model may be most appropriate for predators with fluid social associations. Under mass action, when a naïve and informed predator randomly encounter each other, there is some probability that the naïve predator becomes informed. A well-known result from epidemiology is that mass action infection rates depend on the availability of uninfected individuals (Edelstein-Keshet, 2005).

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Given that naïve predators have not yet been "infected" with information, social learning depends on P_1, and the rate at which P_1 individuals learn, s. Further, we assume social learning requires that a naïve predator observes an informed predator consume a novel prey. Social learning therefore also depends on the rate at which predators encounter and consume novel prey, $a_2N_2P_2E(N_i)$.

An alternative to social learning is individual discovery (i.e., innovation) (Perry et al., 2021). Often, innovation is defined as discovering how to exploit a new resource, or a new way to exploit a familiar resource (Greenberg, 2003; Reader & Laland, 2003). We focus on the former, describing individual discovery of the novel prey by naïve predators with the function $D(P_1)$. Predators transition from P_1 to P_2 through both social learning and discovery. Individuals are removed from P_1 and P_2 by mortality, given by the function $M(P_i)$. This leads to the following general equations:

$$\frac{dN_1}{dt} = N_1[R(N_1) - a_1P_1E(N_1) - a_1P_2E(N_1, N_2)]$$

$$\frac{dN_2}{dt} = N_2[R(N_2) - a_2P_2E(N_1, N_2)]$$

$$\begin{aligned}\frac{dP_1}{dt} = {} & a_1b_1N_1P_1E(N_1) + a_1b_1N_1P_2E(N_1, N_2) \\ & + a_2b_2N_2P_2E(N_1, N_2) - sa_2N_2P_1P_2E(N_1, N_2) \\ & - P_1D(P_1) - P_1M(P_1)\end{aligned}$$

$$\frac{dP_2}{dt} = sa_2N_2P_1P_2E(N_1, N_2) + P_1D(P_1) - P_2M(P_2) \quad (1)$$

We analyze alternative forms of functions R and E for pragmatism and realism. We also switch independent discovery, $D(P_1)$, on and off. In all models, we assume that predators die at a constant per capita rate so that $M(P_i) = mP_i$.

The social Lotka-Volterra system

For an initial, analytical characterization of the model, we assume that prey grow exponentially in the absence of predation. The intrinsic per capita growth rates for prey are given by r_i such that $R(N_i) = r_i$. We also assume that predator attack rate scales linearly with prey abundance, that is, predation follows a Type I functional response where $E(N_i) = 1$ and the total rate of consumption for predator j upon prey i is $a_iP_jN_i$. These assumptions comprise the Lotka-Volterra predator–prey model for a single species of predator and single species of prey.

Likewise, we assume exponential prey growth, a Type I functional response, and no innovation such that $R(N_i) = r_i$, $E(N_i) = 1$, and $D(P_1) = 0$ in (1).

$$\frac{dN_1}{dt} = N_1[r_1 - a_1P_1 - a_1P_2]$$

$$\frac{dN_2}{dt} = N_2[r_2 - a_2P_2]$$

$$\frac{dP_1}{dt} = a_1b_1N_1(P_1 + P_2) + a_2b_2N_2P_2 - sa_2N_2P_1P_2 - mP_1$$

$$\frac{dP_2}{dt} = sa_2N_2P_1P_2 - mP_2 \quad (2)$$

We call this the "social" Lotka-Volterra system.

Equilibria and positivity conditions

Equation (2) has two nontrivial equilibria. At one, all prey and predator types coexist (equilibria indicated by asterisks):

$$\begin{aligned}N_1^* &= \left(\frac{m}{a_1b_1}\right) \cdot \{1 - a_1^2b_2r_2/[sr_1(r_1a_2 - r_2a_1)]\} \\ &= \frac{m}{a_1b_1} - N_2^*(b_2r_2/b_1r_1) \\ &= \frac{m}{a_1b_1}\left[1 - \frac{P_2^*}{P_1^* + P_2^*}N_2^*\left(\frac{a_2b_2}{m}\right)\right] \quad (3)\end{aligned}$$

$$N_2^* = a_1m/[s(r_1a_2 - r_2a_1)] \quad (4)$$

$$P_1^* = r_1/a_1 - r_2/a_2 = r_1/a_1 - P_2^* \quad (5)$$

and

$$P_2^* = r_2/a_2 \quad (6)$$

Notice that $P_1^* + P_2^* = r_1/a_1$. This is equal to predator density in the classic Lotka-Volterra model without social learning. Thus, there is no change in total predator density despite the predator incorporating novel prey into its diet. In contrast, the familiar prey equilibrium density drops from $N_1^* = \frac{m}{a_1b_1}$ to $N_1^* = \frac{m}{a_1b_1}\left[1 - \frac{P_2^*}{P_1^* + P_2^*}N_2^*\left(\frac{a_2b_2}{m}\right)\right]$ with social learning. Thus, (3) indicates apparent competition acting on the familiar prey. Additionally, positivity of (4) and (5) require that $r_1/a_1 > r_2/a_2$, so the familiar prey must be superior to the novel prey in per capita growth reper capita attacks experienced (we do not say "superior competitor" because they do not share a carrying capacity

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or resource). This is reminiscent of coexistence requirements in the classic apparent competition system, which depend on the ratio of growth:attack (Holt, 1977).

