The Lotka-Volterra Predator-Prey Model with Foraging–Predation Risk Trade-Offs

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abstract: This article studies the effects of adaptive changes in predator and/or prey activities on the Lotka-Volterra predator-prey population dynamics. The model assumes the classical foraging–predation risk trade-offs: increased activity increases population growth rate, but it also increases mortality rate. The model considers three scenarios: prey only are adaptive, predators only are adaptive, and both species are adaptive. Under all these scenarios, the neutral stability of the classical Lotka-Volterra model is partially lost because the amplitude of maximum oscillation in species numbers is bounded, and the bound is independent of the initial population numbers. Moreover, if both prey and predators behave adaptively, the neutral stability can be completely lost, and a globally stable equilibrium would appear. This is because prey and/or predator switching leads to a piecewise constant prey (predator) isocline with a vertical (horizontal) part that limits the amplitude of oscillations in prey and predator numbers, exactly as suggested by Rosenzweig and MacArthur in their seminal work on graphical stability analysis of predator-prey systems. Prey and predator activities in a long-term run are calculated explicitly. This article shows that predictions based on short-term behavioral experiments may not correspond to long-term predictions when population dynamics are considered.

Keywords: adaptive foraging, antipredator behavior, predator-prey population dynamics, predator-prey games, trait-mediated interactions, ideal free distribution.

How is it possible that so many species coexist despite the fact that simple models of competition and predation predict species extinction? As Gause (1934) pointed out, in reality, interaction parameters are not constant, as Lotka and Volterra assumed. For example, Gause observed that at low prey densities, some prey can escape when their predators cannot find them. It became clear that to make the Lotka-Volterra model more realistic, behavioral details must be integrated with population dynamics (e.g., MacArthur 1970; Schoener 1973; Oaten and Murdoch 1975; Rapport and Turner 1975; Pulliam 1976; Werner 1977; Comins and Hassell 1979; Rosenzweig 1981). There are many examples of antipredator prey behavior, including increased refuge use and changes in habitat choice and time budget (e.g., Murdoch 1969; Werner and Gilliam 1984; Fraser and Huntingford 1986; Holbrook and Schmitt 1988; Brown and Alkon 1990; Brown 1998; Lima 1998*a*, 1998*b*; Sih 1998; Peacor and Werner 2001; Werner and Peacor 2003; Preisser et al. 2005). It is even more fascinating that rapid morphological and physiological adaptations have recently been observed in prey species (e.g., Wikelski and Thom 2000; Yalden 2000; Relyea and Auld 2004; Losos et al. 2006). For example, Losos et al. (2006) showed that within a single generation, *Anolis sagrei*, a common Bahamian lizard, can change the length of its hindlimbs as a result of habitat shift (from terrestrial to arboreal habitat) in response to increased predation risk in the terrestrial habitat.

Consumer foraging behavior is often assumed to be consistent with the goal of maximizing rate of energy intake (e.g., Emlen 1966; MacArthur and Pianka 1966; Charnov 1976*a*, 1976*b*; Stephens and Krebs 1986; Brown 1998), which is used as a proxy of fitness. Theoretical work that studies the effect of foraging behavior on population dynamics (reviewed in Bolker et al. 2003) focused on the effect of diet selection on resource-consumer population dynamics (e.g., Tansky 1978; Teramoto et al. 1979; Holt 1983, 1984; Abrams 1984; Gleeson and Wilson 1986; Fryxell and Lundberg 1994, 1997; Křivan 1996), habitat choice (e.g., Rosenzweig 1981, 1991; Holt 1983, 1984, 1985, 1987; Morris 1987; Abrams 1996, 2007; Bernstein et al. 1999; Křivan and Sirot 2002; Cressman et al. 2004; Abrams et al. 2007), and activity budget (e.g., Abrams 1984; Brown et al. 1999; Křivan and Sirot 2004). In particular, Křivan (1997, 1998) extended the original Lotka-Volterra model

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to two-patch environments where predators only, prey only, or both predators and prey redistribute in order to maximize their fitness, measured by the instantaneous population growth rate. The last case is an example of a predator-prey game (van Baalen and Sabelis 1993; Hugie and Dill 1994; Křivan 1997; Křivan and Sirot 2002; Cressman et al. 2004; Vincent and Brown 2005). These models predict that aggregative predator response, combined with the Lotka-Volterra predator-prey model, weakens apparent competition (Holt 1984) and promotes coexistence of prey species in both patches. When prey respond to predation risk and predator dispersal between patches is random, Křivan (1998) predicts that at the population timescale, prey will occupy only one patch. When both predators and prey behave adaptively, predators and prey will occupy both patches. In these three cases, the predator-prey equilibrium is always neutrally stable, as for the classical Lotka-Volterra model, but unlike in the classical model, the fluctuations in species densities are bounded by a bound that is independent of the initial species densities.

