

Social Learning of Innovations in Dynamic Predator-Prey Systems

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ABSTRACT: We investigate the social transmission of innovations between predators. We focus on two classic predator-prey models. We assume that innovations increase predator attack rates or conversion efficiencies or that innovations reduce predator mortality or handling time. We find that a common outcome is the destabilization of the system. Destabilizing effects include increasing oscillations or limit cycles. Particularly, in more realistic systems (where prey are self-limiting and predators have a type II functional response), destabilization occurs because of overexploitation of the prey. Whenever instability increases the risk of extinction, innovations that benefit individual predators may not have positive long-term effects on predator populations. Additionally, instability could maintain behavioral variability among predators. Interestingly, when predator populations are low despite coexisting with prey populations near their carrying capacity, innovations that could help predators better exploit their prey are least likely to spread. Precisely how unlikely this is depends on whether naive individuals need to observe an informed individual interact with prey to learn the innovation. Our findings help illuminate how innovations could affect biological invasions, urban colonization, and the maintenance of behavioral polymorphisms.

Keywords: social learning, cultural transmission, foraging, individual variation, behavioral innovation.

Introduction

Social learning produces long-term changes in behavioral phenotype (Mesoudi et al. 2016). The occurrence of social learning is determined by environmental influences (Aoki and Feldman 2014), the structure of social networks (Farine et al. 2015; Shultz et al. 2017; Smolla and Akçay 2019; Cantor et al. 2021; Romano et al. 2022), and population structure (Deffner and McElreath 2020; Deffner et al. 2022). When social learning occurs, it has the potential to change

not only individuals but also the characteristics of a population. Consequently, it might impact population dynamics (Lehmann and Feldman 2009). It might even have cascading effects on populations of other species that are not involved in social learning, altering fundamental interactions in community ecology, such as those between predators and prey. Our study examines these reciprocal effects between social learning and the population dynamics of interacting species.

We focus on social learning in the context of behavioral innovations, in which an animal learns a novel behavior that allows it to exploit a novel resource or to exploit an existing resource in a novel way (Greenberg 2003). Innovations can be critical for responding to invasive species, such as native Australian predators that have learned how to devour toxic, invasive cane toads (Beckmann and Shine 2011; Parrott et al. 2019). They also have relevance for species undergoing range expansion. For example, common mynas on their invasion front in Israel are more innovative and also more accepting of novel foods than in their native range (Cohen et al. 2020). Finally, innovation has the potential to let a species occupy new niches. Great tits in Hungary, for example, have adapted themselves to consuming bats when their traditional food resources are scarce (Estók et al. 2010). Innovations in foraging are by far the most widely documented types of novel behaviors (Lefebvre et al. 1997; Galef and Laland 2005; Overington et al. 2009; Gariépy et al. 2014). Their social transmission occurs in several systems (Hämäläinen et al. 2022). Foraging innovations have also been connected to extinction risk (Ducatez et al. 2020).

Once discovered, innovations can spread between individuals via social learning (e.g., Aplin et al. 2015). Thus, to study innovations, we need to consider how information spreads. There are many modes by which an innovation might pass between individuals. They include various

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forms of vertical (parent to offspring), horizontal (e.g., within a stage/age class), and oblique (between nonparent adults and juveniles) transmission (Cavalli-Sforza and Feldman 1981; Denton et al. 2020). The structure of social networks can affect information spread (Farine et al. 2015; Shultz et al. 2017) and be shaped by the current value of social information (Smolla and Akçay 2019; Cantor et al. 2021; Romano et al. 2022). More granularly, individuals can seek specific role models if they occupy appropriate spots in a social network (e.g., Carter et al. 2016), while the acquisition and deployment of behaviors can also vary with context (Kendal et al. 2018; Chimento et al. 2022).

In this study, we make simplifying assumptions about how information spreads. We examine innovations that are transmitted between randomly mixing individuals. Although this assumption ignores much complexity, it relates innovation spread to some well-studied models for the transmission of disease. This is advantageous for our focus on social learning and population dynamics. In disease ecology, when disease affects fitness, it can create feedback with population size (Ashby et al. 2019). Similarly, socially transmitted innovations could affect population size if they affect how quickly individuals reproduce or die (Ihara and Feldman 2004; Thorogood et al. 2018; Whitehead et al. 2019). They could also impact the populations of other species in a community if they affect a predator's foraging behavior. The spread of innovation happens on the same timescale as population dynamics, so it could produce unexpected system-wide feedbacks.

Some recent theoretical studies have examined social information in predator-prey systems. When social information has only short-term effects on behavior (e.g., alarm calls), it can affect population dynamics (Gil et al. 2018, 2019; Tóth 2021). Borofsky and Feldman (2022) investigated the evolution of conformity and anticonformity in a system where an innovation spreads within a predator population of constant density and prey populations can vary dynamically. Yet to understand feedbacks between social learning and population dynamics, both predator and prey populations must be allowed to vary. This is a realistic assumption for many systems, as predators are often regulated by prey availability (Sinclair 2021). Furthermore, social transmission of foraging innovations can depend not only on the density of individuals in the predator population but also the density of their prey. In the present study, we focus on foraging innovations in a population of predators. We allow both predator and prey populations to vary dynamically. We also consider social learning functions that include the population density of both predators and prey, so that predator learning can be influenced by prey demography. We begin by examining the spread of innovations in a simplistic abstract system based on foundational equa-

tions in population biology and epidemiology. Then we extend our exploration to more realistic models. We ask when an innovation can spread within a predator population, how it impacts equilibrium points and their stability, and how sensitive these results are to our assumptions. We compare our results with classical predator-prey models that do not consider predator innovation or social learning.

Conceptual Framework

We study a single species of predator that feeds on a single species of prey. To depict this interaction, we build on two classic models (Lotka-Volterra, Rosenzweig-MacArthur). Both models assume that the predator attacks one prey type, which, when consumed, is converted to new predators with a linear conversion efficiency. Predators die at a linear per capita rate. In the Lotka-Volterra model, predators capture prey at a rate proportional to the number of prey available for consumption (Murdoch et al. 2003; McPeck 2022). In the absence of predation, prey grow exponentially (see table 1). This model predicts long-term dynamics in which the predator and prey populations cycle around a neutrally stable equilibrium. This means that the properties of the cycle (e.g., amplitude) are determined by starting conditions, and if anything disturbs the system, cycle properties experience long-term changes.