From (3), the positivity condition for N_1^* depends not only upon superiority of familiar prey, but also on the rate of social learning exceeding a threshold, where

$$s > a_1^2 b_2 r_2 / [r_1 (r_1 a_2 - r_2 a_1)] \quad (7)$$

Increasing the rate at which naïve predators become informed predators actually lets the familiar prey coexist with the novel prey. This is odd; social learning is the process that creates apparent competition in the first place – without it, novel prey would exert no influence at all on familiar prey. Yet, instead of fomenting apparent competition that drives familiar prey extinct, *fast* social learning erodes the advantage enjoyed by novel prey. We see this in the negative influence that s has on N_2^* in (4).

Only at low s does apparent competition from novel prey drive familiar prey extinct. Indeed, the only other biologically interesting equilibrium is one where N_1 is extinct: $N_1^* = 0$, $N_2^* = \frac{m}{2a_2 b_2}\left[1 + \left(1 + \frac{4a_2 b_2}{s r_2}\right)^{\frac{1}{2}}\right]$, $P_1^* = \frac{1}{2a_2}\left[\left(r_2^2 + \frac{4a_2 b_2 r_2}{s}\right)^{\frac{1}{2}} - r_2\right]$, and $P_2^* = r_2/a_2$. The invasion criterion for N_1 (i.e., $0 < r_1 - a_1(P_1 + P_2)$) at this equilibrium is identical to its condition for positivity at the coexistence equilibrium. Substituting P_1^* and P_2^* from the N_1-extinct equilibrium into the equation for $\frac{dN_1}{dt}$ from (3) and rearranging reveals the positivity and invasion conditions to be equal. Therefore, if the coexistence equilibrium exists, N_1 can invade a community where only N_2 is present. This is very similar to a result from fundamental apparent competition theory in which positivity conditions and invasion criteria for a prey are coincident (see Holt, 1977, pp. 205–206).

Stability

Neither biologically interesting equilibrium yields characteristic equations with analytically tractable eigenvalues. However, applying the Routh-Hurwitz criteria shows the coexistence equilibrium to be unstable to perturbation (Edelstein-Keshet, 2005; Otto & Day, 2007). The Routh-Hurwitz criteria are analytically intractable for the equilibrium without N_1. Numerical analyses of both equilibria suggest extinction after perturbation.

In sum, when prey grow exponentially and predators have a linear functional response, a feasible coexistence equilibrium exists but is unstable. Coexistence occurs when the familiar prey is superior to the novel prey, and social learning is fast.

The social Rosenzweig-MacArthur system

More realistic models feature self-limiting prey. We represent this with logistic growth. At low density, prey per capita growth is approximately r_i, but slows to zero as the prey population approaches its carrying capacity K_i. To increase realism of the predators, we assume their per capita foraging rate is limited by a saturating (Type II) functional response (Rosenzweig & MacArthur, 1963). This type of response includes a handling time. As prey abundance increases, the proportion of time that each predator spends handling prey also increases such that $E(N_i) = \frac{1}{1 + \sum_{i=1}^{n} a_i h_i N_i}$. The total rate of attack on prey i by predator j is $\frac{a_i N_i P_j}{1 + \sum_{i=1}^{n} a_i h_i N_i}$. These assumptions form the basis for several models of apparent competition (e.g., Abrams et al., 1998; Abrams & Holt, 2002; Křivan & Eisner, 2006).

We assume that an informed predator must successfully handle a novel prey for a naïve predator to learn socially. When predators have a Type I functional response, the rate of social learning is the three-way interaction $sa_2 N_2 P_1 P_2$, but with a Type II functional response, the rate of social learning is $\frac{sa_2 N_2 P_1 P_2}{1 + \sum_{i=1}^{n} a_i h_i N_i}$. Thus, when predators have a Type II functional response, all four populations influence the rate of social learning.

We primarily focus on systems where all learning is social (i.e., $D(P_1) = 0$). However, we can relax that assumption such that individual discovery is slow relative to social learning, that is, $D(P_1) = dP_1$, where d is a small, nonzero number. This evaluates the sensitivity of results to innovation. It also agrees with results from wild populations showing rapid social learning relative to innovation (Farine et al., 2015).