In their graphical analysis of predator-prey interactions, Rosenzweig and MacArthur (1963) hypothesized that selection on the prey toward decreasing the rate of kill increases predator-prey stability, while selection on the predator toward increasing the rate of kill destabilizes the Rosenzweig-MacArthur model. Their model was further elaborated by Brown et al. (1999). These authors assumed that prey vigilance depends on the predator numbers, and they showed that prey perfect knowledge of the predator's whereabouts was destabilizing. When prey had information on the number of predators but no information on their whereabouts, the predator-prey interactions were strongly stabilized. Predictions of other models that consider prey and/or predator responses show that these can be either stabilizing or destabilizing (Schwinning and Rosenzweig 1990; van Baalen and Sabelis 1993; Abrams 1994, 2007; Fryxell and Lundberg 1994, 1997).

In this article, I study effects of adaptive changes in predator and prey activity levels on predator-prey population dynamics described by the Lotka-Volterra model. I show that the effects of prey and/or predator changes in activities on population dynamics can be fully understood (similarly to the classical Lotka-Volterra model) and that the population dynamics are stabilized by adaptive animal behavior. Either the amplitude of maximum oscillations is bounded and the bound is independent of the initial conditions, or population dynamics converge to an equilibrium. Combining animal short-term behavior with population dynamics allows me to make predictions on the evolution of predator and prey activity levels at the population timescale.

Model

I extend the classical Lotka-Volterra predator-prey model by assuming that interactions depend on prey and/or predator activities. Following the spirit of Lotka and Volterra, I assume that these dependencies are linear, which leads to the following model:

$$\frac{dR}{dt} = [r_1 u + r_2 - (\lambda_1 u + \lambda_2 v)P]R,$$

$$\frac{dP}{dt} = [e(\lambda_1 u + \lambda_2 v)R - (m_1 + m_2 v)]P, \qquad (1)$$

where $0 \le u \le 1$ ($0 \le v \le 1$) denotes prey (predator) activity. The model assumes the foraging–predation risk trade-offs undertaken by both species. Increased prey activity (u) increases prey growth rate ($r_1 u + r_2$), but it also increases the encounter rate with predators ($\lambda_1 u + \lambda_2 v$). Similarly, increasing predator activity (v) increases both predator growth rate ($e(\lambda_1 u + \lambda_2 v)R$) and mortality rate ($m_1 + m_2 v$). Here, r_2 and m_1 are the prey background growth rate and predator mortality rate, respectively, that are independent of activity level. Positive (negative) r_2 models the case where prey population grows (declines) if prey are completely inactive ($u = 0$). In what follows, I assume that $r_1 + r_2 > 0$, which means that active prey always reach a positive population growth rate. All other parameters in model (1) are positive, and they have the same meaning as in the original Lotka-Volterra model. Various special cases can be worked out. When activity levels (u and v) are fixed, I get the classical neutrally stable Lotka-Volterra predator-prey model. By fixing predator activity (v), I can study the effect of prey behavior alone on the population dynamics. Alternatively, by fixing prey activity level (u), I can study the effect of predator behavior alone. Finally, I consider the predator-prey game where both species choose their activity level.

Adaptive Predators

To model predators that adjust their activity to current prey density, I fix prey activity level at some arbitrary value (set to maximum prey activity $u = 1$ in this article), and I assume that predators behave so that their per capita population growth rate maximizes. Thus, predators should be maximally active, provided that their population growth rate exceeds the mortality rate associated with predator activity (i.e., $v = 1$ if $e\lambda_2 R > m_2$), and they should be inactive otherwise (i.e., $v = 0$ if $e\lambda_2 R < m_2$). This switch causes the prey isocline to be Z-shaped (fig. 1, *horizontal dotted line*; van Baalen et al. 2001). The isocline consists of three parts: two horizontal lines and the vertical line

