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Pick your trade-offs wisely: Predator-prey eco-evo dynamics are qualitatively different under different trade-offs

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ABSTRACT

In recent decades, myriad studies have explored the population dynamics of coevolving populations of predator and prey. A variety of choices are made in these models: exponential or logistic prey growth in the absence of a predator, various forms of predator functional response, and uni- or bi-directional trait axes. In addition, some form of trade-offs are assumed in order to prevent run-away evolution of the prey and predator traits. While there is a considerable amount of theory regarding various forms of prey growth rates and predator functional responses, only a few studies have explored how different types of trade-offs affect predator-prey dynamics. Here, we compared two ditrophic coevolution models incorporating different trade-offs via dual effects of the prey trait on attack rate and either prey carrying capacity or intrinsic growth rate. We employed a standard dynamical systems approach to analyze the equilibrium conditions of each model and find conditions for non-equilibrium oscillatory coexistence. The exact effect of various parameters on the outcome of predator-prey interactions depends on whether the trade-offs affect the intrinsic growth rate or carrying capacity. In particular, coexistence is more likely when prey growth rate is affected by the evolving trait. In addition, in parameter regimes where cycles occur in both models, oscillations typically have larger periods and amplitudes when prey growth rate is affected by the evolving trait.

1. Introduction

Interactions between predators and their prey are among the most frequently studied ecological interactions in nature. Classic ecological theory led to hundreds of experiments that have documented the relative importance of these interactions (Englund et al., 1999; Gurevitch et al., 2000) and their cascading effects on other trophic levels (Schmitz et al., 2000; Shurin et al., 2002). Classic theory predicts various outcomes in terms of coexistence of predator and prey, but a common prediction is that predator and prey coexist in oscillations (Beddington et al., 1975; Berryman, 1992; Lotka, 1925; Volterra and Brelot, 1931). In these cases, predator abundances increase with increasing prey density until a threshold level where predators overexploit prey, resulting in a decrease in prey abundance, followed by a decrease in predator abundance, which ultimately allows the prey population to recover. Theoretically, predator population cycles should lag behind prey population cycles by a quarter of a cycle phase (Case and Roughgarden, 2000). These dynamics are well supported in some systems (Lynx-hare (Krebs et al., 2001), rotifer-algae (Yoshida et al., 2003)), but in other systems, stable coexistence between predator and prey have proved unlikely (Fujii, 1999; Huffaker, 1958), or predator-prey cycles do not match those predicted by theory (Hiltunen et al., 2014; Yoshida et al., 2007, 2003).

One reason that dynamics in natural systems may not match theoretical predictions is the context-dependency of species interactions. The strength of interactions between species may depend on the environment in which those interactions occur (Bertness and Callaway, 1994). Moreover, we could broadly define environmental context to include the genetic environment of the predator and prey populations. Intraspecific trait variation plays an important role in the strength of interactions between predator and prey (Bolnick et al., 2011; Gross et al., 2009; Litchman and Klausmeier, 2008). For example, different individuals of three-spined sticklebacks differ in morphology, depending on whether they come from benthic or limnetic habitats, which affects what they eat, or by whom they are eaten (Reimchen, 1980; Reimchen and Nosil, 2001). In addition to such spatial variation in traits,

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temporal trait variability over evolutionary time may also affect predator-prey interactions.

Recent evidence suggests that evolution can occur on contemporary time scales that affect ecological interactions, particularly when selection pressure is very strong, or when generation times are very short (Hairston Jr. et al., 2005; Schoener, 2011; Thompson, 1999). DeLong et al. (2016) recently quantified that rates of change of phenotypes are on average $\frac{1}{4}$ of the concurrent rates of change of population sizes. In many cases, predators serve as important selective agents on prey populations (Brodie III., 1992; Endler, 1991; Walsh and Reznick, 2008) and, conversely, prey can serve as important selective agents on predator populations (Lill, 2001; Motychak et al., 1999; West et al., 1991). When predators evolve in response to prey, attack rates or consumption of prey should increase, thus increasing the strength of ecological interactions between predator and prey (Strauss et al., 2006). Conversely, prey that evolve increased escape ability or avoidance of predators should decrease the strength of the ecological interaction (Strauss et al., 2006).

Evolution can have important consequences for predator-prey cycles (Hiltunen et al., 2014). Previous models have shown that incorporating prey evolution can shift predator-prey population dynamics between equilibrium, stable cycles, and chaotic coexistence (Abrams and Matsuda, 1997; Saloniemi, 1993). Yoshida et al. (2007) modeled prey that evolve on ecological time scales and found that prey evolution largely masked the predator-prey cycles that occured in the absence of predation. These results were supported by experiments in laboratory microcosms, in which algal evolution in response to rotifer predation eliminated the oscillating cycles that occured when algal population lacked sufficient genetic variation to evolve (Yoshida et al., 2007; 2003). Becks et al. (2010) extended this work and found that in the presence of sufficient genetic variation, populations underwent ecological predator-prey oscillations, as defended prey were favored when predators were abundant and undefended prey were favored when predators were rare; without initial genetic variation, populations quickly converged on a steady state equilibrium.

Because both predator and prey species may be important selective agents on each other, coevolution between predator and prey might be important for determining the stability of the system. Early models found that an evolutionary arms race leads to Red Queen dynamics, in which both predator and prey evolve in response to fluctuating selection that maintains their ecological interaction over time (Brodie III and Brodie Jr., 1999; Van Valen, 1973). However, coevolution need not lead to a stable ecological equilibrium (Abrams and Matsuda, 1997; Bengfort et al., 2017; Cortez and Weitz, 2014; Klauschies et al., 2016; Mougi, 2012; Mougi and Iwasa, 2011; Saloniemi, 1993; Tien and Ellner, 2012; Tirok et al., 2011; van Velzen and Gaedke, 2017). Small adaptive trait changes in predator or prey can result in changes in attack rates that lead to antiphase oscillations (Bengfort et al., 2017). Similarly, Mougi (2012) suggested that antiphase cycles or cryptic cycles could occur in systems in which both predator and prey evolve, but not when only a single species evolves. Mougi's results seemingly contradict those of Yoshida et al. (2007), who find cryptic cycles in models with on prey evolution. However, their modeling approaches vary in a critical way: Yoshida et al. assume a unidirectional axis in the prey trait, while Mougi assumes bidirectional axes in both predator and prey. Predator and prey often have dramatically different generation times, which could lead to differences in rates of evolution in each species. Even if generation times are similar, selection on prey may be stronger because a single interaction between predator and prey individuals has a huge effect on prey fitness, but often less effect on predator fitness (life vs. lunch; (Brodie III and Brodie Jr., 1999)). Furthermore, traits in one species may be more heritable than traits in another, resulting in different rates of evolution even under equivalent selection pressure.

Coevolutionary models can result in unrealistic runaway evolution, unless models incorporate some form of trade-off. For example, some models assume an increase in predator or prey traits on a uni-directional axis linearly also decreases the growth rate of that species. (e.g. Tien and Ellner, 2012. Other models assume that increases in predator traits along a uni-directional axis result in reductions in conversion efficiency (Klauschies et al., 2016; Mougi and Iwasa, 2011; Tirok et al., 2011; van Velzen and Gaedke, 2017) or increased death rate (Cortez and Weitz, 2014; Mougi, 2012; Tien and Ellner, 2012; van Velzen and Gaedke, 2017). Few studies have explored how the natures of different trade-offs affect ecological dynamics (Tien and Ellner, 2012).

Because of the variety of results which have arisen out of recent eco-evolutionary models of coevolving predator and prey, it is crucial that we gain a deeper understanding of how modeling choices surrounding trade-offs affect the outcomes of population dynamics. Here we analyze and compare two simple models of predator and prey which contain different trade-offs for the prey population. We assume bi-directional trait axes for both predator and prey traits (e.g. body size), where attack rates of predator on prey are maximized if trait matching occurs. Run-away evolution of the prey is prevented by the tethering of the prey trait to an optimal value via some form of trade-off, while runaway evolution of the predator is prevented via the trait matching requirement for attack rate. For this reason, we do not include additional trade-offs in the predator. Our goal in this study is to understand how predator-prey eco-evolutionary dynamics differ under two different trade-offs in prey.