For analysis, we make the appropriate substitutions into $R(N_i)$ and $E(N_i)$ in (1). Then, we rescale the equations (see Appendix S1 for details):

$$\frac{dN_1'}{dt'} = N_1'\left[(1 - N_1') - \frac{P_1'}{1 + \beta_1 N_1'} - \frac{P_2'}{1 + \beta_1 N_1' + \beta_2 N_2'}\right]$$

$$\frac{dN_2'}{dt'} = N_2'\left[\gamma(1 - N_2') - \frac{\alpha P_2'}{1 + \beta_1 N_1' + \beta_2 N_2'}\right]$$

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$$\frac{dP'_1}{dt'} = \frac{\omega_1 P'_1 N'_1}{1+\beta_1 N'_1} + \frac{\omega_1 P'_2 N'_1 + \omega_2 P'_2 N'_2}{1+\beta_1 N'_1 + \beta_2 N'_2} - \frac{\varphi P'_1 P'_2 N'_2}{1+\beta_1 N'_1 + \beta_2 N'_2} - \delta P'_1 - \mu P'_1$$

$$\frac{dP'_2}{dt'} = \frac{\varphi P'_1 P'_2 N'_2}{1+\beta_1 N'_1 + \beta_2 N'_2} + \delta P'_1 - \mu P'_2 \quad (8)$$

We call this the social Rosenzweig-MacArthur system. We ask whether coexistence requires that novel prey be superior to familiar prey, or that social learning exceed a certain rate. In addition, we ask how apparent competition impacts population dynamics. Do populations gravitate towards an equilibrium density, oscillate around an equilibrium in limit cycles (fluctuations that repeat in period and amplitude), or exhibit other behaviors? How much does one species impact the other?

We address these questions using numerical integration – specifically, bifurcation analyses, where one parameter is varied while others are held constant to determine the behavior of the system (Otto & Day, 2007). We focus our analysis on the social learning rate φ and the predator death rate μ. Social learning lets informed predators access a resource subsidy (the novel prey), while predator death removes informed predators from the population. Together, these parameters help determine the degree of apparent competition between prey, whether the population cycles or remains at a point equilibrium, and the intensity and synchrony of cycling.

When populations exhibit limit cycles, it can be more useful to measure population densities averaged over time than equilibrium densities (Abrams, 2009; Abrams et al., 1998). Time-averaged densities may be lower or higher than equilibrium densities depending on whether populations spend most of their time near their minimum density or their maximum density (due to Jensen's inequality; see Abrams et al., 1998). Thus, we focus analysis on time-averaged population densities rather than equilibrium densities. Note that when populations are at point equilibria, the two coincide.

We performed bifurcation analyses across combinations of φ and μ. We performed these bifurcation analyses at three combinations of prey parameters to test the effects of prey species superiority: (1) novel prey have slower growth and suffer higher attacks than familiar prey ($\gamma < 1$; $\alpha > 1$), (2) the prey are identical ($\gamma = 1$; $\alpha = 1$), and (3) novel prey grow faster and are attacked less than familiar prey ($\gamma > 1$; $\alpha < 1$). We explored values of μ up to the maximum that allow predators to persist in the original one-predator, one-prey Rosenzweig-MacArthur model. Values of φ ranged from 0 to 1. For each parameter combination, we started the system (N'_1, N'_2, P'_1, and P'_2) at equilibrium densities from Rosenzweig and MacArthur's original model. We obtain the same results when half the equilibrium population densities are used. During numerical integration, we used the following criteria to classify point equilibria and limit cycles. We initially integrated over 2000 time steps, discarding the first 1000. If a population remained within a range of 1e-5 for 1000 time steps, we considered it to be at a point equilibrium. If it did not, we tested for periodicity by finding local maxima in P'_1 and P'_2 that repeated at regular intervals. Predator populations have no upper bound, which made it easier to identify variability among maxima. Once a cycle period was identified, we calculated the maximum, minimum, difference between maximum and minimum, and time-averaged mean, across the last five cycles. These all needed to fall within 1e-5 across the five cycles (except the difference between maxima and minima, which needed to exceed 1e-5). If a point equilibrium or a limit cycle was not reached, we extended the integration time until one was. In all cases tested, point equilibria or limit cycles were the only outcomes. When a population near zero met the criteria for point equilibria, we considered it extinct if its maximum density over the last 1000 time steps did not exceed 1e-5. This criterion admitted some biologically unrealistic population cycles but was reasonable for describing qualitative behavior of the system.

We repeated bifurcation analyses to analyze sensitivity to starting conditions and individual discovery of innovations. We also performed removal experiments by setting the abundance of either prey equal to zero. In the sensitivity analyses and removal experiments, we assumed the prey were identical except in which predators could attack them.

To explore sensitivity to starting conditions, we tested the ability of N'_1, N'_2, and P'_2 to invade from rarity by setting their abundance to 1e-4 one at a time and repeating the bifurcation analysis. We did not do this for P'_1, because it would be immediately repopulated by P'_2. Separately, we examined the effect of a low rate of individual innovation discovery with $\delta = 1e\text{-}4$, as $\delta = 0$ for most of the results.

The removal experiments were done to determine the intensity of apparent competition (or apparent mutualism or apparent predation). In apparent mutualism, both species benefit from each other's populations, while in apparent predation, one species benefits and the other suffers (Abrams et al., 1998; Holt, 1977). For the removal experiments, we followed methods from Abrams et al. (1998). Abrams et al. (1998) measured indirect effects in a one-predator, two-prey system with self-limiting prey and predator with a Type II functional response. They measured the time-averaged population density of one prey after removing the other. Using the same sets of

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parameters that Abrams et al. (1998) used, we set either N_1' or N_2' equal to 0 and compared the results of bifurcation analyses with those obtained when all populations started at their Rosenzweig-MacArthur equilibria. We also measured the effect of social learning on apparent competition per se by contrasting the present model with one without social learning, that is, the model of Abrams et al. (1998) in which the predator always forages on both prey if available.