In contrast, the Rosenzweig-MacArthur model assumes that consumption of prey is not instantaneous following capture but instead takes some time to handle (Rosenzweig and MacArthur 1963; McPeck 2022). Handling time is incorporated using a type II functional response: the rate of prey consumption per predator increases rapidly with prey density when prey are rare but increases very slowly when prey are common (Holling 1959; Murdoch et al. 2003). In the absence of predation, prey grow logistically. Depending on parameter values, this system approaches either a stable equilibrium point or a stable limit cycle (Rosenzweig 1969; Edelstein-Keshet 2005). A limit cycle is a fixed pattern of oscillation toward which a system is drawn when it is near a particular equilibrium (Otto and Day 2007).

We now ask whether innovations, particularly when spread by social learning, change the qualitative dynamics of predator-prey systems.

A Dynamic System of Social Learning

Let us assume that a single innovation spreads in a population of predators but that all predators are otherwise identical in their demographic rates. Predators are born without knowledge of the innovation (we call such individuals "naive") and must acquire it from another predator that has already learned the behavior (we call such individuals "informed") or, in rare cases, independently discover the

Table 1: Forms of prey growth $R(N)$, predator functional response $F(P_i, N)$, and social learning $\Phi(P_1, P_2)$ used in this study

Function	Form		Interpretation
	L-V	R-M	
Population dynamics			
$R(N)$	rN	$\frac{rN(k-N)}{k}$	Prey grow at intrinsic rate r with carrying capacity k (when self-limitation applies)
$F(P_i, N)$	$a_i P_i N$	$\frac{a_i P_i N}{1 + a_i h_i N}$	Predators encounter prey with rate a_i and take h_i time to handle a prey item
Discovery			
$D(P_1)$	0		No independent discovery
	δP_1		Independent discovery occurs in proportion to the density of naive predators
	$\delta P_1 N$		Individuals are likely to discover an innovation only when encountering a prey item
Social learning			
$\Phi(P_1, P_2)$	$\varphi P_1 P_2$		Social learning depends only on a naive individual observing an informed individual
	$\varphi N P_1 P_2$		Social learning depends on a naive individual observing an informed individual interact with a prey
	$\frac{\varphi a_2 N P_1 P_2}{1 + a_2 h_2 N}$		Social learning depends on a naive individual observing an informed individual handle prey

Note: L-V = Lotka-Volterra; R-M = Rosenzweig-MacArthur.

innovation without learning from others. Both naive and informed individuals consume prey. Both give birth only to naive individuals. The innovation spreads according to the law of mass action, meaning that encounters between naive and informed individuals lead to the spread of the innovation in proportion to their population densities. We assume overlapping generations, so transmission is horizontal dominated, but it also includes some vertical and oblique transmission, as we cannot distinguish between cohorts. This assumption is common in classic epidemiological models, where it is simply called horizontal transmission (Cavalli-Sforza and Feldman 1981).

We assume that an innovation has a beneficial effect on an individual predator's demographic rates, although neutral (or even deleterious) innovations could also spread in principle. We assume that individuals do not forget or abandon the innovation once they have learned it (which would be conceptually analogous to recovering from a disease or back mutation). Figure 1 provides a conceptual overview of the models we develop here (fig. 1A) and highlights our main results (fig. 1B).

We use $P_i \in (P_1, P_2)$ to represent the densities of naive (P_1) and informed (P_2) individuals. We assume that prey density N increases according to the function $R(N)$. Prey are captured according to $F(P_i, N)$, the functional response of naive and informed predators ($i = 1, 2$). Prey dynamics are described by the equation

$$\frac{dN}{dt} = R(N) - \sum [F(P_i, N)]. \quad (1)$$

The predator population dynamics are described by

$$\frac{dP_1}{dt} = \sum [b_i F(P_i, N)] - D(P_1) - \Phi(P_1, P_2) - m_1 P_1, \quad (2)$$

$$\frac{dP_2}{dt} = \Phi(P_1, P_2) + D(P_1) - m_2 P_2. \quad (3)$$

All parameters in equations (1)–(3) are positive. The function $\Phi(P_1, P_2)$ describes the rate at which naive individuals learn socially on contact with an informed individual. We consider multiple forms of this function: specifically, one in which social learning depends only the density of naive and informed individuals, and two forms in which social learning additionally depends on the density of the prey. The differences among them are central to the dynamics of social learning. We discuss the specifics of each functional form further below (and in table 1).

In many systems, small perturbations can have major effects (McPeck 2022; Simon et al. 2022). We therefore consider the possibility that naive predators may innovate via nonsocial learning (i.e., independent discovery). This is represented by the function $D(P_1)$ in equations (2) and (3). We assume that independent discovery is slow relative to social learning. Functional forms are summarized in table 1.

We assume that innovation can increase reproduction (by increasing attack rate, increasing conversion efficiency, or, when applicable, reducing handling time) as well as reduce mortality. Prey are captured at rate a_1 by naive predators but at rate a_2 by informed predators ($a_2 > a_1$). Likewise, naive and informed predators convert captured prey