2. Model formulation

Consider predator and prey species with densities $P = P(t)$ and $N = N(t)$ at time t, respectively. Assume the predator and prey populations have mean quantitative traits $\overline{p} = \overline{p}(t)$ and $\overline{n} = \overline{n}(t)$, respectively, and that these traits can be measured in the same unit, or can be transformed into the same unit. Also assume these traits are normally distributed through the populations with constant phenotypic variances σ^2 and β^2, respectively (Schreiber et al., 2011). In other words, their trait distributions are given by

$$q_p(p, \overline{p}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(p-\overline{p})^2}{2\sigma^2}\right],$$

$$q_n(n, \overline{n}) = \frac{1}{\sqrt{2\pi\beta^2}} \exp\left[-\frac{(n-\overline{n})^2}{2\beta^2}\right],$$

where phenotypic variances σ^2 and β^2 have additive genetic (subscript G) and environmental (subscript E) components (i.e., $\sigma^2 = \sigma_G^2 + \sigma_E^2$ and $\beta^2 = \beta_G^2 + \beta_E^2$).

Assume predator individuals with trait value p attack prey individuals with trait value n with attack rate $a = a(p, n)$. Also assume predators have a linear functional response and convert consumed prey in to offspring with efficiency e and have a constant death rate d. Then the fitness of predators with trait value p and consuming prey individuals with trait value n is

$$W(N, n, p) = ea(p, n)N - d,$$

and the per-capita mean fitness of the predator population is

$$\overline{W}(N, \overline{n}, \overline{p}) = \int_{\mathbb{R}^2} W(N, n, p) q_p(p, \overline{p}) q_n(n, \overline{n}) \mathrm{d}p\mathrm{d}n. \tag{1}$$

Assume prey with trait value n experience density-dependent logistic-type growth with growth rate $r = r(n)$ and carrying capacity $K = K(n)$ in the absence of predation. Since the prey trait n affects the predator-prey interaction a in addition to ecological variables in the absence of predation, we consider the prey trait to be ecologically pleiotropic. Thus the fitness of prey with trait value n interacting only with predators with trait value p is

$$Y(N, P, n, p) = r(n)\left(1 - \frac{N}{K(n)}\right) - a(p, n)P,$$

and the per-capita mean fitness of the prey population is

$$\overline{Y}(N, P, \overline{n}, \overline{p}) = \int_{\mathbb{R}^2} Y(N, P, n, p)q_n(n, \overline{n})q_p(p, \overline{p})\mathrm{d}n\mathrm{d}p. \tag{2}$$

Thus, the ecological dynamics are given by

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\overline{W}(N, \overline{n}, \overline{p}), \qquad \frac{\mathrm{d}N}{\mathrm{d}t} = N\overline{Y}(N, P, \overline{n}, \overline{p}). \tag{3}$$

Assuming each evolutionary variable stays normally distributed with unchanging variance, then the change of each evolutionary variable is proportional to the partial derivative of their mean fitness function with respect to that variable. In other words, evolution is always in the direction which immediately increases the mean fitness of the population (Lande, 1976). Specifically, the constant of proportionality is the genetic component of the phenotypic variances. This gives rise to the evolutionary components of this model:

$$\frac{\mathrm{d}\overline{p}}{\mathrm{d}t} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{p}}, \qquad \frac{\mathrm{d}\overline{n}}{\mathrm{d}t} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}.$$

If there is no evolution, i.e., all of the ecological parameters are constant ($\sigma_G = \beta_G = 0$), the dynamics of the resulting purely-ecological system (4) are well known.

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P[eaN - d], \qquad \frac{\mathrm{d}N}{\mathrm{d}t} = N\left[r\left(1 - \frac{N}{K}\right) - aP\right] \tag{4}$$

As a review, the three equilibria of this simplified model are extinction $(P^*, N^*) = (0, 0)$, (unstable), exclusion $(P^*, N^*) = (0, K)$ (locally asymptotically stable if $d > Kea$), and coexistence $(P^*, N^*) = \left(\frac{r}{a}\left(1 - \frac{N^*}{K}\right), \frac{d}{ea}\right)$, (biologically feasible and locally asymptotically stable if $d < Kea$). Since the exclusion and coexistence stability conditions are equal and opposite, there is no non-equilibrium dynamic. In other words, either the predator becomes extinct and the prey population asymptotically approaches its carrying capacity, or the predator and prey asymptotically approach a stable coexistence state.

However, ecological interactions are often dependent on which genetic variants are involved in the interactions. Evolutionary changes in traits may shift the strength of ecological interactions, which may in turn cause feedback by shifting the evolutionary variables via selection by ecological interactions. This eco-evolutionary feedback loop can affect both ecological and evolutionary outcomes. Since the purely-ecological model (4) is completely asymptotically stable, incorporating evolution here can only serve to destabilize the ecological equilibria.

2.0. Model 0 – no stabilizing selection

First we define the attack rate of a predator individual with phenotype p on a prey individual with phenotype n as a Gaussian function of their difference. For this study, we assume prey have a bidirectional axis of vulnerability to predation, which means they can reduce the successful predation rate by having a phenotype either greater or less than the matching predator phenotype. Examples of foraging traits on bidirectional axes are relative body sizes of predator and prey, and number and size of gill rakers in predatory freshwater fish (i.e. threespine stickleback) compared to body size of insect larvae or zooplanktonic prey (Saloniemi, 1993). Similar to Schreiber et al. (2011), the attack rate is maximized when $p - n$ is equal to some optimal difference θ_a and decreases hyper-exponentially as $|p - n|$ diverges from θ_a:

$$a(p, n) = \alpha \exp\left[-\frac{((p - n) - \theta_a)^2}{2\tau_a^2}\right],$$

where α is the maximal attack rate and τ_a determines how steeply the attack rate declines with distance from the optimal trait difference θ_a. In effect, τ_a determines how phenotypically specialized the predator must be to consume the prey (Schreiber et al., 2011). In other words, for large τ_a only large deviations from the optimal trait difference will result in large reductions in the attack rate, while for small τ_a even small deviations from the optimal trait difference have large fitness consequences. Under these assumptions, the average attack rate of the predator species on the prey species is

$$\begin{aligned}\overline{a}(\overline{p}, \overline{n}) &= \int_{\mathbb{R}^2} a(p, n)q_p(p, \overline{p})q_n(n, \overline{n})\mathrm{d}p\mathrm{d}n \\ &= \frac{\alpha\tau_a}{\sqrt{A}} \exp\left[-\frac{((\overline{p} - \overline{n}) - \theta_a)^2}{2A}\right],\end{aligned}$$

where $A := \tau_a^2 + \sigma^2 + \beta^2$. If all other ecological parameters (r, K, d, and e) are constant, this model may result in asymptotically stable ecological equilibrium, but runaway evolution, i.e., an evolutionary arms race where the population densities are constant but trait values are unbounded in time (Appendix D). This is not realistic because all characters have some constraints on their evolution (Saloniemi, 1993). Below we introduce two expanded models which tether the prey character $\overline{n}$ to an optimal value via decreases of vital ecological functions.