RESULTS

Coexistence and stability

Bifurcation analyses of the social Rosenzweig-MacArthur model revealed that the system exhibits three main regions of coexistence. In one (green colors in Figure 1) the familiar prey is extinct. In another (violet and purple colors in Figure 1), social learning cannot take hold so informed predators are extinct. In the blue areas of Figure 1, both prey coexist with naïve and informed predators. Stable point equilibria exist, but there are many areas dominated by persistent limit cycles (Figure 1). In contrast to the social Lotka-Volterra system, when prey are equal, and even when novel prey are superior, familiar prey are not necessarily excluded. However, when novel prey are superior, familiar prey were driven extinct over greater proportions of the φ and μ values we explored (compare the three panels in Figure 1).

The rate of social learning plays a similar role in this system as in the social Lotka-Volterra system. High social learning rates promote coexistence by reducing the advantage that novel prey enjoy (right end of arrow in Figure 1B). However, social learning at low rates can cause the familiar prey to be driven extinct because they permit apparent competition in the first place (green and light green in Figure 1). Interestingly, for some levels of predator mortality, prey coexist at very low rates of social learning (left end of arrow in Figure 1B). At those very low rates of social learning, trophic connectivity via informed predators is small, so apparent competition is weak and familiar prey are not overexploited. As the social learning rate increases, familiar prey become extinct, but are able to coexist again at the highest social learning rates. Within regions of coexistence, increasing the social learning rate tends to shift stable point equilibria to limit cycles.

Predator mortality also has a strong influence on the system. Increasing predator mortality tends to decrease the propensity for the system to cycle when social learning occurs and prey coexist. It also tends to promote prey coexistence. From (8), we can see that the ability of informed predators to persist in the population is governed by an inverse relationship between the rates of social learning φ and predator mortality μ. This is evident in the concave shape of the pink and purple regions of Figure 1. This shape limits the region where apparent competition can arise, and hence the left border of the region where N_1' is extinct.

Evaluating conditions for the invasion of social learning emphasizes the importance of μ and φ, and an easily overlooked role of consumption rate. The informed predator can invade if the novel prey and naïve predator populations have sufficiently high abundance relative to the ratio of predator mortality to social learning, such that

$$\frac{\mu}{\varphi} < P_1'^{*} N_2'^{*} E\left(N_1'^{*}, N_2'^{*}\right) \tag{9}$$

Thus, invasion requires low predator mortality or fast social learning. Satisfying (9) also requires fast consumption rates (low handling time) because social learning only happens when an informed predator successfully *completes* handling a novel prey (Appendix S2). We also

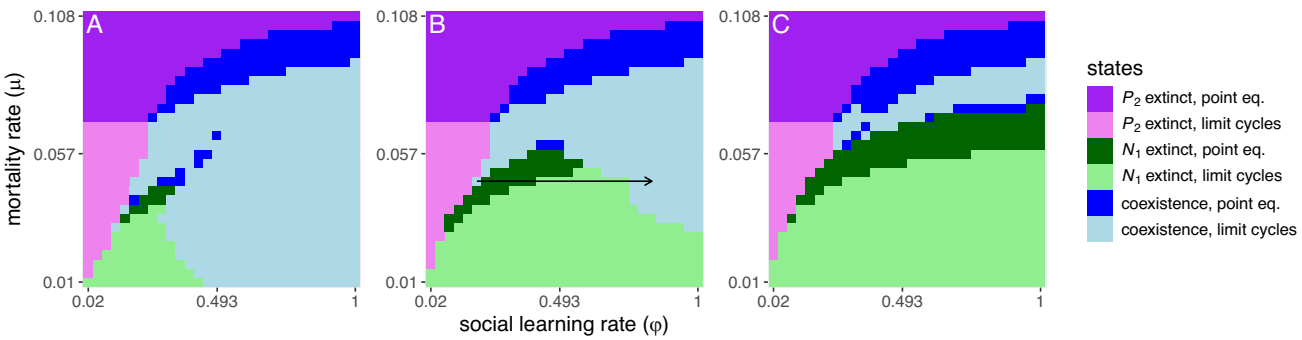

FIGURE 1 Bifurcation analyses in μ and φ. From left to right, novel prey shift from inferior to superior versus familiar prey. (A) Novel prey suffer higher attacks ($\alpha = 1.2$) and have slower growth ($\gamma = 0.8$) than familiar prey, (B) prey are identical; $\alpha = 1$, $\gamma = 1$, (C) novel prey suffer fewer attacks ($\alpha = 0.8$) and grow more quickly ($\gamma = 1.2$). In all panels, $0.01 \le \mu \le 0.1075$ and $0.02 \le \varphi \le 1$, and $\beta_i = 2.7$, $\omega_i = 0.4$, $\delta = 0$. The arrow in B depicts changes in the system due to increasing φ while holding μ constant (see text).