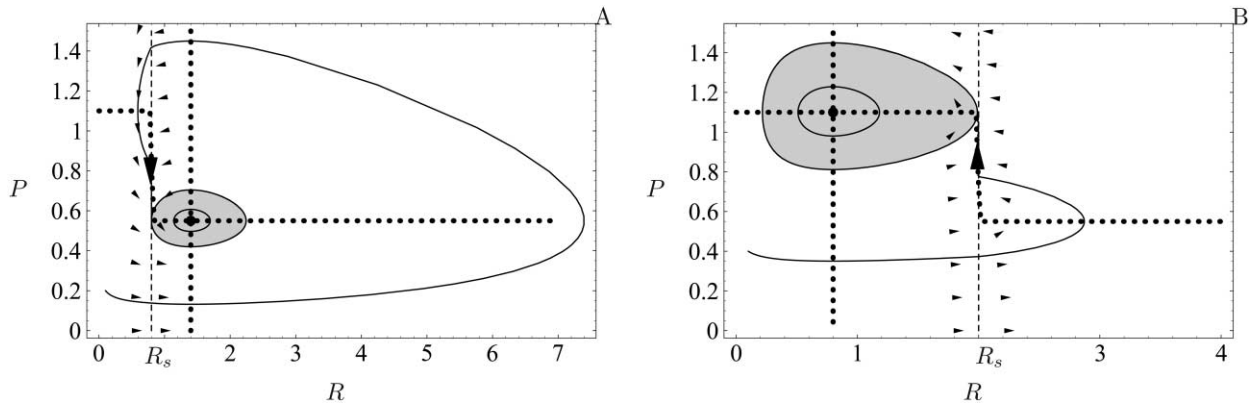

Figure 1: Solutions of model (1) where only predator behavior is adaptive. The dotted lines are isoclines, and the dashed line shows the critical prey density $R_s = m_2/e\lambda_2$, below (above) which predators are inactive (active). The global attractor is shown in gray. The arrows along the switching line show direction of trajectories. In *A*, the predator benefit/cost ratio (λ_2/m_2) is high, inequality (2) holds, and the population equilibrium is in the region of the prey-predator density phase space where predator activity is at its maximum ($v = 1, m_1 = 0.2, m_2 = 0.08$). *B* considers the opposite case, where inequality (2) does not hold and predators are inactive at the population equilibrium ($v = 0, m_1 = 0.08, m_2 = 0.2$). Other parameters: $r_1 = 1$, $r_2 = 0.1$, $\lambda_1 = 1$, $\lambda_2 = 1$, $e = 0.1$.

segment joining them. The vertical segment is located at the prey density ($R_s = m_2/e\lambda_2$) where predators switch between active and inactive states. In the vicinity and to the right of the vertical part of the isocline, prey population decreases, while to the left, it increases (fig. 1, *arrows*). It is clear that trajectories are "pushed" from both sides to the vertical part of the prey isocline and that they cannot cross it. Thus, by definition (Rosenzweig and MacArthur 1963), the vertical segment is indeed a part of the prey isocline. This is clearly shown in figure 1, where upon reaching the vertical part of the prey isocline, trajectories cannot cross it, and they "slide" (Křivan 1997; van Baalen et al. 2001) along it (downward in fig. 1*A* and upward in fig. 1*B*) before they settle on a Lotka-Volterra cycle.

The predator isocline is a vertical line (fig. 1, *vertical dotted line*), exactly as in the classical Lotka-Volterra case. The position of this isocline depends on the benefit/cost ratio (λ_2/m_2) that is due to predator activity. This ratio relates the added benefit, expressed as the increased predator cropping rate (λ_2), to the added cost, expressed as the increased predator mortality rate (m_2). If the predator benefit/cost ratio is high, so that

$$\frac{\lambda_2}{m_2} > \frac{\lambda_1}{m_1}, \tag{2}$$

then the predator isocline is to the right of the switching threshold R_s (fig. 1*A*), and it is to the left if the opposite inequality holds (fig. 1*B*; app. A). In the first case, the population equilibrium is in the part of the prey-predator density phase space where predator activity is at its maximum ($v = 1$), while in the second case, predators are inactive at the equilibrium ($v = 0$). Using Lyapunov functions (Boukal and Křivan 1999), it can be proved that trajectories converge to a global attractor, shown in figure 1 as the gray area. This attractor is formed by Lotka-Volterra neutrally stable cycles. Contrary to the classical case, where the amplitude of oscillations depends on the initial population densities, this attractor is bounded; that is, the amplitude of maximum prey and predator oscillations is bounded. The bound is proportional to the distance of the equilibrium from the switching line ($R = R_s$). Because the attractor is either to the right (fig. 1*A*) or to the left (fig. 1*B*) of the predator isocline (except the unlikely case where $\lambda_2/m_2 = \lambda_1/m_1$), in a long-term perspective, predators will be either completely active or completely inactive (e.g., sessile). For predators to be inactive, either activity has to be very risky (high m_2) or the predator cannot increase its cropping rate by being active (small λ_2). In other words, an observer would see some switching in predator behavior only before population numbers settle on the attractor. Afterward, there will be no observable switching in predator activity, despite the fact that population numbers fluctuate. This means that the short-term predator behavioral response to changing prey densities will attenuate on the population timescale.