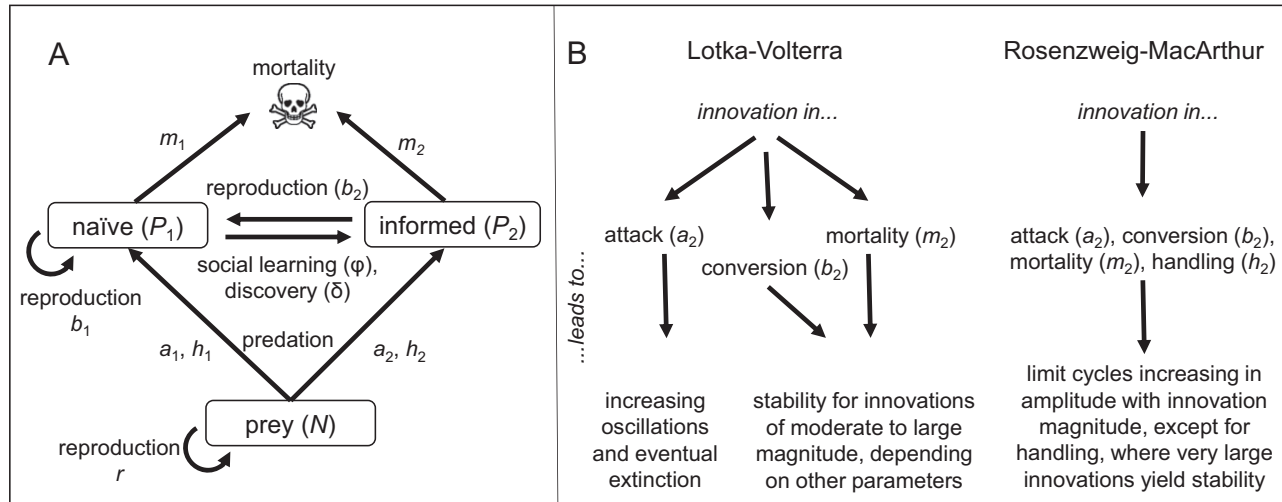


Figure 1: A, Structure of the predator-prey community assumed for our models. Prey occupy the bottom trophic level. Predators reproduce by converting their prey into new naïve predators. Social learning and discovery of innovations transforms naïve predators into informed individuals. Per capita predator mortality is linear. B, Summary of results under Lotka-Volterra and Rosenzweig-MacArthur assumptions. In Lotka-Volterra systems, attack rate innovations cause eventual extinction. Innovations in conversion and mortality cause either stability or limit cycles. In Rosenzweig-MacArthur systems, innovations above a certain magnitude cause limit cycles except for handling time, where stability can be restored with innovations of very large magnitude.

with efficiency b_1 and b_2 , respectively ($b_2 > b_1$). Some types of innovations may reduce predator mortality, so we assume separate death rates for naïve and informed individuals, respectively (m_1 and m_2 ; $m_2 < m_1$). In the Rosenzweig-MacArthur formulation of $F(P_i, N)$, we consider the time to handle prey. Handling time for naïve individuals is h_1 , and for informed individuals it is h_2 ($h_2 < h_1$). Note that we assume that $\Phi(P_1, P_2)$ is independent of the magnitude of the innovation. We define the magnitude of an innovation as the difference between parameter values for informed and naïve individuals (e.g., $b_2 - b_1$).

Methods

We analyze the Lotka-Volterra and Rosenzweig-MacArthur forms of equations (1)–(3) to determine whether foraging innovations, spread by social learning, change the qualitative dynamics of predator and prey populations. We first find conditions for which the innovation’s rate of increase in the population would be positive ($R_0 > 1$). When analytical solutions are possible, we solve for equilibria by setting each set of equations to zero and then assess the stability of those equilibria by solving for the Jacobian matrix, characteristic equation, and, when possible, eigenvalues using Mathematica (Wolfram Research 2010). Whenever eigenvalues for the more complicated equilibria are difficult to interpret, we derive the Routh-Hurwitz conditions for stability. If analytical solutions are not possible, we present nu-

merical results investigating stability using R (R Core Team 2021; R code is available in the Dryad Digital Repository; <https://doi.org/10.5061/dryad.2z34tmpqn>; Kikuchi and Simon 2023). We ignore all biologically infeasible equilibria.

For completeness, we ask how the stability of the system is impacted by ongoing independent discovery of an innovation. For the Rosenzweig-MacArthur system, we also examine how dynamics are affected by variation in prey productivity and social learning rate. Under parameter values where the innovation can invade, we use bifurcation analyses to see whether larger-magnitude innovations shift the Rosenzweig-MacArthur system from a stable point equilibrium to limit cycles.

Analyses and Results

Lotka-Volterra Assumptions: R_0 and Equilibria

First, we analyze the model under Lotka-Volterra assumptions (table 1). That is, prey grow exponentially in the absence of predation: $R(N) = rN$, where r is the intrinsic rate of increase. Predation follows a type I functional response (prey capture rate scales linearly with prey density; Holling 1959, 1965), where $F(P_i, N) = a_i P_i$ and indicates a negligible handling time ($h_i = 0$). We assume social learning takes the form $\Phi(P_1, P_2) = \varphi P_1 P_2$, where φ is a constant. Additionally, we assume independent discovery does not occur (i.e., $D(P_1) = 0$).

Although the assumptions of the Lotka-Volterra equations may lack realism for many empirical systems, they let us arrive at some analytical conclusions. For a new innovation to have relevance beyond the individual that discovers it, it must initially spread in (invade) a population. Invasion can occur when R_0 exceeds 1 and depends on the number of naive individuals available to learn (Cavalli-Sforza and Feldman 1981). We can find R_0 by seeking conditions that satisfy the inequality $dP_2/dt > 0$. From equation (3) we see that $dP_2/dt = P_2(\varphi P_1 - m_2)$. Then, for a positive rate of change in informed individuals, the condition $\varphi P_1/m_2 > 1$ must be met. This gives

$$R_0 = \frac{\varphi P_1}{m_2}. \quad (4)$$

Biologically, this means that, on average, an informed individual must encounter a sufficient number of naive individuals to pass the innovation on to more than one of them before dying. The minimum number of naive individuals they must encounter depends on φ and m_2 . Additionally, innovations that decrease mortality will spread more easily because they lower the minimum number of naive individuals required for sustained innovation spread, much like a less virulent disease.

In the absence of innovators (i.e., $P_2^* = 0$), the density of naive individuals is $P_1^* = r/a_1$, and the density of their prey is $N^* = m_1/(a_1 b_1)$ (equilibrium is denoted by a superscript asterisk). Readers should note that this is the neutrally stable equilibrium of the classic Lotka-Volterra model. We also find a coexistence equilibrium where both types of predators coexist with the prey. At this equilibrium,

$$\begin{aligned} P_2^* &= \frac{r\varphi - a_1 m_2}{a_2 \varphi}, \\ P_1^* &= \frac{m_2}{\varphi}, \\ N^* &= \frac{P_1^*(\varphi P_2^* - m_1)}{a_1 b_1 P_1^* + a_2 b_2 P_2^*}. \end{aligned}$$

A condition for this equilibrium to exist is $\varphi/a_1 - m_2/r > 0$ (i.e., $P_2^* > 0$). Note that this is also required for an innovation to invade a population of solely naive predators because

$$\frac{dP_2}{dt} \frac{1}{P_2} = \varphi P_1^* - m_2 = \frac{\varphi r}{a_1} - m_2 > 0.$$

Equivalently, $R_0 = \varphi r/a_1 m_2 > 1$. Biologically speaking, for an innovation to spread and be maintained in the population, prey reproduction and predator social learning

must be fast relative to the attack rate of naive predators and the death rate of informed predators. If this condition is not met, the innovation cannot spread or be sustained.