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find that for some ranges of predator mortality, increases in mortality can create a hydra effect that actually increases predator populations. Finally, in the social Rosenzweig-MacArthur system, social learning increases total predator abundance relative to a system without social learning (Appendix S2).

The system is somewhat sensitive to starting conditions (Appendix S3: Figure S1). On the borders between regions where different sets of populations coexist in Figure 1, system behavior can change depending on whether a particular population is initialized near the original Rosenzweig-MacArthur equilibrium. Most alternative states have to do with persistence of familiar prey. Familiar prey is often excluded when we set its abundance to 1e-4. Its ability to coexist but not invade is indirect evidence for an Allee effect. Informed predators can also suffer from an Allee effect (Appendix S3: Figure S1).

A low ongoing rate of innovation has little influence on the results, although it can maintain informed predators at a rate just above the extinction threshold (Appendix S3: Figure S2).

Removal experiments: Apparent competition and apparent predation

The familiar prey always suffers from the presence of the novel prey as long as informed predators can persist in the community (Figure 2A–C). When the novel prey is removed, familiar prey can exist in the community where

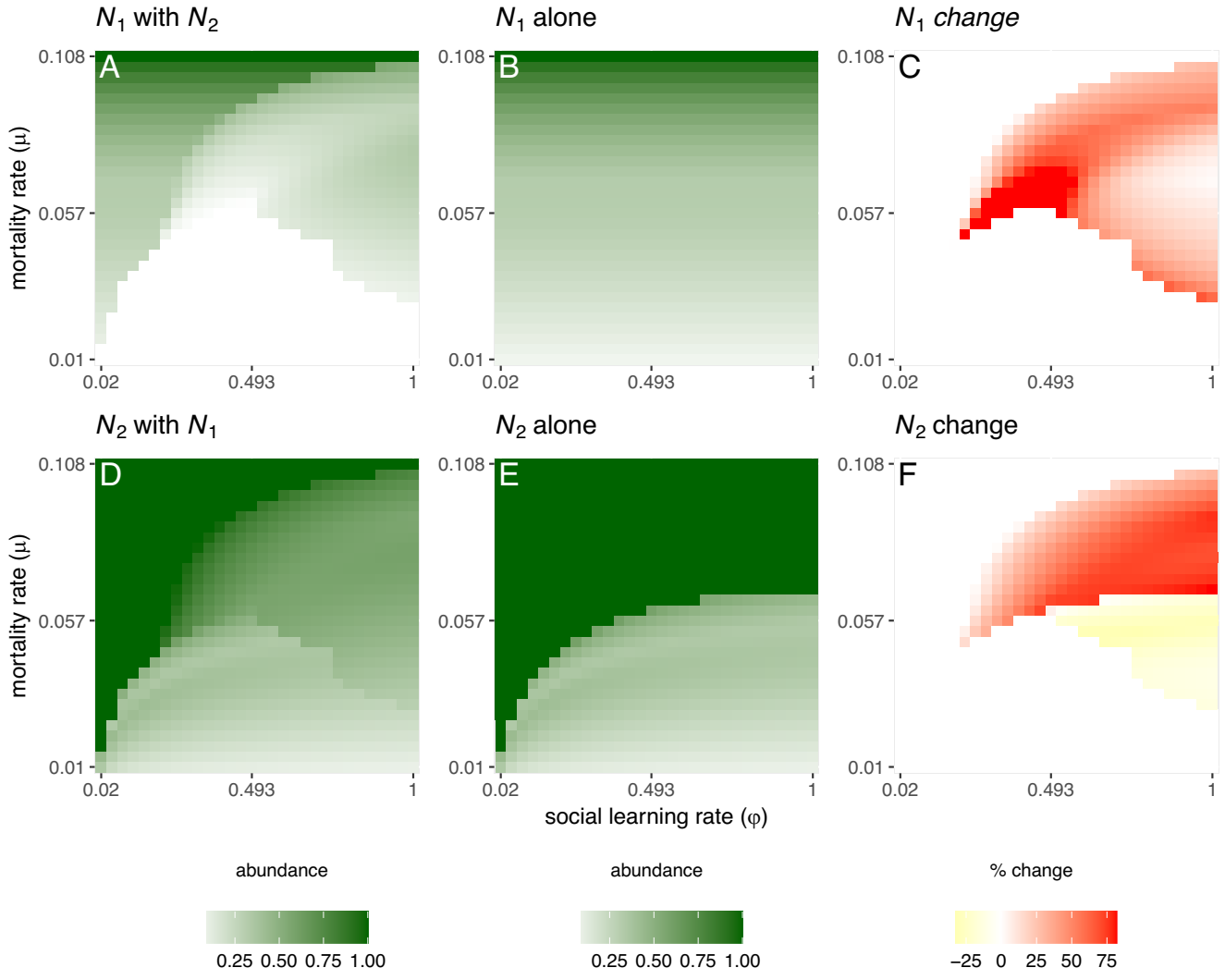

FIGURE 2 Prey density and their changes following removal of one species. (A, D) densities with both prey present. (B, E) density of each prey after removal of the other. (C, F) the percentage change in density from (A–E) Positive change indicates apparent competition, whereas negative change indicates either apparent mutualism or apparent predation. In (C, F), only regions where all populations coexist prior to removal of either prey make valid comparisons. Parameter values as in Figure 1B.