Adaptive Prey

Here I consider the complementary case where only prey behave adaptively. I set predator activity level to some fixed value (here to the maximum value $v = 1$). In this case, the optimal prey strategy that maximizes the per capita prey population growth rate is to be inactive when pred-

ator density is above a critical threshold, given by $P_s = r_1/\lambda_1$, and to be active if the opposite inequality holds. This switching leads to a steplike predator isocline (fig. 2, *vertical dotted line*). By definition, trajectories cannot cross the predator isocline in the vertical direction, which is clearly documented in figure 2*A*, where a trajectory slides along the horizontal part of the predator isocline before it settles on a Lotka-Volterra cycle.

The prey isocline is the horizontal dotted line in figure 2. Its position depends on the component of the benefit/cost ratio (r_1/λ_1) that is due to prey activity. This ratio relates the added benefit, expressed as the increased intrinsic per capita prey population growth rate, to the added cost, expressed as the increased prey mortality rate due to increased predation. If the prey benefit/cost ratio is high, so that

$$\frac{r_1}{\lambda_1} > \frac{r_2}{\lambda_2}, \tag{3}$$

then the prey isocline is below the switching line (fig. 2*A*; app. B), while if the opposite inequality holds, then it is above the switching line (fig. 2*B*). If the background prey population growth rate is negative ($r_2 < 0$), inequality (3) always holds. To maximize population growth rate at low predator density, prey must be active. This leads to a high encounter rate between prey and predators (which is given by $\lambda_1 + \lambda_2$). The corresponding part of the predator isocline is the vertical segment at the point $R_1 = (m_1 + m_2)/[e(\lambda_1 + \lambda_2)]$ (app. B). When predator density is higher than the switching density, prey are inactive, which shifts the predator isocline to the point $R_2 = (m_1 + m_2)/e\lambda_2$, that is, to the right of R_1 (fig. 2; app. B). All trajectories converge to a global attractor (shown as the gray area) that is formed by closed Lotka-Volterra cycles. Once again, prey and predator amplitude is bounded, which prevents predator and prey densities from becoming too low. When population densities settle on the attractor, the short-term prey behavior effects attenuate: prey are either completely active (fig. 2*A*) or completely inactive (fig. 2*B*), and no changes in their activities should be observed.

Both Species Are Adaptive

Finally, I consider the case where both prey and predators adjust their activity levels adaptively. This results in a predator-prey game because prey activity level depends on predator activity and vice versa. I assume that the activity levels reach the ideal free distribution (Fretwell and Lucas 1970); that is, neither prey nor predators can increase their fitness by changing their strategy. The corresponding activity levels combine the activity levels for adaptive prey with those for adaptive predators.

In what follows, I consider two possibilities: either the prey population can increase when prey are completely inactive ($r_2 > 0$) or it cannot ($r_2 < 0$). First, I consider the case where prey can increase when inactive ($r_2 > 0$). The two switching thresholds (R_s and P_s) split the prey-predator population density phase space into four parts (fig. 3, *dashed lines*; app. C). The short-term predictions at the behavioral timescale for fixed prey and predator densities suggest that when prey density is lower (higher) than the threshold (R_s), predators are inactive (active). Similarly, when predator density is higher (lower) then the threshold (P_s), prey are inactive (active) because of high (low) predation risk. To obtain predictions at the population time-