Lotka-Volterra Assumptions: Stability Analyses

When only prey and naive predators exist, the system is identical to the classic Lotka-Volterra model and is hence neutrally stable. How does innovation impact this result? It is difficult to make meaningful general statements about the stability of the coexistence equilibrium because of the large number of parameters involved. However, in that full system, we assumed that the innovation beneficially affects all predator demographic parameters (i.e., $a_1 < a_2$, $b_1 < b_2$, $m_1 > m_2$). This may not be realistic for most innovations. We therefore examine specific scenarios in which an innovation causes only a single pair of parameters to differ between naive and informed individuals.

First, we consider innovations that increase attack rate ($a_1 < a_2$, $b_1 = b_2$, $m_1 = m_2$). This could represent an innovation that elevates foraging success, such as imitating a successful search strategy or microhabitat choice. We examine the Routh-Hurwitz conditions for stability (see the supplemental PDF, sec. 1), which reveal the equilibrium to be unstable. Numerical analyses show that attack rate innovations generate oscillations of increasing amplitude, eventually leading to extinction. This is a consequence of the innovation directly increasing predator populations and reducing prey populations, resulting in positive feedback. The larger the innovation is, the more quickly either the predator or the prey reaches extinction.

Next we examine the case where an innovation increases conversion efficiency ($b_2 > b_1$; $a_1 = a_2$, $m_1 = m_2$), as might happen when predators learn how to more efficiently exploit prey tissues. For example, some species of rodents cut and store toxic plants and return to consume them only after the plant's toxicity has decreased (Glendinning 2007). This behavior presumably increases the net value of toxic plants as a resource. Routh-Hurwitz criteria reveal that stability depends on the value of φ (see the supplemental PDF, sec. 1). The system is stable when social learning is moderate in speed. Predator populations are gradually supplemented by reproductive output of informed individuals back into the naive population to such a degree that the whole predator population does not collapse at lower prey abundances (fig. 2A). Informed predators can be thought of as storing energy for release back into the naive predator population, as though a segment of the population were in a temporal refuge buffered from starvation. However, when social learning occurs too slowly or too quickly, the predator population either does not receive a critical level of supplement or receives too much, such that it overshoots prey abundances. Either φ too large or too small therefore

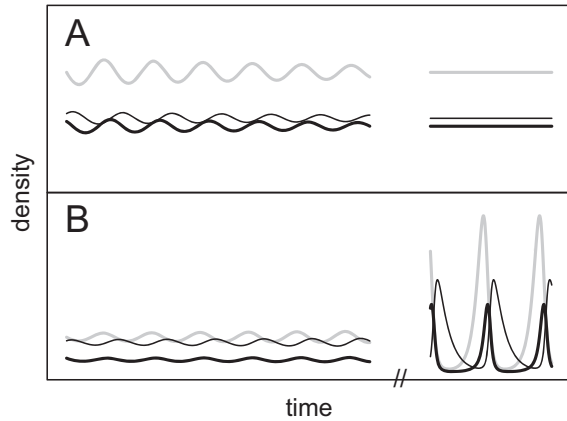


Figure 2: Lotka-Volterra outcomes of conversion rate innovations depend on social learning. *A*, Moderate social learning speed yields a stable equilibrium over time ($\varphi = 0.16$). *B*, Social learning speed exceeds a critical threshold, destabilizing the system into limit cycles ($\varphi = 0.25$). Thick gray line = prey; thick black line = naive predators; thin black line = informed predators. In both panels, other parameters are $a = 0.15$, $b_1 = 0.4$, $b_2 = 0.7$, $m = 0.2$, and $r = 0.4$.

causes limit cycles (fig. 2*B*). The conditions for stability can also be framed in terms of b_2 . If $a > \varphi$, only $b_1 < b_2$ is required for stability (i.e., any innovation). When $a < \varphi$, stability requires $b_2 < a^2 b_1 m / (a^2 m - a m \varphi - a r \varphi + r \varphi^2)$ (i.e., there is an upper bound on innovation magnitude beyond which the system is not stable).

For completeness, we also consider innovations that decrease mortality ($m_2 < m_1$; $a_1 = a_2$, $b_1 = b_2$). These are not directly related to foraging but still constitute innovations when they arise from individuals learning to utilize their environments in a new way (resource use in a broad sense). This could include new shelter-use behaviors like hiding in cars (Cauchard and Borderie 2016) or nesting in artificial structures (Lowry et al. 2013; Dias et al. 2017). Predator survival could also increase in response to social learning to avoid dangerous or toxic prey (other than the focal prey modeled here; e.g., Thorogood et al. 2018). The Routh-Hurwitz criteria, our analysis of R_0 , and a biologically feasible equilibrium (above) require $0 < \varphi/a - m_2/r < 1$ for a stable equilibrium (see the supplemental PDF, sec. 1). This means that for stability, m_2 , a , and φ have both upper and lower bounds (in some cases zero for m_2). Additionally, r may have both an upper and lower bound or only a lower bound depending on the relationships between the other parameters. If parameters exceed these bounds, the system exhibits limit cycles.

Generally speaking, the spread of innovations in conversion rate and mortality reduces the tendency of pred-

ator populations to crash during periods of low prey abundance, resulting in a weaker prey boom at the start of the subsequent cycle. However, when social information spreads too quickly, this damping effect is limited and instead a stable limit cycle results. This is similar to the effect on the Lotka-Volterra model when a prey species uses multiple habitat patches: as long as predators disperse randomly between the two patches, stability results (Holt 1984). The system reverts to neutral stability only when predators disperse with infinite speed (Holt 1984). Likewise, in our system, if social information spreads at such a fast rate that demographic parameters are irrelevant, this separation of timescales returns the system to the original Lotka-Volterra equations (supplemental PDF, sec. 1).