2.1. Model 1 – stabilizing selection via prey intrinsic growth rate

It may be the case that there is an optimal prey body size which maximizes prey intrinsic growth rate (Werner et al., 1984). If trait matching must occur for the prey species and their resource, then it is appropriate to model prey growth rate r as a Gaussian function of its trait value n, given by

$$r(n) = \rho \exp\left[-\frac{(n - \theta_r)^2}{2\tau_r^2}\right],$$

where ρ is the maximal growth rate of the prey species and τ_r determines how steeply the growth rate declines with distance from the optimal trait value θ_r. In effect, τ_r determines how far the prey trait value can deviate from the optimal trait value while still maintaining an adequate growth rate. In other words, for large τ_r only large deviations from the optimal trait value θ_r can result in large reductions in prey growth rate, while for small τ_r even small deviations from θ_r can result in large reductions in prey growth rate. Under these assumptions, the average growth rate of the prey species is

$$\overline{r}(\overline{n}) = \int_{\mathbb{R}} r(n)q_n(n, \overline{n})\mathrm{d}n = \frac{\rho\tau_r}{\sqrt{B}} \exp\left[-\frac{(\overline{n} - \theta_r)^2}{2B}\right]$$

where $B := \tau_r^2 + \beta^2$. For this first model, we assume the prey trait does not affect its resource use, i.e., the prey population carrying capacity K is constant. Thus the ecological and evolutionary dynamics of Model 1 are:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[e\overline{a}(\overline{p}, \overline{n})N - d\right], \tag{5a}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right) - \overline{a}(\overline{p}, \overline{n})P\right], \tag{5b}$$

$$\frac{\mathrm{d}\overline{p}}{\mathrm{d}t} = \sigma_G^2\left[\frac{eN(\theta_a - (\overline{p} - \overline{n}))}{A}\overline{a}(\overline{p}, \overline{n})\right], \tag{5c}$$

$$\frac{\mathrm{d}\overline{n}}{\mathrm{d}t} = \beta_G^2\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right)\frac{\theta_r - \overline{n}}{B} + \frac{P(\theta_a - (\overline{p} - \overline{n}))}{A}\overline{a}(\overline{p}, \overline{n})\right]. \tag{5d}$$

2.2. Model 2 – stabilizing selection via prey carrying capacity

It may be the case that suboptimal investment in prey body size can result in reduced ability to process resources, which causes an uptake in prey foraging effort and an increase in intraspecific competition. A reduction in the carrying capacity K is synonymous with an increase in intraspecific competition. Thus, for the second model, we assume the prey trait does not affect its intrinsic growth rate, i.e., r is constant. Rather, the prey population carrying capacity K is a Gaussian function of its trait value n.

$$K(n) = \kappa \exp\left[-\frac{(n - \theta_K)^2}{2\tau_K^2}\right]$$

where κ is the maximal carrying capacity of the prey species and τ_K determines how steeply the carrying capacity declines with distance from the optimal trait value θ_K. In effect, $1/K(n)$ gives the strength of competition of a prey individual with trait value n, and $K(n)$ gives the carrying capacity of a population consisting entirely of individuals with trait value n. Thus the ecological and evolutionary dynamics of Model 2 are:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[e\overline{a}(\overline{p}, \overline{n})N - d\right], \tag{6a}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left[r\left(1 - \frac{N}{\overline{K}(\overline{n})}\right) - \overline{a}(\overline{p}, \overline{n})P\right], \tag{6b}$$

$$\frac{\mathrm{d}\overline{p}}{\mathrm{d}t} = \sigma_G^2\left[\frac{eN(\theta_a - (\overline{p} - \overline{n}))}{A}\overline{a}(\overline{p}, \overline{n})\right], \tag{6c}$$

$$\frac{\mathrm{d}\overline{n}}{\mathrm{d}t} = \beta_G^2\left[-\frac{rN(\overline{n} - \theta_K)}{\overline{K}(\overline{n})C} + \frac{P(\theta_a - (\overline{p} - \overline{n}))}{A}\overline{a}(\overline{p}, \overline{n})\right], \tag{6d}$$

where the harmonic mean of prey carrying capacity is given by

$$\overline{K}(\overline{n}) = \left(\int_{\mathbb{R}} \frac{1}{K(n)} q_K(n, \overline{n})\mathrm{d}n\right)^{-1} = \frac{\kappa\sqrt{C}}{\tau_K}\exp\left[-\frac{(n - \theta_K)^2}{2C}\right],$$

and $C := \tau_K^2 - \beta^2$ (note that our use of the harmonic mean here is a result of the calculation of mean prey fitness (Eqs. (2), (3)). This formulation requires $\tau_K > \beta$ because C is contained inside a square root, so no rigorous analysis can be done if $\tau_K \leq \beta$. However, if τ_K approaches β from above, then the peak of the average carrying capacity function $\overline{K}$ decreases to 0, which causes immediate extinction of the prey and thus extinction of the predator. The biological justification for varying the "carrying capacity" in the prey population in Model 2 is that a bidirectional trait like body size could affect how individuals are able to consume resources, which in turn affects intraspecific competition and decreases the effective carrying capacity of the population in that environment. If this is the case, then prey populations with high phenotypic variation (large β) are either unable to adequately consume resources or there is too much intraspecific competition. In either case, the prey population will not survive. This suggests there is a threshold value of phenotypic variation (τ_K) which determines whether or not the prey population is able to survive in that environment in the absence of predation. This is also mathematically intuitive since the harmonic mean is highly sensitive to small numbers. All parameters and their descriptions are listed in Table 1. See Appendix A for model derivation details.

Table 1
All model parameters and their biological meaning.

Parameter	Description
r, K	Prey intrinsic growth rate and carrying capacity
d, e	Predator death rate and efficiency
σ	Predator trait distribution variance; $\sigma^2 = \sigma_G^2 + \sigma_E^2$
β	Prey trait distribution variance; $\beta^2 = \beta_G^2 + \beta_E^2$
α, τ_a, θ_a	Maximum value, variance, and mean value of the Gaussian average attack rate function $\overline{a}(\overline{p}, \overline{n})$
ρ, τ_r, θ_r	Maximum value, variance, and mean value of the Gaussian average intrinsic growth rate function $\overline{r}(\overline{n})$
κ, τ_K, θ_K	Maximum value, variance, and mean value of the Gaussian average carrying capacity function $\overline{K}(\overline{n})$
A	$\tau_a^2 + \sigma^2 + \beta^2$
B	$\tau_r^2 + \beta^2$
C	$\tau_K^2 - \beta^2$

3. Results

3.1. Equilibria and stability analysis

In addition to using standard numerical techniques to simulate the model (Figs. 1 and 2), we analyze both models by employing a standard dynamical systems approach, which includes solving for equilibrium points and determining conditions for local linear stability. Both models have three types of equilibria $(N^*, P^*, \overline{n}^*, \overline{p}^*)$: extinction (of both species), exclusion (of the predator species), and coexistence. The extinction equilibria are given by

$$(N^*, P^*, \overline{n}^*, \overline{p}^*) = (0, 0, *, *), \tag{7}$$

and are unstable for all biologically relevant parameters (* represents an arbitrary quantity). The exclusion equilibria are given by

$$(N^*, P^*, \overline{n}^*, \overline{p}^*) = \left(K^*, 0, \theta_{\text{excl}}, \theta_{\text{excl}} + \theta_a\right), \tag{8}$$

where

$$\theta_{\text{excl}} = \begin{cases} *, & \text{for Model 1,} \\ \theta_K, & \text{for Model 2,} \end{cases} \qquad \text{and}$$

$$K^* = \begin{cases} K, & \text{for Model 1,} \\ \dfrac{\kappa\sqrt{C}}{\tau_K}, & \text{for Model 2,} \end{cases}$$

and are stable if

$$d > \frac{K^* e\alpha\tau_a}{\sqrt{A}}. \tag{9}$$

The coexistence equilibrium is given by

$$(N^*, P^*, \overline{n}^*, \overline{p}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau_a}, \frac{r^*\sqrt{A}}{\alpha\tau_a}\left(1 - \frac{N^*}{K^*}\right), \theta_{\text{coex}}, \theta_{\text{coex}} + \theta_a\right), \tag{10}$$

where

$$\theta_{\text{coex}} = \begin{cases} \theta_r, & \text{for Model 1,} \\ \theta_K, & \text{for Model 2,} \end{cases} \qquad \text{and}$$

$$r^* = \begin{cases} \dfrac{\rho\tau_r}{\sqrt{B}}, & \text{for Model 1,} \\ r, & \text{for Model 2,} \end{cases}$$

and is stable if

$$\frac{\sigma_G^2}{\beta_G^2} > \frac{r_{\text{stab}}}{d}\left(1 - \frac{d\sqrt{A}}{K_{\text{stab}} e\alpha\tau_a}\right), \tag{11}$$

where

$$r_{\text{stab}} = \begin{cases} \frac{\rho\tau_r}{\sqrt{B}}\left(1 - \frac{A}{B}\right), & \text{for Model 1,} \\ r, & \text{for Model 2,} \end{cases} \qquad \text{and}$$