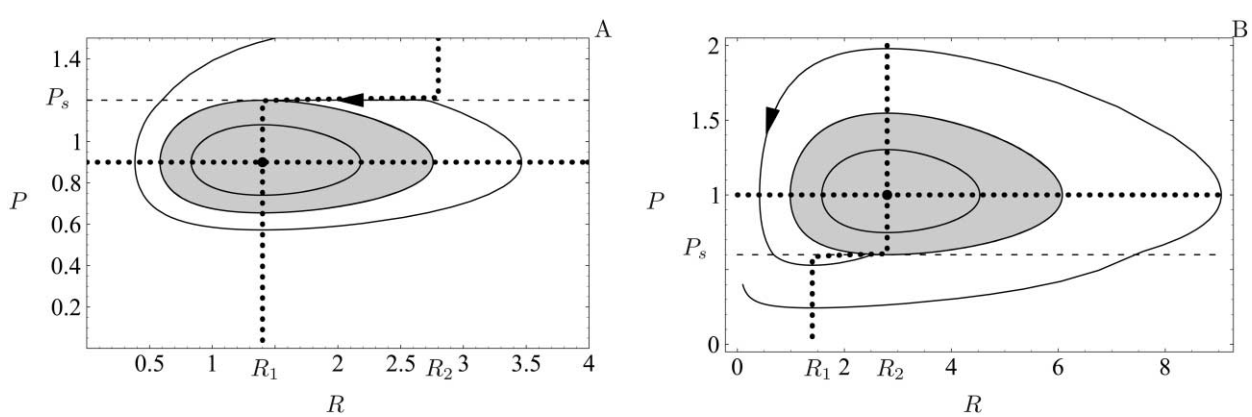

Figure 2: Solutions of model (1) when prey are adaptive. The dotted lines are isoclines, the dashed line is the predator critical density $P_s = r_1/\lambda_1$, above (below) which prey are inactive (active). The global attractor is shown in gray. *A* shows the case where prey benefit/cost ratio (r_1/λ_1) is high and inequality (3) holds ($r_1 = 1.2$, $r_2 = 0.6$). *B* shows the opposite case ($r_1 = 0.6$, $r_2 = 1.2$). Other parameters: $\lambda_1 = 1$, $\lambda_2 = 1$, $m_1 = 0.08$, $m_2 = 0.2$, $e = 0.1$.