Lotka-Volterra Assumptions: Independent Discovery

To test the influence of independent discovery on the system's dynamics, we investigate two modes of nonsocial learning (table 1). We let $\Phi(P_1, P_2) = 0$ in equation (3), so that social learning does not occur. First, we examine discoveries that occur in proportion to the density of naive predators, such that $D(P_1) = \delta P_1$, where δ is a constant. This could represent the adoption of a novel foraging strategy independent of encounters with prey, such as foraging in hedges rather than fields. Under this assumption, innovations in attack rate cause instability, whereas innovations in conversion rate and mortality always yield stability at the lone nontrivial equilibrium (for details, see the supplemental PDF, sec. 1). Second, we assume that discovery requires that a predator encounter a prey, which we represent by letting $D(P_1) = \delta P_1 N$. In this case, at the nontrivial and biologically feasible equilibrium, innovations in attack rate and conversion rate cause instability; mortality innovations produce stability (see the supplemental PDF, sec. 1).

Next, we examine the system's behavior when predators can either discover an innovation independently ($D(P_1) \neq \delta 0$) or use social learning ($\Phi(P_1, P_2) = \varphi P_1 P_2$). Analytically, such systems are difficult to interpret. However, numerical analysis reveals that when $D(P_1) \ll \Phi(P_1, P_2)$, the system behaves primarily like one where social learning takes place alone (see the supplemental PDF, sec. 2, fig. S1). Therefore, the ecological effects of innovation discovery are likely to be swamped by social learning in systems that meet Lotka-Volterra assumptions.

Rosenzweig-MacArthur Assumptions: R₀ and Numerical Approaches

The assumptions of the Lotka-Volterra model are poorly supported for many systems. Here, we incorporate Rosenzweig-MacArthur assumptions to develop a model that applies to

a larger proportion of predator-prey ecologies. Recall that these assumptions are that prey (when alone) exhibit sigmoidal population dynamics (reaching a carrying capacity at high abundance) and that individual predators exhibit saturating functional responses to prey abundance (e.g., Holling type II; Rosenzweig and MacArthur 1963; Rosenzweig 1969; for an overview, see McPeck 2022). Self-limiting prey grow according to $R(N) = rN(k - N)/k$, where k is the carrying capacity of the prey and the type II functional response takes the form $F(P_i, N) = a_i P_i N / (1 + a_i h_i N)$ (table 1).

Under these assumptions, equations (1)–(3) do not yield analytical equilibria, nor can their stability be assessed with analytical methods. We can, however, predict how innovations are likely to affect the system by comparing them to the nullclines of a system without innovation (nullclines are combinations of variables where the net growth of a population is zero; Rosenzweig and MacArthur 1963). Nullclines partition state space (fig. 3) into regions of positive or negative growth for each of the populations. The Rosenzweig-MacArthur model approaches a stable equilibrium when the predator nullcline is to the right side of a hump in the prey nullcline (fig. 3A). If the predator nullcline falls on the left side of a hump, stable limit cycles result (Rosenzweig 1969; fig. 3B). Because they can be sustained by fewer prey, predators that are more efficient at exploiting their prey will have nullclines further to the left than less efficient predators. Beneficial innovations may therefore create segments of the predator population that tend to push the system away from the stable equilibrium on the right side of figure 3A, toward limit cycles. In other words, rather than changing the behavior of the system entirely (as we saw with

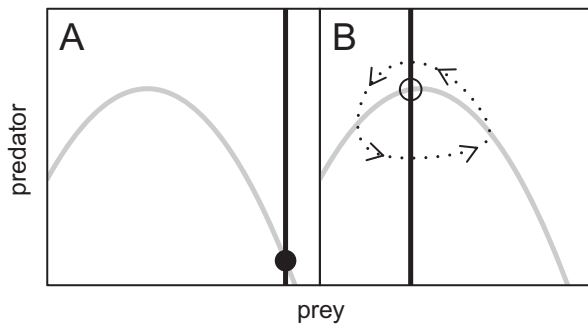


Figure 3: Prey nullclines (gray curves) and predator nullclines (black vertical lines) in the classic Rosenzweig-MacArthur model where prey are self-limiting and predators use type II functional responses. A, Stable equilibrium shown by the black circle (e.g., without innovation). B, Limit cycles following the dotted line around an unstable equilibrium shown by the open circle (as we might expect to observe once an innovation has spread among the predator population).

the Lotka-Volterra model with social learning), the impact of social learning on the Rosenzweig-MacArthur system may be conceptually similar to changing its parameter values.

To test this hypothesis, we examine systems where populations of only naive individuals and their prey have stable equilibria. For an innovation to initially invade a system at stable equilibrium, the naive predator population must be above the threshold density $R_0 = \phi P_1^* / m_2$, where again P_1^* denotes equilibrium density. This suggests that predator populations living a marginal existence may be the least likely to foster innovations that would help them succeed (i.e., if the vertical line in fig. 3A were even further to the right). An innovation that reduces mortality (m_2) would increase R_0 at a given P_1^* and so might be more likely to invade a small predator population than other innovations. It is easy to see why mortality innovations are special by considering extreme cases. If a predator discovers an innovation that makes it immortal, it will eventually encounter another predator to share the discovery with no matter how long it takes. By contrast, if a predator discovers an innovation to massively increase its rate of converting prey, it may produce a flood of naive offspring but die before any of its children can learn its secret.