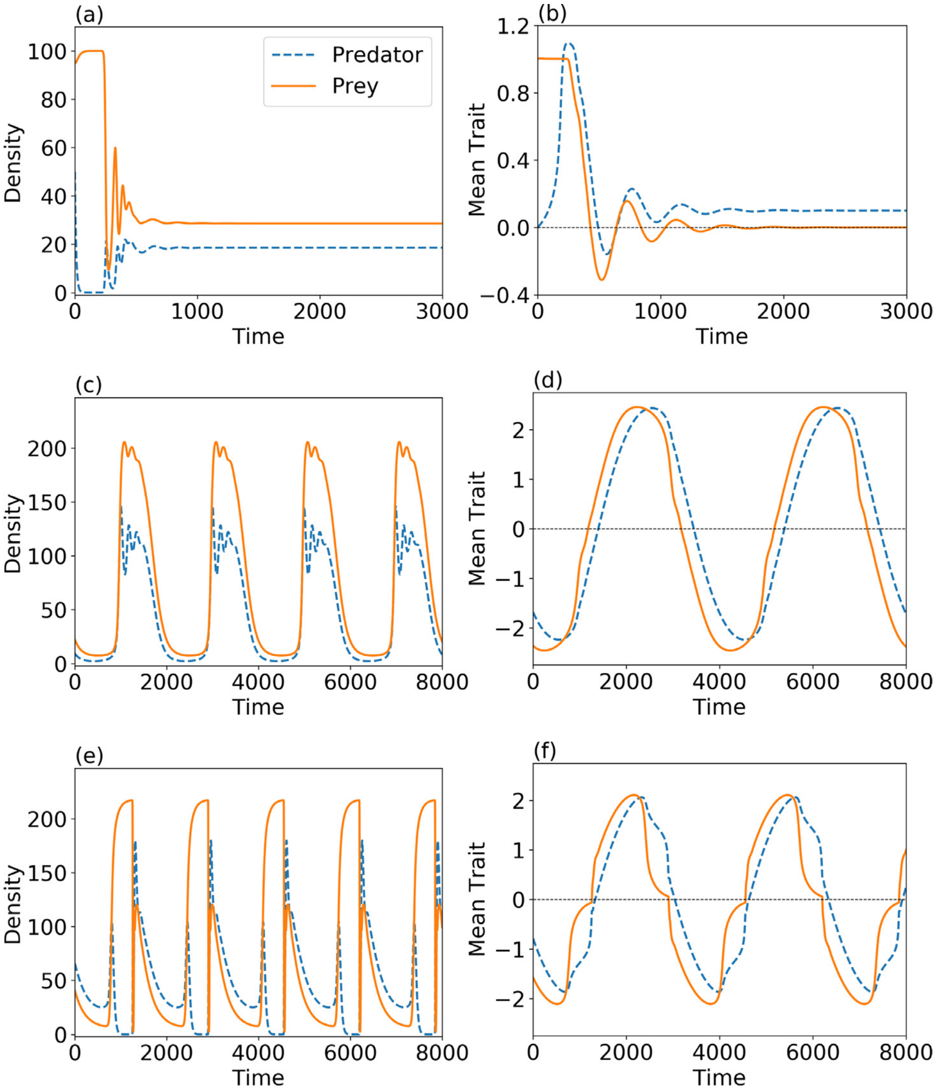

Fig. 1. Timeseries. The left panels (Fig. 1(a), (c), (e)) depict predator and prey population densities. The right panels (Fig. 1(b), (d), (f)) depict predator and prey mean trait values. Fig. 1(a) and (b) show stable coexistence equilibrium dynamics in Model 1. Fig. 1(c) and (d) show cyclic coexistence dynamics in Model 1. Fig. 1(e) and (f) show cyclic coexistence dynamics in Model 2. Parameter values: $e = 0.5,\ \alpha = 0.05,\ \sigma = \beta = 0.25,\ \theta_a = 0.1,\ \theta_r = \theta_K = 0$. Fig. 1(a) and (b) parameter values: $d = 0.1,\ \tau_a = 0.05,\ \tau_r = 0.55,\ \sigma_G = 0.18,\ \beta_G = 0.17,\ \rho = 0.2,\ K = 100$. Fig. 1(c)–(f) parameter values: $d = 0.05,\ \tau_a = 0.1,\ \tau_r = \tau_K = 1.0,\ \sigma_G = 0.106,\ \beta_G = 0.1,\ \rho = r = 0.5,\ \kappa = K = 225$.

$$K_{\text{stab}} = \begin{cases} K, & \text{for Model 1,} \\ \dfrac{\kappa\sqrt{C}}{\tau_K\left(1 + \dfrac{A}{C}\right)}, & \text{for Model 2,} \end{cases} .$$

See Appendices B and C for details of equilibria stability analysis.

In both models, the prey face a trade off between evolution of anti-predator traits and optimization of growth rate or carrying capacity. The size of this trade off $|\overline{n} - \theta_{\text{coex}}|$ is irrelevant when determining stability of the coexistence equilibrium (11). This is because Models 1 and 2 do not reduce to Model 0 when $\theta_{\text{coex}} = \theta_a$; rather, Model 1 and Model 2 reduce to Model 0 when growth rate and carrying capacity are constant, respectively. This happens when $\tau_r \to \infty$ and $\tau_K \to \infty$ because τ_r and τ_K describe the variation of prey growth rate and carrying capacity caused by variation in prey genotype. As $\tau_r \to \infty$ or $\tau_K \to \infty$, growth rate or carrying capacity approaches a constant value for the population because there are few individuals with extreme genotypes. Therefore coexistence stability is independent of the relative values of θ_a and θ_{coex} and dependent on the variance terms τ_r and τ_K.

Note that if both populations are extinct, their trait values can be arbitrary because the populations are in ecological equilibrium for any values of $\overline{p}^*$ and $\overline{n}^*$. Since θ_{excl} is arbitrary for Model 1, there are an infinite number of exclusion equilibria for Model 1. Thus, when (9) holds, the evolutionary dynamics will approach an equilibrium based on initial conditions. The prey trait at carrying capacity is arbitrary since selection on traits which affect intrinsic growth rate is weak when the prey population is near its carrying capacity. On the other hand, Model 2 has a unique exclusion equilibrium since selection on traits which affect prey population carrying capacity is strong when the population is near its carrying capacity. This is intuitive since increasing prey carrying capacity always increases average prey fitness. The predator population will be excluded if its death rate is sufficiently high. Also, higher prey carrying capacity, predator efficiency and predator maximum attack rate can destabilize the exclusion equilibrium in favor of the internal coexistence equilibrium, which is unique for each model. When (11) holds, the prey character $\overline{n}$ reaches its optimal value for the trait undergoing stabilizing selection, and the predator character $\overline{p}$ reaches the optimal difference to maximize attack rate.