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they were otherwise driven extinct with the novel prey (Figure 2B), or increase in density by large margins where they existed before (Figure 2C).

Novel prey also suffer from the familiar prey in some areas of parameter space. Indeed, when apparent competition happens, it is because the familiar prey lets predators persist in the community when predators would otherwise go extinct (Figures 2D–F and 3). Removal of familiar prey causes large increases in the density of novel prey in that area of parameter space (Figure 2F). Surprisingly, however, in another part of parameter space, when familiar prey are removed, the density of novel prey *decreases* (Figure 2F). This is the area between where familiar prey are driven extinct by indirect effects of novel prey and where familiar prey are needed for predators to persist. In this area, novel prey benefit from familiar prey but familiar prey suffer from novel prey. This is an instance of apparent predation. In the apparent predation area, the total *predator* population increases when the familiar prey is removed (Figure 3C). Timeseries suggest that the presence of both species of prey destabilizes predator populations (top vs. bottom rows of Figure 4). With both prey present, predator populations spend most of the time near their minima, and consequently, novel prey populations spend most of the time near their maxima (Figure 4B). This appears to be due to time lags created by the three-way interaction required for social learning (Appendix S4).

Prey are usually apparent competitors over a range of values for β, ω, and μ, with familiar prey usually faring worse than novel prey. Relative to systems without social learning, apparent competition is greater, although such systems are not always comparable (Appendix S5).

DISCUSSION

We show that when one prey is vulnerable to all predators, but another must be learned about or discovered, the system's dynamics favor the novel prey. The novel prey is very difficult to exclude from a community even when the familiar prey is superior. In the social Rosenzweig-MacArthur system, novel prey were never driven extinct over the parameter values we explored. Further, in the social Lotka-Volterra system, the novel prey always had a positive density at the coexistence equilibrium, whereas a higher growth:attack rate was necessary for familiar prey to have a positive density.

In classic apparent competition systems, a higher growth:attack rate makes a prey species dominant to others (Holt, 1977). A reversal of dominance can occur when a prey species with lower growth:attack rate benefits from a refuge from predation (Holt, 1977). We find that novel prey enjoy a release from predation relative to familiar prey, so social learning creates a refuge for the novel prey. This "information refuge" is probabilistic rather than absolute because novel prey still have a non-zero probability of being consumed (Hochberg & Holt, 1995). The refuge also fluctuates dynamically, rather than being defined by an absolute proportion or number of prey that are protected (Hochberg & Holt, 1995). It is difficult to measure the refuge in a concise, intuitive form. Both the per capita attacks directed towards each prey (Sih, 1987) and the proportion of novel predators depend on multiple dynamic quantities (see Appendix S4 for more details). However, the general conclusion that refuges can modify the outcome of apparent competition is supported. The refuge is an evolving concept in ecology and evolution (Berryman & Hawkins, 2006; Fahimipour et al., 2025; Orrock et al., 2010). A major contribution of our study is to show that social learning expands the range of mechanisms that produce refuges and drive their dynamics.

Our model illuminates a need for data on how populations of predators and prey change following the spread of socially transmitted diet preferences. We are not aware of any conclusive cases. However, a compelling potential example may be the invasion of Israeli pine forests by black rats. Black rats that feed on pine nuts, a novel, socially learned resource, have become notable nest predators for birds native to the pine forests (Dagan & Izhaki, 2020). Black rats are important nest predators around the world (Amarasekare, 1993; Smith et al., 2016), so it seems likely that eggs are an innately recognized, and hence familiar, food source. Measuring the effect of black rat removal on birds in Israeli pine forest would be one way to test an unconventional apparent competition relationship—one between pine cones and birds! Other invasive predators exhibit social learning, such as Italian wall lizards in Portugal (Damas-Moreira et al., 2018). The impact of the lizards' social learning on food web connectivity remains unknown but seems likely to be a component of their success.

Another way to test our model is to consider systems of native predators and native prey in which the predator uses social learning to consume an invasive prey. Invasive prey species can be more tolerant of predation than native species (David et al., 2017), making them superior apparent competitors. If invaders also benefit from a refuge because native predators must learn to exploit them, any asymmetry in apparent competitive ability could be exacerbated. Native predators do learn to exploit invasive species, as we saw with Australian birds that consume cane toads (Donato & Potts, 2004). However, it is very difficult to infer any effect of cane toad consumption on the dynamics of populations