Across innovation types, the bifurcation analyses show that stable systems are destabilized by the spread of innovations of large magnitude (fig. 4). Innovations that confer only a small advantage do not destabilize the system. All innovations large enough to destabilize the system shift the trophic structure of the community, such that predator populations are (on average) higher relative to prey (shown on a log scale in fig. 4). With innovations in handling time, the amplitude of cycles increases, then decreases as innovations bring handling time close to zero (fig. 4). This occurs because the shape of the prey isocline loses its hump as handling time approaches zero. In other words, the predator becomes “stable” in its foraging behavior because its functional response becomes approximately linear (sensu Abrams and Holt 2002). With other innovations, populations remain unstable as innovation magnitude increases (fig. 4). Perhaps surprisingly, the larger the magnitude of an innovation in attack rate or conversion efficiency, the lower the average proportion of informed individuals in the predator population. This happens because there is a critical density of naive individuals required for R_0 to exceed 1, allowing an innovation to spread. The innovation has difficulty spreading during periods of low predator density, so during these times most predators are naive. A fluctuating proportion of informed individuals is predicted in a population with cyclic dynamics because the cycles include periods of abundance where $R_0 < 1$. A parallel to this exists in wildlife disease, where the population cycles of great gerbils drive periodic outbreaks of the bacterium that causes bubonic plague (Davis et al. 2004). Mortality innovations produce slightly

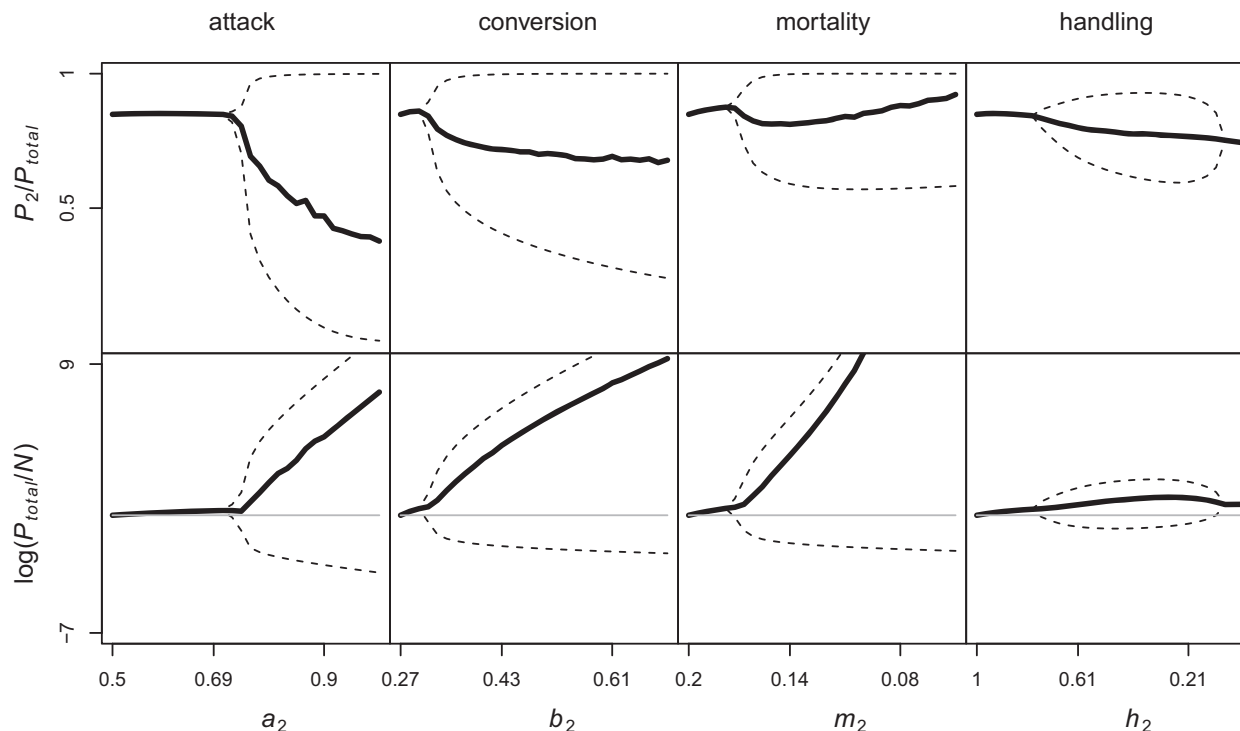


Figure 4: Effect of increasing innovation magnitude on the proportion of informed individuals in the population (*top*) and the log ratio of predator to prey (*bottom*) in the Rosenzweig-MacArthur system. Black line = time-averaged mean; dashed line = bounds of limit cycles; gray line = population equilibrium in the absence of innovation. Except for the varying parameter on the abscissa, naive and informed predators shared the same parameter values: $a = 0.5$, $b = 0.27$, $m = 0.2$, $h = 1$, $\varphi = 0.2$, $r = 2$, and $k = 10$.

different patterns from attack rate and conversion efficiency innovations, with the proportion of informed individuals increasing at very large magnitude innovations (because informed individuals live a very long time).

It is also helpful to have predictions about how a single type of innovation affects population dynamics and behavioral variability across an ecological gradient, for example, prey productivity or general proclivity toward social learning. We examine the influences of r and φ on how a population is impacted by the spread of an innovation. Stable equilibria exist only at low values of r and φ , which have qualitatively similar effects on stability. Once limit cycles emerge, their amplitudes typically increase with increases in r or φ (fig. 5A). Trends in limit cycles are similar to those displayed in figure 5A regardless of innovation type (i.e., a_2 , b_2 , m_2 , or h_2) or whether we examine predator and prey populations separately, predator-to-prey ratios, or the proportion of informed to naive predators. The average proportion of informed individuals in the population also increases with r and φ (fig. 5B). This happens because higher prey populations support

more predators and larger φ increases the rate of social information spread. Both of these increase R_0 , so the innovation is adopted by more predators.

When Social Learning Depends on Observing an Informed Individual Interact with Prey

So far, we have considered only mass action spread of innovations between two individuals. Many other modes of spread exist (Cavalli-Sforza and Feldman 1981; McCallum et al. 2001; Galef and Laland 2005; Denton et al. 2020). The transmission of foraging innovations may depend not only on interactions between naive and informed individuals but also on interactions with prey. There are many circumstances where naive individuals need to observe an informed individual interact with an object to acquire the relevant skill. For example, capuchin monkeys need to see another monkey interact with a nut to learn how to crack it open (Coelho et al. 2015), and a bird needs to observe another bird interact with a warning-colored prey item to learn avoidance (Hämäläinen et al. 2021). Unlike