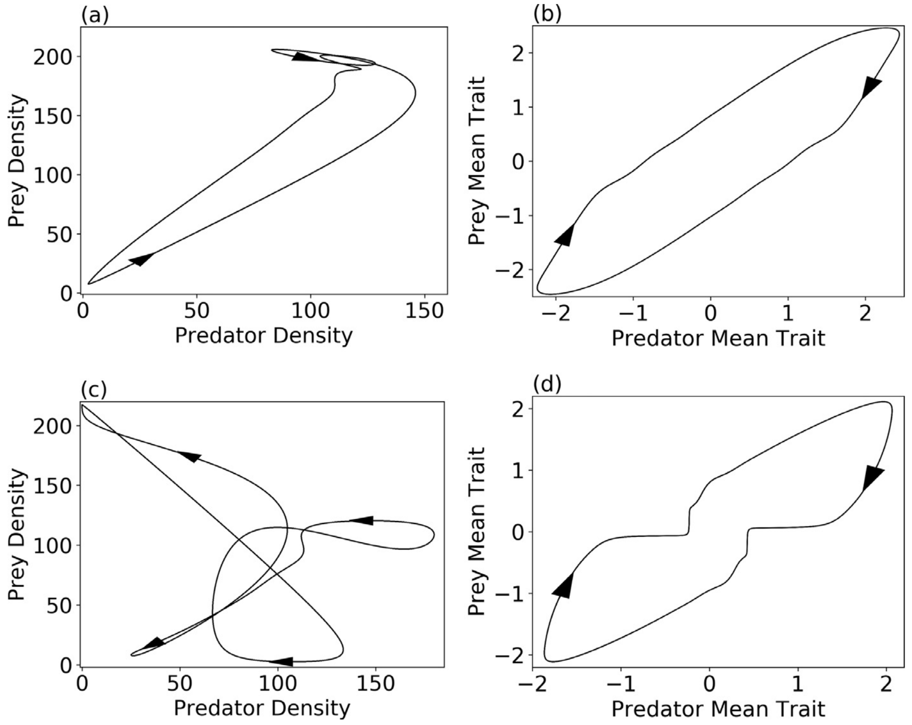

Fig. 2. Cycle Phaseplanes for Model 1 (Fig. 2(a) **and** (b)) **and Model 2** (Fig. 2(c) **and** (d)). The left panels (Fig. 2(a), (c)) depict phaseplanes of predator and prey population densities. The right panels (Fig. 2(b), (d)) depict phaseplanes of predator and prey mean trait values. Fig. 2(a) and (b) are the phaseplanes of the cyclic dynamics of Model 1 shown in Fig. 1(c) and (d). Fig. 2(c) and (d) are the phaseplanes of the cyclic dynamics of Model 2 shown in Fig. 1(e) and (f).

In (11), σ_G/β_G is the ratio of predator and prey speeds of evolution given equivalent selection pressure. This means the coexistence equilibrium (10) is stable if predator evolution can be fast enough in comparison to prey evolution. More precisely, stable equilibrium coexistence is more likely if the predator's trait is more heritable than the prey's trait. If this happens, the predator trait value "catches up" to the prey trait value, which increases the attack rate, hence decreasing prey density, and decreasing $|d\bar{n}/dt|$. The trait dynamics stabilize, resulting in decaying ecological oscillations.

In Model 1, if $\tau_a^2 > \tau_r^2 - \sigma^2$, then $r_{\text{stab}} < 0$. This always results in stable coexistence provided that (10) is biologically feasible. The biological feasibility condition for coexistence is the opposite condition as the exclusion stability condition (9). That is, provided $d < \frac{Ke\alpha\tau_a}{\sqrt{A}}$, then stable coexistence is inevitable if the variance of the attack rate curve τ_a is high enough. Biologically, this means that if the attack rate does not require high predator specificity, then stable equilibrium coexistence is more likely.

In Model 2, however, the coexistence stability condition boundary can be arranged so that only d is on the left hand side:

$$d = \frac{r\kappa e\alpha\tau_a\sqrt{C}}{\frac{\sigma_G^2}{\beta_G^2}\kappa e\alpha\tau_a\sqrt{C} + r\sqrt{A}\tau_K\left(1+\frac{A}{C}\right)}$$

and we find that d decreases to 0 as τ_a grows without bound to ∞ (since all terms are positive, the numerator is $\mathcal{O}(\tau_a)$ and the denominator is $\mathcal{O}\left(\tau_a^3\right)$). This means that for any value of τ_a, there is always a value of d such that (9) is not satisfied (Fig. 3). This is a key difference between the models: in Model 1, high values of τ_a never result in cyclic coexistence, whereas in Model 2, high values of τ_a may result in cycles for sufficiently low d. For fixed d in Model 2, however, the stable coexistence condition (11) will hold for sufficiently high τ_a. The notation $\mathcal{O}(\tau_a)$ and $\mathcal{O}\left(\tau_a^3\right)$ here mean that as τ_a grows indefinitely, the expression grows proportionally to τ_a or τ_a^3, respectively. The notation $\mathcal{O}(1)$ means an expression approaches a constant value in a given limit.

Note that $B = \mathcal{O}\left(\tau_r^2\right)$ as τ_r increases, and thus $\frac{\rho\tau_r}{\sqrt{B}} = \mathcal{O}(1)$. This means r_{stab} (for Model 1) is eventually an increasing function of τ_r. Since the right hand side of the coexistence stability condition (11) is an increasing function of r_{stab}, then increasing τ_r can destabilize the coexistence equilibrium. Similarly, note that $C = \mathcal{O}\left(\tau_K^2\right)$ as τ_K increases, and thus $\frac{\kappa\sqrt{C}}{\tau_K} = \mathcal{O}(1)$. This means K_{stab} is eventually an increasing function of τ_K. Since the right hand side of (11) is an increasing function of K_{stab}, then increasing τ_K can also destabilize the coexistence equilibrium. Biologically, these results mean that if prey are not required to be particularly close to the optimal trait value in order to have adequate growth rate or carrying capacity, then cyclic coexistence is more likely. More precisely, the coexistence stability condition boundaries are

$$d = \begin{cases} \dfrac{\rho\tau_R Ke\alpha\tau_a\left(\tau_r^2-\tau_a^2-\sigma^2\right)}{\frac{\sigma_G^2}{\beta_G^2}Ke\alpha\tau_a\left(\tau_r^2+\beta^2\right)^{3/2}+\rho\tau_r\left(\tau_r^2-\tau_a^2-\sigma^2\right)\sqrt{\tau_a^2+\sigma^2+\beta^2}} & \text{for Model 1,} \quad (a) \\ \dfrac{r\kappa e\alpha\tau_a\left(\tau_K^2-\beta^2\right)^{3/2}}{\frac{\sigma_G^2}{\beta_G^2}\kappa e\alpha\tau_a\left(\tau_K^2-\beta^2\right)^{3/2}+r\tau_K\left(\tau_K^2+\tau_a^2+\sigma^2\right)\sqrt{\tau_a^2+\sigma^2+\beta^2}} & \text{for Model 2.} \quad (b) \end{cases} \tag{12}$$

In Model 1, $d \to \frac{rKe\alpha\tau_a}{\frac{\sigma_G^2}{\beta_G^2}Ke\alpha\tau_a+\rho\sqrt{A}}$ as $\tau_r \to \infty$, and in Model 2 $d \to \frac{r\kappa e\alpha\tau_a}{\frac{\sigma_G^2}{\beta_G^2}\kappa e\alpha\tau_a+r\sqrt{A}}$ as $\tau_K \to \infty$. These limiting values of d are less than the predator exclusion boundary, so as τ_r or $\tau_K \to \infty$, there is an intermediate range of d values which results in stable coexistence,

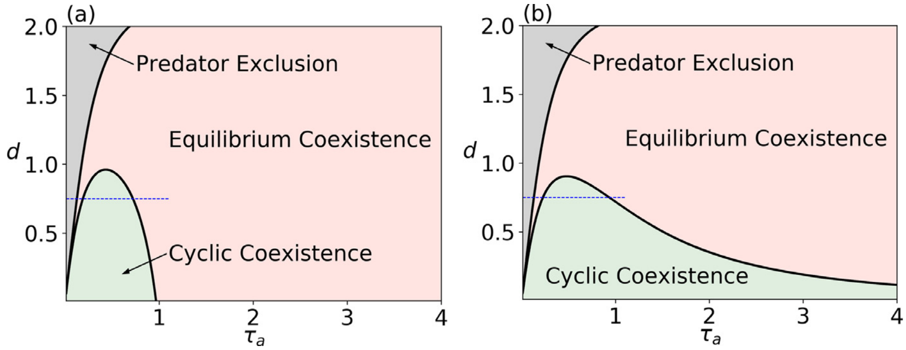

Fig. 3. Bifurcation diagrams for model 1 (Fig. 3(a)) **and model 2** (Fig. 3(b)), **with predator death rate** (d) vs. predator specialization (τ_a)**.** In Fig. 3(a), the coexistence stability boundary crosses the τ_a axis, while in Fig. 3(b), the coexistence stability boundary approaches the τ_a axis as $\tau_a \to \infty$. There is a much larger region in parameter space that results in cyclic behavior in Model 2 than in Model 1. Parameter values: $\sigma = \beta = 0.25$, $e = \alpha = 0.1$, $\tau_r = \tau_K = 1$, $\sigma_G/\beta_G = 0.4$, $\rho = r = 0.5$, $K = \kappa = 225$. Fig. 6 c shows cycle maxima, minima, and periods for the parameter values indicated by the dotted line ($d = 0.75$, $0 \leq \tau_a \leq 1.1$).