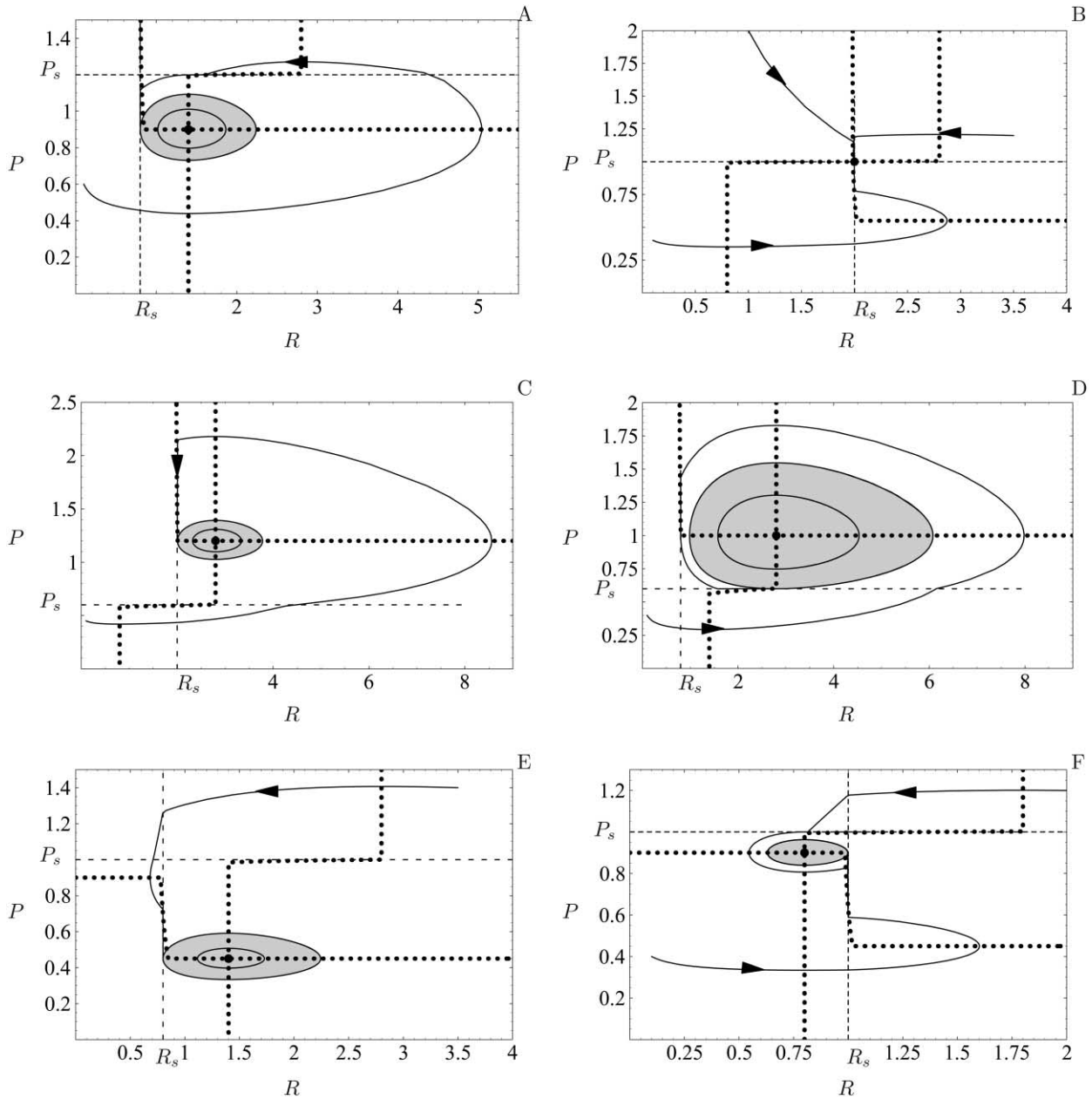

Figure 3: Solutions of model (1) when both prey and predators are adaptive. The dotted lines are isoclines, the dashed lines correspond to prey ($R_s = m_2/e\lambda_2$) and predator ($P_s = r_1/\lambda_1$) switching densities. The gray area denotes the attractor. Parameter r_2 is positive in *A–D* and negative in *E* and *F*. Parameters used in simulations: *A*, $r_1 = 1$, $r_2 = 0.6$, $m_1 = 0.2$, $m_2 = 0.08$; *B*, $r_1 = 1$, $r_2 = 0.6$, $m_1 = 0.08$, $m_2 = 0.2$; *C*, $r_1 = 0.6$, $r_2 = 1$, $m_1 = 0.08$, $m_2 = 0.2$; *D*, $r_1 = 0.6$, $r_2 = 1$, $m_1 = 0.2$, $m_2 = 0.08$; *E*, $r_1 = 1$, $r_2 = -0.1$, $m_1 = 0.2$, $m_2 = 0.08$; *F*, $r_1 = 1$, $r_2 = -0.1$, $m_1 = 0.08$, $m_2 = 0.1$. Parameters $\lambda_1 = 1$, $\lambda_2 = 1$, and $e = 0.1$ were the same in all simulations.

scale, I study population dynamics (model [1]), where I substitute the optimal prey and predator activity levels. The graphical analysis shown in figure 3 is based on the position of isoclines (*dotted lines*). The prey isocline is either L-shaped (when $r_2 > 0$; fig. 3*A*–3*D*) or Z-shaped (when $r_2 < 0$; fig. 3*E*, 3*F*). This is because to the left of the predator switching line (fig. 3, *vertical dashed line*) and above the prey switching line (*horizontal dashed line*), that is, in the upper left corner in figure 3, both predators and prey are inactive, they do not interact, and prey population growth is always positive (if $r_2 > 0$) or negative (if $r_2 < 0$); see appendix C. Thus, the prey isocline cannot intersect

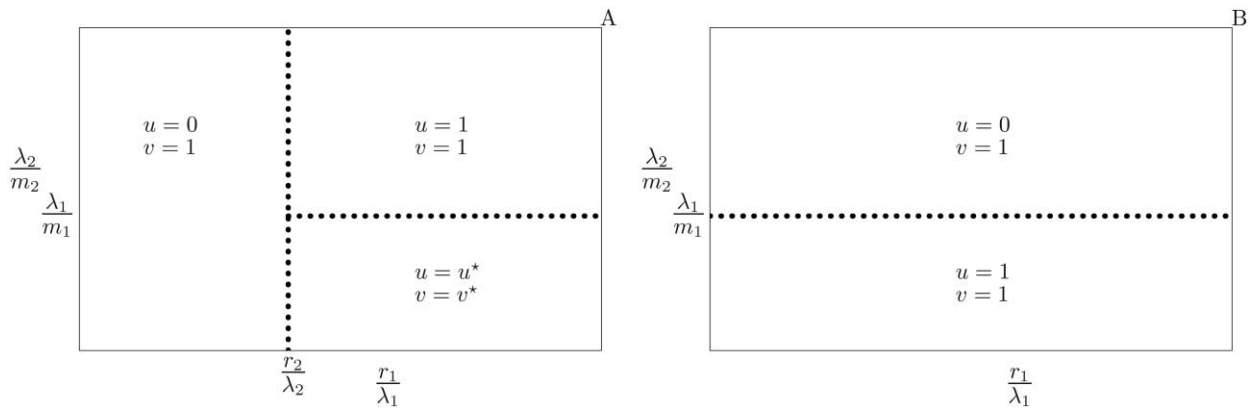

Figure 4: Long-term predictions for prey and predator activities as a function of model parameters. *A* assumes positive r_2, while *B* assumes negative r_2. Values of u^* and v^* are given by equation (4).