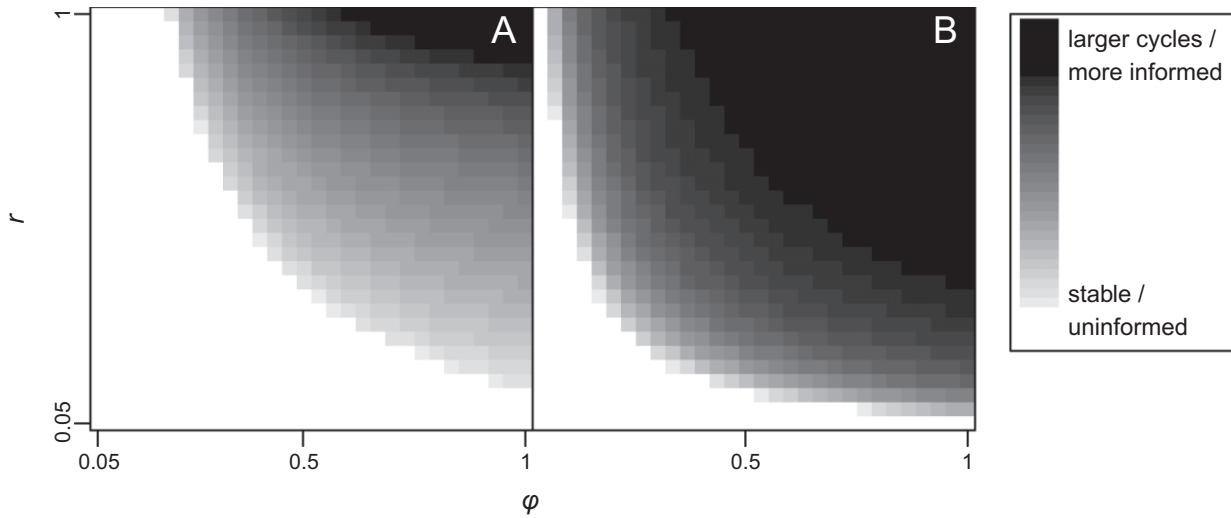


Figure 5: A, Bifurcation analyses of the total predator population size across a range of r and ϕ values for attack rate innovations in the Rosenzweig-MacArthur system. Increasing either parameter shifts the system from stability toward increasingly high-amplitude limit cycles. B, Corresponding plot showing that the mean proportion of the population composed of informed individuals increases with r and ϕ . In both panels, $a_1 = 0.5$ and $a_2 = 0.75$; all other parameter values are the same as in figure 4.

the models we explored above, such models of information transfer are not as directly analogous to epidemiological transfer functions.

We explore this scenario by letting $\Phi(P_1, P_2)$ include prey density. We do this in two ways (table 1). First, we extend the mass action assumption to require three agents: $\Phi(P_1, P_2) = \phi NP_1 P_2$. We interpret this as social learning that requires a naive individual observe only a momentary interaction between an informed individual and prey. Second, we add the rate at which informed individuals process prey, meaning that we reduce the rate of social learning by prey handling time and encounter rate: $\Phi(P_1, P_2) = \phi a_2 NP_1 P_2 / (1 + a_2 h_2 N)$. This means that social learning is limited by the rate at which informed individuals capture and handle prey. It is based on the type II functional response that governs predator foraging. Using bifurcation analyses as above, we examine the effect of these functions on the system across a range of values for a_2 , b_2 , and h_2 (the spread of mortality-reducing innovations should not depend on prey density, so we ignored them).

If $\Phi(P_1, P_2) = \phi NP_1 P_2$, then the proportion of informed individuals in the predator population increases relative to when $\Phi(P_1, P_2) = \phi P_1 P_2$. We find it also reduces the amplitude of cycles in P_2/P_{total} , so the population is less variable in the proportion of informed individuals (fig. S2). Why does this happen? After a prey population crash, naive and informed predators both decline steeply; often, it is difficult for an innovation to spread. However, the R_0 value for information spread is $N\phi P_1/m_2$. The addition

of the N term to R_0 causes prey populations to increase the rate of social learning within the predator population as the prey population recovers following a crash. This prevents the proportion of informed individuals from falling as low as when $\Phi(P_1, P_2) = \phi P_1 P_2$. Including N in the transmission function also increases the prey abundance at which R_0 is highest in populations of entirely naive predators, so innovations are more likely to spread at lower predator abundances (i.e., fig. 3A).

When $\Phi(P_1, P_2) = \phi a_2 NP_1 P_2 / (1 + a_2 h_2 N)$, the proportion of informed individuals in the population decreases compared with when $\Phi(P_1, P_2) = \phi P_1 P_2$ (fig. S3). This pattern is driven by a decrease in the upper bound on the proportion of informed individuals, while the lower bound remains similar to the case where $\Phi(P_1, P_2) = \phi P_1 P_2$. Overall, the amplitude of the cycles decreases. See figure S4 for a comparison of the three transmission functions using time series.

Rosenzweig-MacArthur Assumptions: Independent Discovery

How does the capacity of individuals to learn nonsocially impact the dynamics of the Rosenzweig-MacArthur system? We examine two cases. In the first, we let $D(P_1) = \delta P_1$ and $\Phi(P_1, P_2) = \phi P_1 P_2$. This assumes that encountering prey is unnecessary for discovery and social learning. In the second, we let $D(P_1) = \delta P_1 N$ and $\Phi(P_1, P_2) = \phi P_1 P_2 N$. In this latter case, both ways of learning the

innovation require interaction with a prey item. Again assuming that $D(P_1) \ll \Phi(P_1, P_2)$, numerical analyses reveal that regardless of the nature of the innovation (attack, conversion, etc.), the system is dominated by the influence of social learning, and discovery has little impact on their dynamics (fig. S5). This is intuitive; adding a newly discovered innovation essentially performs a perturbation analysis, nudging the system away from an equilibrium point or cycle. Because Rosenzweig-MacArthur systems have stable point equilibria or limit cycles as attractors, it is unsurprising that perturbations caused by independent discovery have little impact on long-term system behavior.

Discussion

Our models show that behavioral innovations among predators in dynamic populations have the potential to alter the stability of a system and to shift the distribution of energy to higher trophic levels. Furthermore, larger-magnitude innovations tend to be more destabilizing in the more realistic Rosenzweig-MacArthur system. Although we do not explicitly consider extinction probability as a function of population size, other work shows that periods of low population size can increase the likelihood of this outcome due to stochastic processes (Bartlett 1960; Lande 1993) or Allee effects (Gil et al. 2019; Aubier 2020). Thus, innovations in stable systems could act as catalysts of change that qualitatively alter dynamics by pushing them toward cyclic behavior or local extinction when predators depend on a single species of prey.