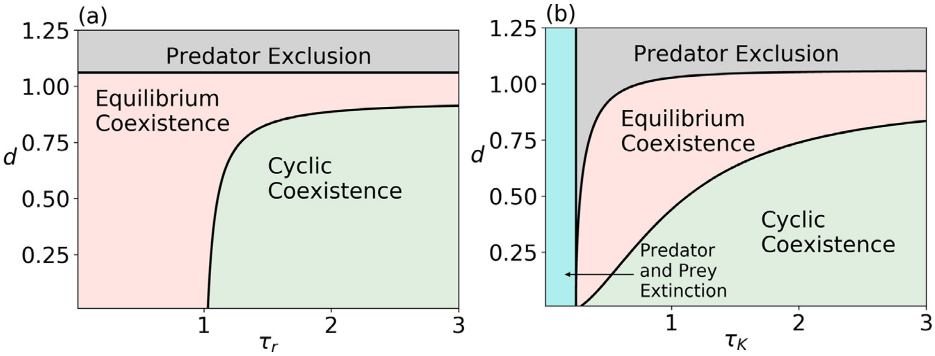

Fig. 4. Bifurcation diagrams for model 1 (Fig. 4(a)) **and model 2** (Fig. 4(b)), **with predator death rate** (d) vs. prey trade-off strength (τ_r or τ_K)**.** Parameter values: $e = 0.1$, $\alpha = 0.05$, $\tau_a = 1$, $\sigma_G/\beta_G = 0.2$, $\rho = r = 0.3$, $K = \kappa = 225$, $\sigma = \beta = 0.25$.

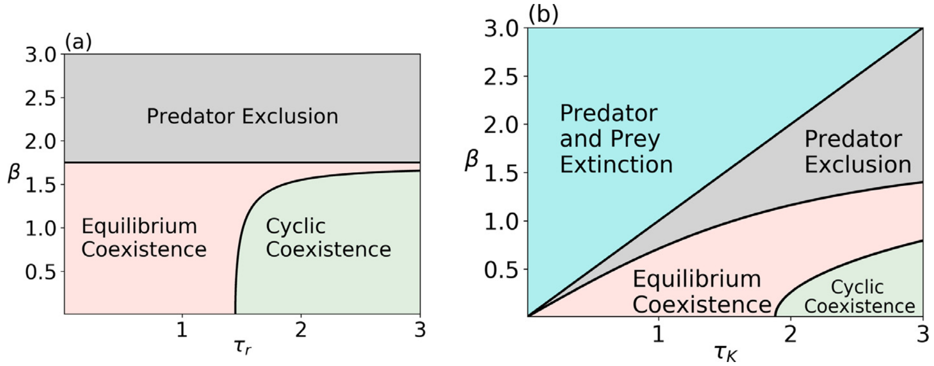

Fig. 5. Bifurcation diagrams for model 1 (Fig. 5(a)) **and model 2** (Fig. 5(b)), **with prey trait distribution variance** (β) vs. prey trade-off strength (τ_r or τ_K)**.** Parameter values: $e = 0.1$, $\alpha = 0.05$, $d = 0.5$, $\tau_a = 1$, $\sigma = 1$, $\sigma_G/\beta_G = 0.1$, $\rho = r = 0.3$, $K = \kappa = 225$.

while low d values will result in cyclic coexistence and high d values result in predator exclusion (Fig. 4). The models differ, however, as τ_r or τ_K decrease. First, Model 2 predicts both predator and prey go extinct for $\tau_K \leq \beta$, while coexistence is possible for arbitrarily small τ_r in Model 1. In addition, while the denominator of (12b) is positive for $\tau_K > \beta$ in Model 2, the denominator of (12a) is negative for sufficiently small τ_r in Model 1.

Fig. 5 shows similar distinctions between the models. The predator exclusion stability condition (9) is independent of τ_r, and thus the boundary between the “Predator Exclusion” and “Equilibrium Coexistence” regions is flat for Model 1. However, (9) is dependent on τ_K which accounts for the different shape for Model 2. We also see a larger region of coexistence in Model 1 than in Model 2.

3.2. Qualitative differences in the models’ cycles

Fig. 1(a) and (b) display a stable coexistence dynamic from Model 1. In this simulation, the initial prey and predator mean trait values, $\overline{n}_0$ and $\overline{p}_0$, respectively, are far enough apart that the predator is not a threat. Their initial difference is $\overline{p}_0 - \overline{n}_0 = 1$, which is large in comparison to the variance of the attack rate curve $\tau_a = 0.05$. This means that only a very small percentage of predators are initially well suited to attack the prey, resulting in very strong selective pressure on the predators. In contrast, the prey population is not initially threatened by the predator, resulting in very weak selective pressure on the prey. Once the predator mean trait value is close enough to the optimal difference θ_a, the predator becomes a viable threat to the prey, increasing predator density and decreasing prey density. The predator and prey then undergo dampening oscillations to coexistence equilibrium as their mean trait values stabilize. Model 2 simulations resulting in stable equilibrium coexistence show similar dynamics.

In contrast to the purely ecological system (4), both models' exclusion and coexistence stability conditions are not equal or opposite, which implies there is at least one type of non-equilibrium dynamic. Fig. 1(c) and (d) depict long-term stable oscillatory behavior in Model 1, and Fig. 1(e) and (f) depict long-term stable oscillatory behavior in Model 2. In order to achieve a good comparison between Models 1 and 2, we matched the parameters as closely as possible. In particular, we set the constant carrying capacity K from Model 1 equal to the maximum carrying capacity κ from Model 2, the constant intrinsic growth rate r from Model 2 equal to the maximum intrinsic growth rate ρ from Model 1, and the growth rate variance τ_r from Model 1 equal to the carrying capacity variance τ_K from Model 2.

The oscillations seen in Fig. 1(c)–(f) are similar in many ways, and we can intuitively understand them by considering the inverse effects that the evolution of the prey mean trait value sometimes has on its own fitness. In particular, consider the periods of time in which the prey mean trait value is undergoing selection *away* from the optimal value (θ_r for Model 1; θ_K for Model 2). Since the predator is a threat, the prey evolves away from the predator, decreasing attack rate $\overline{a}$, and hence increasing its fitness. However, as the prey evolves away from its optimal value, the trade off $|\overline{n} - \theta_{\text{coex}}|$ increases, reducing the average growth rate $\overline{r}$ (Model 1) or carrying capacity $\overline{K}$ (Model 2), and thus reducing prey fitness. These two inverse effects nullify each other whenever the prey mean trait value reaches a minimum or maximum. At these extrema, both populations are suppressed to low levels (due to either low growth rate in Model 1 or low carrying capacity in Model 2), and thus the selection pressure toward the optimal trait value outweighs the selection pressure of predation. The prey trait value then reverses direction and evolves *toward* its optimal value. During this time, prey mean fitness increases for two reasons: a negative effect on attack rate and a positive effect on the prey trait undergoing selection. Immediately after passing through the optimal value, however, the inverse effects take hold and the cycle begins again.

Predator and prey density cycles can be in phase in the larger evolutionary time scale, and out of phase in the smaller ecological time scale (Fig. 2). Note the density phase trajectory of Model 1 is generally positively sloped, which means prey and predator densities reach their minima and maxima at around the same time (Figs. 2(a) and 1(c)). However, when prey and predator densities are near their relative maxima, their cycles are temporarily out of phase, as indicated in Fig. 2(a) by the negative slope of the top part of the density phase trajectory. In other words, as the genetic environment changes to favor a high-density equilibrium, predator and prey densities diverge from the low-density equilibrium together, but on the ecological time scale predator and prey densities undergo out-of-phase, dampening oscillations toward this high-density equilibrium.