this region of the prey-predator phase space. Similarly, in the lower left corner of figure 3*A*, prey are active ($u = 1$) and predators are inactive ($v = 0$). Substituting these activity values in model (1), we observe that the corresponding prey isocline is the horizontal line given by $P = (r_1 + r_2)/\lambda_1$ (app. C). However, this line is in the lower left region of the prey-predator phase space only provided that $r_2 < 0$ (and $r_1 + r_2 > 0$; fig. 3*E*, 3*F*), which then leads to Z-shaped prey isocline. For positive r_2, this line segment is not in the lower left corner of the phase space, and the prey isocline is L-shaped.

For positive r_2, depending on other parameters, there are four qualitative possibilities for position of predator and prey isoclines (fig. 3*A*–3*D*; app. C). First, I consider the case where the prey benefit/cost ratio is high ($r_1/\lambda_1 > r_2/\lambda_2$; fig. 3*A*, 3*B*).

If the predator benefit/cost ratio is high ($\lambda_2/m_2 > \lambda_1/m_1$; fig. 3*A*), the population equilibrium is located in the part of the population density phase space where both predators and prey are active ($u = v = 1$), because prey density is high and predator density is low. This equilibrium is neutrally stable, and trajectories converge to a bounded attractor (fig. 3*A*).

If the predator benefit/cost ratio is low ($\lambda_2/m_2 < \lambda_1/m_1$; fig. 3*B*), the intersection of the two isoclines coincides with the intersection of the two switching lines ($R_s = m_2/e\lambda_2$ and $P_s = r_1/\lambda_1$), and population dynamics converge to this equilibrium. It is interesting to note that predator and prey activities at this equilibrium are intermediate and can be calculated explicitly. Indeed, at this equilibrium, the right-hand side of model (1) must be 0 by definition. Substituting the prey and predator equilibrium values allows me to calculate the activity levels at the population equilibrium:

$$u^* = \frac{m_1\lambda_2}{m_2\lambda_1},$$

$$v^* = \frac{r_2\lambda_1}{r_1\lambda_2}. \tag{4}$$

Second, I consider the case where the prey benefit/cost ratio is low ($r_1/\lambda_1 < r_2/\lambda_2$). The two cases (fig. 3*C* assumes $\lambda_2/m_2 < \lambda_1/m_1$, and fig. 3*D* assumes $\lambda_2/m_2 > \lambda_1/m_1$) are qualitatively similar because when population dynamics reach the attractor, predators are active ($v = 1$) and prey inactive ($u = 0$). In both cases, the equilibrium is neutrally stable, and all trajectories converge to the bounded attractor.

If $r_2 < 0$, there are two possibilities, shown in figure 3*E* ($\lambda_2/m_2 > \lambda_1/m_1$) and figure 3*F* ($\lambda_2/m_2 < \lambda_1/m_1$). In both cases, the equilibrium predator density is in the region of the prey-predator phase space where prey are active ($u = 1$). Predators can be either active (fig. 3*E*) or inactive (fig. 3*F*) at the population equilibrium.

The above analysis is useful in making long-term predictions with respect to model parameters that classify various environments (fig. 4). In this figure, the horizontal axis is parameterized by the prey benefit/cost ratio (r_1/λ_1) and the vertical axis is parameterized by the predator benefit/cost ratio (λ_2/m_2). Various environments are identified by these two ratios. First, I assume that the background prey population growth rate (r_2) is positive (fig. 4*A*). For example, if increased prey activity does not make prey more conspicuous to their predators, λ_1 is small, and the ratio r_1/λ_1 will be high in productive environments, where prey can increase their consumption by increasing their activity ($r_1 > 0$). For example, this can be the case of cryptic prey. Similarly, in environments where predators have no

other natural enemies, m_2 will be low. If predators can increase prey capture rate by increasing their activity, the ratio λ_2/m_2 will be high. Thus, in environments where both prey and predator activities lead to a high benefit/cost ratio, both species will be maximally active at the population timescale (fig. 4*A*). In environments where the benefit/cost ratio is high for prey and low for predators (e.g., because of high predation risk, m_2), both prey and predator activities will be intermediate and are given by equation (4). As a function of prey and predator benefit/cost ratio, this dependence is shown in figure 5. In environments with low benefit/cost for prey, prey will be inactive while predators will be active. Second, if the background prey population growth rate (r_2) is negative, predators are always active, and prey are inactive if the predator benefit/cost ratio is high (fig. 4*B*).