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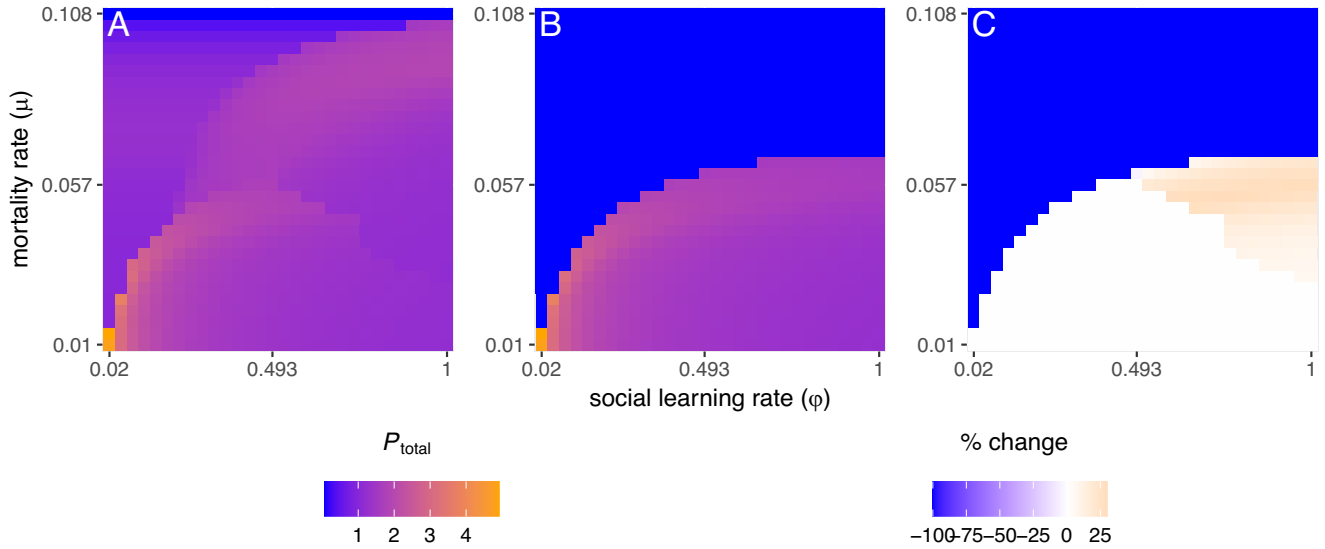

FIGURE 3 (A) P_{total} with both prey, (B) P_{total} after removing familiar prey, and (C) percentage change in P_{total} after removal. Parameter values as in Figure 1B. Panel A shows a hydra effect: for any vertical slice where $\varphi > 0$, as mortality increases, P_{total} shows initial increase.