There are qualitative differences between the cycles in these two models, however, which may be attributed to the decrease in $|d\overline{n}/dt|$ (5d) as growth rate decreases, as opposed to the increase in $|d\overline{n}/dt|$ (6d) as carrying capacity decreases. This results in more rapid prey evolution when the prey mean trait is at an extrema in Model 2, and less rapid prey evolution when the prey mean trait is at an extrema in Model 1. In addition, prey growth rate in Model 2 is never as low as the mean prey growth rate in Model 1. Higher prey growth rate causes an increased predator equilibrium density, which increases selective pressure on the prey, causing bouts of more rapid prey evolution. On the other hand, the predators in Model 2 cannot adequately respond to this rapid evolution, resulting in a lag time where predator density is exponentially decreasing and the rate of predator evolution is diminished. In the simulations shown in Fig. 1(c)–(f), the increase in the Model 2 period due to the lag time is outweighed by its decrease due to the increase in $|d\overline{n}/dt|$ as carrying capacity decreases, and thus we see longer oscillatory periods in Model 1 ($T \approx 4000$ in Figs. 1(c), (d), 2(a), and (b)) than in Model 2 ($T \approx 3300$ in Figs. 1(e), (f), 2(c), and (d)). In Fig. 6 we see that the oscillation periods in Model 1 are greater than that in Model 2 for intermediate values of τ_a. This is intuitive since generalist predators are more able to respond to bouts of rapid prey evolution than specialist predators, thus removing the period of the exponentially decaying predator population. However, at larger values of τ_a, the oscillation periods in Model 2 are greater than that of Model 1. This may seem counterintuitive, but an increased ability to respond decreases the overall selective pressure on predators, ultimately resulting in slower evolution and greater oscillatory periods.

Finally, we proved the existence of Hopf bifurcations (Hale and Koçak, 1991) as parameters are shifted from satisfying the coexistence equilibrium stability condition of either model to not satisfying them. Hopf bifurcations occur when a shifting parameter causes a stable equilibrium to become unstable, while also creating cyclic behavior around the equilibrium. The existence of Hopf Bifurcations in both models suggests the existence of asymptotically stable limit cycles, which we conjecture are globally stable given positive density initial conditions. In this study we have shown the models exhibit stable cyclic behavior using simulations, but we stop short of rigorously proving the asymptotic stability of the attractors.

4. Summary and discussion

We formulated two coevolutionary predator-prey models which differ only in the form of an evolutionary trade-off. For both models, we found all equilibria and their local stability conditions. We showed the existence of Hopf bifurcations in both models, which suggests the existence of stable limit cycles (and which we conjecture are globally stable provided positive density initial conditions). While predator-prey cycles are possible without evolution if the predator has a saturating functional response, our models show that coevolution can cause ecological cycles even under the assumption of a linear functional response. This is important because the predator-prey model with logistic growth and linear functional response is well-known to not produce stable cycles.

In the first model, prey evolution to avoid predation is halted by a trade-off due to reductions in growth rate. This is a common form of trade-off incorporated into models and is a reasonable choice in many systems (Klauschies et al., 2016; Mougi, 2012; Mougi and Iwasa, 2010; 2011; van Velzen and Gaedke, 2017). In the second model, prey evolution is halted by a trade-off due to reuctions in carrying capacity. This is a less common choice but can be reasonable if shifting a continuous trait (i.e. body size) affects how prey are able to consume resources, altering their effective carrying capacity.

Previous models of coevolution in exploiter-victim systems have incorporated evolutionary trade-offs in various ways. Iwasa et al. (1991) modeled mate preference as a fitness cost, and in later analyses, Mougi and Iwasa (2010) found that the coexistence equilibrium is stable if the evolutionary adaptation of the prey is faster than that of the predator. These studies assumed unidirectional trait axes and trade-offs in prey and predator basal per-capita growth rates. Later, Mougi (2012) analyzed a coevolutionary model with bidirectional traits with trade-offs in prey growth rate and predator death rate. In contrast to their earlier studies, they found that the coexistence equilibrium is stable if the predator can adapt faster than the prey. These conflicting results may have been a result of choosing unidirectional or bidirectional

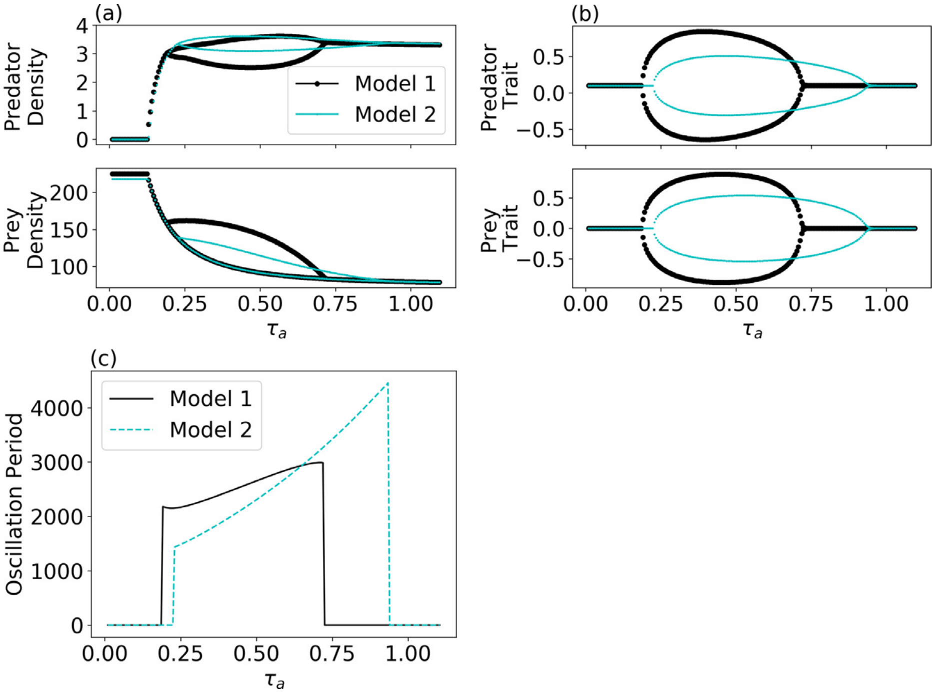

Fig. 6. Models 1 and 2 Bifurcation Diagrams (Fig. 6(a) **and** (b)) **and oscillation periods** (Fig. 6(c)). Parameter values match Fig. 3 for predator death rate $d = 0.75$. Also, $\theta_a = 0.1$, $\theta_r = \theta_K = 0$, $\sigma_G = 0.04$, and $\beta_G = 0.1$. As τ_a increases the population moves from predator exclusion, to coexistence equilibrium, to cyclic coexistence, and back to coexistence equilibrium. There is a small region of τ_a where Model 1 exhibits oscillatory coexistence and Model 2 exhibits coexistence equilibrium (τ_a between 0.18 and 0.2, approximately) and a larger region of τ_a where Model 2 exhibits oscillatory coexistence and Model 1 exhibits coexistence equilibrium (τ_a between 0.71 and 0.93, approximately). In Fig. 6(c), oscillation periods of 0 indicate non-oscillatory behavior.

trait axes, but they also may have been a result of choosing different forms of evolutionary trade-offs.

While many modeling choices can be jusitified by various biological examples, relatively few studies have explored how these choices affect results. Tien and Ellner (2012) compared two models with unidirectional trait axes and density independent and density dependent trade-offs. Interestingly, they found that stable coexistence is more likely if both predator *and* prey have fast adaptation in the density independent trade-off model, while stable coexistence is more likely if predator has faster adaptation than the prey in the density dependent trade-off model. In our study, both models resulted in stable coexistence if the ratio of predator to prey speeds of adaptation is sufficiently high. These conflicting results highlight the need for theoreticians to consider how the forms of trade-offs can affect model analyses. It is surprising this has not been a larger area of research given that trade-offs are so widely accepted as a necessary component of eco-evo models.