Within the Rosenzweig-MacArthur systems, when social learning requires interaction between only naive and informed predators, the R_0 for innovation spread ($R_0 = \phi P_1 / m_2$) could preclude the innovation from taking hold in small populations that subsist on prey populations near their carrying capacity. Such innovations, like foraging in particular microhabitats or using a particular movement style, might be most likely to spread in established populations. Innovations that spread through a three-way interaction of naive predator, informed individual, and prey have a maximum R_0 at lower predator abundances (and higher prey abundances; fig. S6). These innovations might be more likely to spread in less established predator populations—for example, among introduced species (i.e., a species starting at low abundance) that have yet to become locally invasive. In fact, in newly colonized pine forests, black rats (*Rattus rattus*) learn to open pinecones by observing conspecifics perform this behavior (Aisner and Terkel 1992). Conversely, marginalized native species responding to an invader might be likely to learn to forage on the invader via the same three-way interaction. This appears to be occurring when some

Australian predators encounter cane toads (Beckmann and Shine 2011; Parrott et al. 2019). Innovations that reduce mortality independently of prey can spread more easily than other types of innovations, so their spread might not be reliably correlated with population size or mode of information transmission. Once an innovation is established in a predator population, the temporal pattern of innovation prevalence is also somewhat sensitive to the type of transmission function (fig. S4). We also note that our results hinge on our assumption of density-dependent social learning. Certain systems may be better described by frequency-dependent transmission. This could apply when individuals actively seek one another out or are in constant contact because of group living. An example might likely be meerkats, which actively teach their young to handle scorpions (Thornton and McAuliffe 2006). Thus, our assumption is not the only biologically reasonable one, and systems better described by other social learning functions may produce different results.

In a spatially structured system, more complex outcomes are possible, and they might make innovations less likely to cause predator or prey extinction. If the spread of an innovation is heterogeneous across the landscape, populations might cycle asynchronously with the temporal and spatial spread of the innovation (a phenomenon seen in other, nonbehaviorally labile systems and termed the “inflationary effect”; Roy et al. 2005; Kortessis et al. 2020). Another potentially interesting factor we do not explicitly consider is the possibility of stochastic extinction of the innovation (even if the predator species persists). This might be quite important if the innovation routinely becomes extinct in some subpopulations of a metapopulation only to be rediscovered in another subpopulation. This appears to be common in animal societies. For example, predatory behavior appears to have been acquired several times by great tits (*Parus major*), with isolated reports of attacks on other birds in the literature (Saunders 1889; Caris 1958; Barnes 1975) and in the popular news (Jokinen 2013). A population of great tits in Hungary apparently also learned to find and kill bats as they emerged from their hibernation caves (Estók et al. 2010). However, these behaviors are not commonly observed in the species across its very large geographic range. Thus, they may represent an instance of spontaneous emergence and extinction of innovations (although more research is needed to determine whether there is a genetic predisposition toward carnivory). The probability of extinction and reemergence of an innovation would add an additional layer of nuance to our predictions for behavioral variability. Generally speaking, it would be of great interest to expand the spatial complexity of the systems in which innovation transmission is modeled.

There must be some limits placed on the use of social information for its rate of transmission to be held in check.

Why would an animal not adopt an advantageous novel behavior from another member of its species? Costs specific to social learning include increased competition from conspecifics (Seppänen et al. 2007) as well as increased chances of acquiring pathogens (Cantor et al. 2021). Indeed, the evolution of sociality and pathogen virulence may codetermine animal social networks (Prado et al. 2009). Organisms can also use information from genetic biases, early developmental effects, and personal experience (Laland 2004; Dall et al. 2005). A critical alternative to social information is personal information. Which one an animal uses can be context dependent (reviewed in Kendal et al. 2005). It would be interesting to integrate models on the evolution of personal versus social information use (e.g., Wakano and Aoki 2007; Borofsky and Feldman 2022) with the ecological dynamics of predators and prey in this study.

An open question is how social (and personal) information affects the dynamics of multispecies communities. Adaptive foraging can stabilize the dynamics of ecological networks (Valdovinos et al. 2010). The results of the present study make it tempting to hypothesize that highly innovative species may depend on continuous innovation to exploit new populations of prey if foraging innovations drive local prey extinct or to abundances so low that predator populations cannot sustain themselves. Among birds, innovative species tend to have lower extinction risk and more stable or increasing populations than less innovative species (Ducatez et al. 2020). However, this is attributed to informed individuals responding less aversely to habitat destruction, so the results of Ducatez et al. (2020) do not speak directly to our study of predator-prey relationships. A promising future direction is examining the ecological dynamics of innovation in more diverse systems.

Although we focused on innovations among predators, prey may reciprocally change their behavior in response to predator innovations. Prey responses are well documented in the context of predator evolutionary innovations (e.g., Hanifin et al. 2008) but could occur in response to predator behavioral innovations too (Whitehead et al. 2019; Cantor et al. 2021). Furthermore, countermeasures by prey are socially transmitted, such as alarm calling (Magrath et al. 2015) and habitat use (Fortin et al. 2005). Cultural arms races between predators and prey have the potential to create a constantly shifting landscape of fear over which predators and prey contest their existence (Brown et al. 1999; Laundré et al. 2001).

In general, emerging theory suggests that social information can have significant impacts on population persistence (Schmidt et al. 2015; Schmidt 2017), competitive outcomes (Gilpin et al. 2016; Gil et al. 2018, 2019; Wakano et al. 2018), and predatory behavior (Borofsky and Feldman 2022). Exploring further scenarios such as those we have discussed here will help us broadly understand the

role information plays in ecological processes and maintaining phenotypic diversity within populations.

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Statement of Authorship

Conceptualization: D.W.K., M.W.S.; methodology: D.W.K., M.W.S.; investigation: D.W.K., M.W.S.; visualization: D.W.K.; writing—original draft: D.W.K.; writing—review and editing: D.W.K., M.W.S.

Data and Code Availability

All code is available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2z34tmpqn>; Kikuchi and Simon 2023).

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