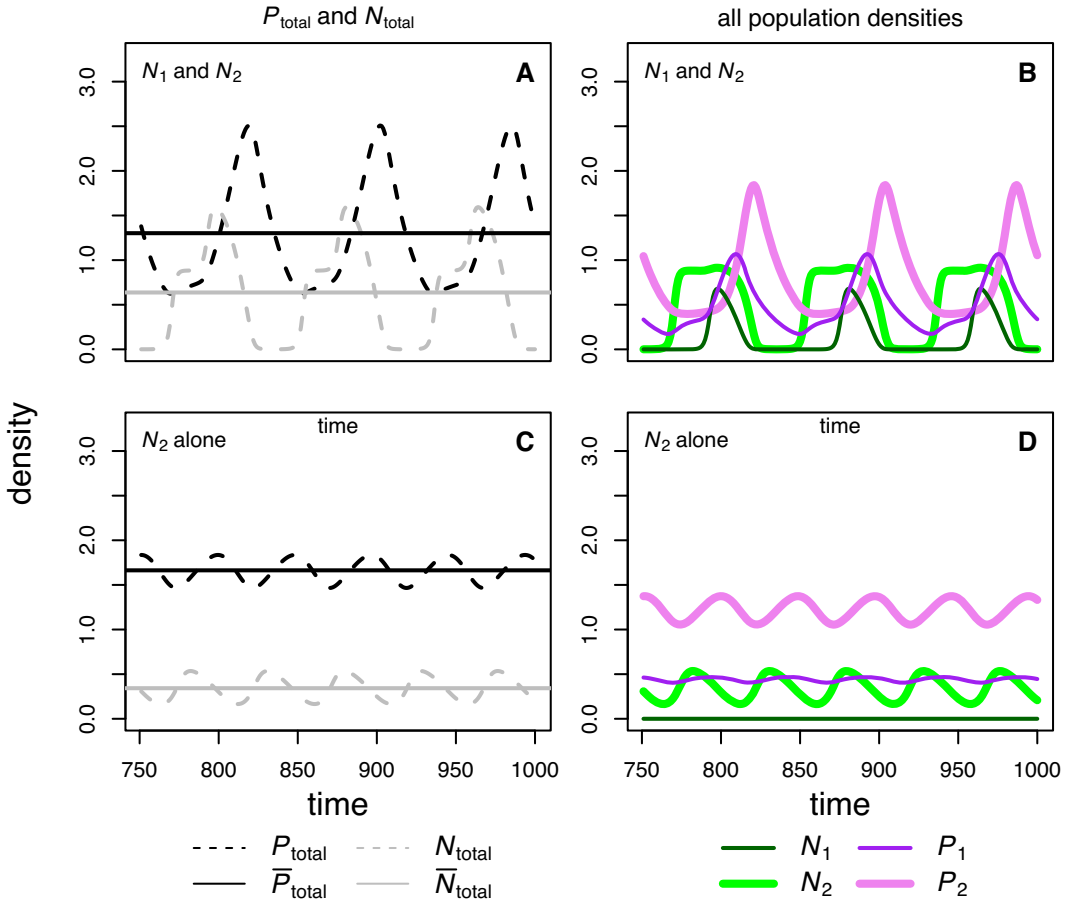

FIGURE 4 (A) Total predator and prey populations when both prey are present. (B) Fluctuations among the four populations. In the absence of familiar prey, (C) oscillations in total predators and prey are dampened as (D) naïve predators serve as a reservoir to replenish informed predators. $\varphi = 0.32$, $\mu = 0.05$, other parameter values as in Figure 1B.

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(Shine, 2010). A separate, fascinating case comes from the invasion of Australia by cockroaches. Researchers have tried to teach native predators to eat invasive cockroaches. Parker et al. (2023) found that at sites where they released trained bush rats, predation rates on the invasive cockroaches nearly doubled. The authors suggest that their training regimen resulted in bush rats actively seeking invasive cockroaches, which in our model would correspond to increasing the attack rate. Our model suggests that if eating invasive cockroaches subsidizes bush rat populations, native prey could suffer. Understanding how bush rats acquire prey preferences for native prey and invasive prey is critical because this will determine the relative predation pressure on native prey versus invasive cockroaches. Are preferences for invasive cockroaches socially transmitted following human-initiated education? If so, how does this compare with the way bush rats target their native prey? If bush rats learn all prey preferences socially, native prey may be at no special disadvantage in apparent competition. However, if native prey are innately preferred, the present model is more applicable: Bush rat consumption of invasive cockroaches could be surprisingly detrimental for native prey.

We find that time lags caused by social learning in the social Rosenzweig-MacArthur system often affect the mean densities of predators and prey. When familiar and novel prey coexist, cycles can be larger than when familiar prey are absent, resulting in lower mean predator densities and higher mean prey densities (Figure 4). However, cycles can be less extreme than when the system is devoid of social learning (Appendix S4: Figure S1). Further, the mean density of predators *and* prey are often, but not always, higher with social learning (Appendix S5: Figures S3 and S4). This suggests that relative to the fixed apparent competition system investigated by Abrams et al. (1998), overexploitation is less common, since novel prey have a refuge. Negative effects of large-magnitude cycles on mean predator density are also less prevalent. In the social Rosenzweig-MacArthur system, prey populations do not perfectly covary, and the compartments of the predator population vary asynchronously as well, reducing extreme cycles.

Direct empirical tests of cyclic dynamics are notoriously difficult (Myers, 2018). One way to test how populations are influenced by social learning may be to examine metacommunities across environmental gradients that determine a key parameter such as predator mortality. Mortality varies widely among bird populations and species (e.g., Bastianelli et al., 2021; Scholer et al., 2020). Across bird populations that exhibit a socially learned preference for a particular prey, this model predicts that in subcommunities with higher avian mortality, more prey will be able to coexist with the socially learned prey (moving upwards on the panels of Figure 1). Although the present model is not stochastic, it also seems likely that socially learned prey preferences would be more likely to go extinct in populations with high predator mortality, leading to less connected trophic networks. The massive archives of predatory interactions in citizen science databases may be one way to test these patterns (e.g., de Souza et al., 2022; Mallavarapu et al., 2026). Observations of socially transmitted feeding behaviors could be identified in photos to infer their prevalence across subpopulations in time and space. These could then be correlated with spatial estimates of avian mortality (e.g., Martin, 2015; Wolfe et al., 2025). Comparative phylogenetic patterns could also be tested. A striking result of our model is that at higher mortality rates, predators will depend on familiar prey for subsistence (Figure 3B,C). Social learning and foraging on novel prey may occur but must be accompanied by consumption of innately preferred prey. By contrast, predators with low mortality rates can subsist entirely on novel prey that they must learn about socially. Thus, our model predicts two patterns. First, innate capacities to recognize and capture prey will be stronger in taxa with high mortality rates. Second, all else being equal, heavy reliance on social learning for prey recognition and capture will be restricted to taxa with the lowest mortality rates.

We did not find noteworthy effects of rare individual discovery on the dynamics of our system. However, predators may invest more in individual discovery or exhibit more complex social learning strategies than we considered here. Borofsky and Feldman (2022b) used adaptive dynamics to show that social learning among predators could balance predation on two-prey species, while Kikuchi (2024) found that foragers change investment in discovery depending on their own condition and prey abundance. Examining indirect effects when predators exhibit adaptive behavior in both learning and prey choice should be a priority.

Generally, as novel interactions between predators and prey become more frequent under anthropogenic changes to ecosystems, we can expect increased scope for social learning to create new linkages in food webs. This study provides a mechanism that directly links animal culture to altered predator–prey dynamics and food web structure.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Kikuchi & Simon, 2026) is available in Zenodo at https://doi.org/10.5281/zenodo.21400968.

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

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