While this study follows the work of Mougi and Iwasa (2010, 2011), Mougi (2012) and Tien and Ellner (2012), who used a quantitative genetics framework to model trait evolution, others have utilized adaptive dynamics frameworks (Nuismer et al., 2005) and/or individual-based frameworks (Calcagno et al., 2010; DeLong and Gibert, 2016). Quantitative genetics eco-evo models typically assume that traits stay normally distributed with constant variance and that selection pressure is proportional to that variance (Abrams and Matsuda, 1997; Lande, 1976). This is a reasonable assumption according to studies by Gaylord (1953) and Van Valen (1969), who have noted that variance of morphological traits in a lineage often remains roughly constant (Lande, 1976). Others have assumed variance is constant but there is some other evolutionary force which decreases selective pressure as the mean trait approaches one or more boundary values (Bengfort et al., 2017; Cortez and Weitz, 2014; Klauschies et al., 2016; Saloniemi, 1993; Tien and Ellner, 2012; van Velzen and Gaedke, 2017). Nuismer et al. (2005) used an adaptive dynamics framework to model the evolution of trait variance for normally distributed traits, and Tirok et al. (2011) used a quantitative genetics framework to derive differential equations to model the evolution of trait mean and variance for normally distributed traits.

Any of the above evolutionary modeling choices also greatly affect analytical results. When using the framework of Tirok et al. (2011) to incorporate the dynamics of the trait variance σ_G^2 and β_G^2, we obtain results different from the main text, as seen in the comparison between Figs. 1 and 7. The shorter periods seen in the oscillating solutions is a result of increased and evolving trait variances. We also see coexistence is threatened if prey variance can increase without bound in Model 1. This is because reductions in growth rates are of little consequence to prey when their population is at its carrying capacity. Calcagno et al. (2010) utilized an individual-based framework to model the full distribution of traits and found that rapid predator evolution resulted in prey and/or predator speciation and fewer interactions between predator and prey. They also found that the predator went extinct if its adaptation speed was too slow, suggesting that predators are more successful if the ratio of speeds of adaptation of predators and prey is at some optimal level. We expect that comparing models with different evolutionary trade-offs and full trait distributions will yield similar results to Calcagno et al. (2010), and future work will entail modeling the evolution of the full trait distribution of both predator and prey.

Our study shows that analytical outcomes are affected greatly by the choice of trade-off in prey species; the specific traits under consideration matter. We investigated the qualitative differences between cycles produced by the two models using simulations. Since the prey rate of evolution $|d\bar{n}/dt|$ generally decreases as prey growth rate decreases but increases as carrying capacity decreases, there are bouts of more rapid prey evolution in Model 2 that are not present in Model 1 (Fig. 1(d), (f)) These bouts of rapid evolution present an evolutionary challenge to the predators, who are suddenly unequipped to deal with the changing genetic land-

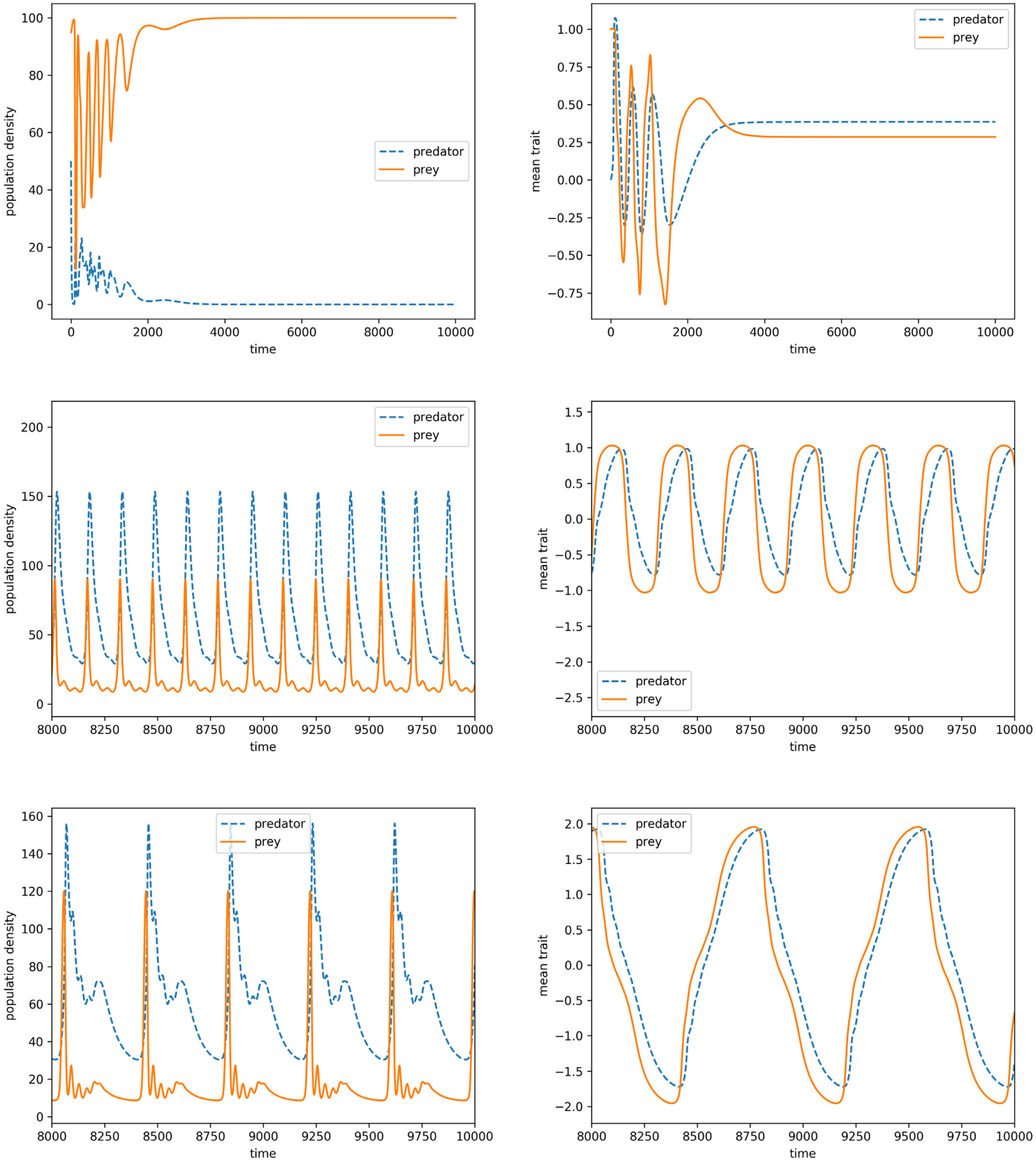

Fig. 7. Timeseries. Parameters are identical to those from Fig. 1, but results were obtained by running the model with evolving variance according to the framework of Tirok et al. (2011).

scape. This results in periods of time in which the predator population decays exponentially and would go extinct if evolution were to cease (Fig. 1(e)). At these low densities, the predator population is able to quickly respond evolutionarily, making them a threat to the prey, enabling them to recover ecologically. Since generalist predators (higher τ_a) are more able to respond to rapid prey evolution than specialist predators, they spend less time at extremely low densities. This decrease in selective pressure results in cycles of longer periods (Fig. 6(c)).

Our models produce cycles with generally in-phase ecological dynamics over the longer evolutionary time scale, and out-of-phase fluctuations on an ecological time scale immediately following bouts of more rapid evolution. These ecological fluctuations are not offset by a quarter cycle, as predicted by classical ecological models, but rather resemble dynamics seen in Khibnik and Kondrashov (1997) and Mougi (2012) and supported by studies incorporating rapid prey evolution (Cortez et al., 2010; Yoshida et al., 2003).

This study expands our theoretical understanding of predator-prey eco-evolutionary dynamics. In particular, we explored the effects of two types of trait linkage on ecological dynamics and concluded that one must be mindful of the type of stabilizing selection included in theoretical models. In reality, many groups of traits which affect ecological interactions are correlated with varying strengths, and predator and prey species interact in the context of a larger food web. Future studies can potentially expand on this model by considering more complex trait linkage in the context of multiple prey species, multiple predator species, intraguild predation, or more general multitrophic food webs.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2018.08.013.

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