Discussion

In this article, I combined the adaptive prey and/or predator activity with the classical Lotka-Volterra population dynamics. I proved that when both predators and prey adjust their activity level simultaneously, the neutral stability of the classical Lotka-Volterra predator-prey model is destroyed, and an upper bound on the amplitude of maximum oscillations in population numbers exists. This bound is independent of the initial population densities. Depending on the parameters, adaptive adjustment of both prey and predator activity level can globally stabilize the population equilibrium (fig. 3*B*). If prey only or predators only respond to the presence of the other species, the population equilibrium is neutrally stable, as in the case of the classical Lotka-Volterra model, but the amplitude of population fluctuations is bounded. In other words, while large perturbations of the classical Lotka-Volterra model lead to population cycles with large amplitude, the amplitude decreases when prey or predators behave adaptively. Once again, animal behavior has a stabilizing effect on predator-prey population dynamics, although these do not converge to a population equilibrium. In short, whether or not population dynamics settle at the equilibrium, optimal adjustment of prey and/or predator activity has a stabilizing effect on the Lotka-Volterra predator-prey population dynamics.

The model studied in this article is the simplest extension of the classical Lotka-Volterra predator-prey model that considers adaptive response in activity for predators and/or prey. It assumes rapid changes in activity level, as compared to changes in population numbers. This assumption leads to models with instantaneous switchings, in the sense that animal strategies abruptly change when population numbers cross some critical thresholds. This is similar to the case of the optimal-diet-choice model, where the alternative prey type is included in the consumer diet only if the density of the more profitable prey type decreases under a given threshold (the 0-1 rule; Charnov 1976*a*). Similarly, in the case of habitat choice, the ideal free distribution predicts that individuals will go to the patch that provides them with the highest food intake rate (Fretwell and Lucas 1970). Thus, if one patch becomes better than the other, the optimal strategy abruptly changes, so that all individuals move to the better patch (Křivan 1997). Empirical observations support the idea that animals behave in order to maximize their fitness, although switching can be more gradual (e.g., Murdoch 1969; Krebs et al. 1977; Milinski 1979; Berec et al. 2003,

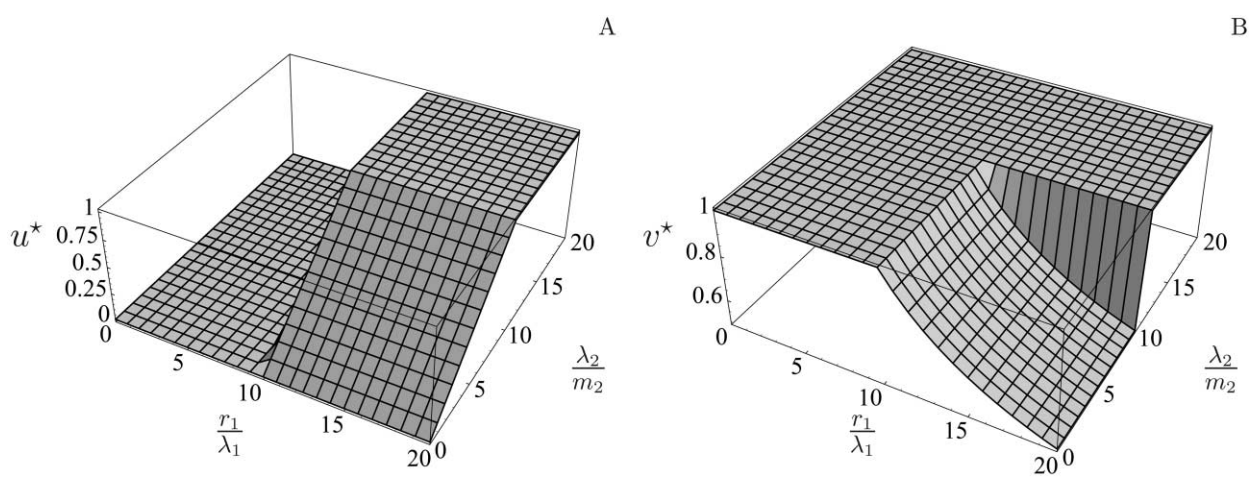

Figure 5: Dependence of the prey (u^*, *A*) and predator (v^*, *B*) activity level on prey and predator benefit/cost ratios along the population attractor (shaded area in fig. 3). The figure corresponds to the situation shown in figure 4*A*.

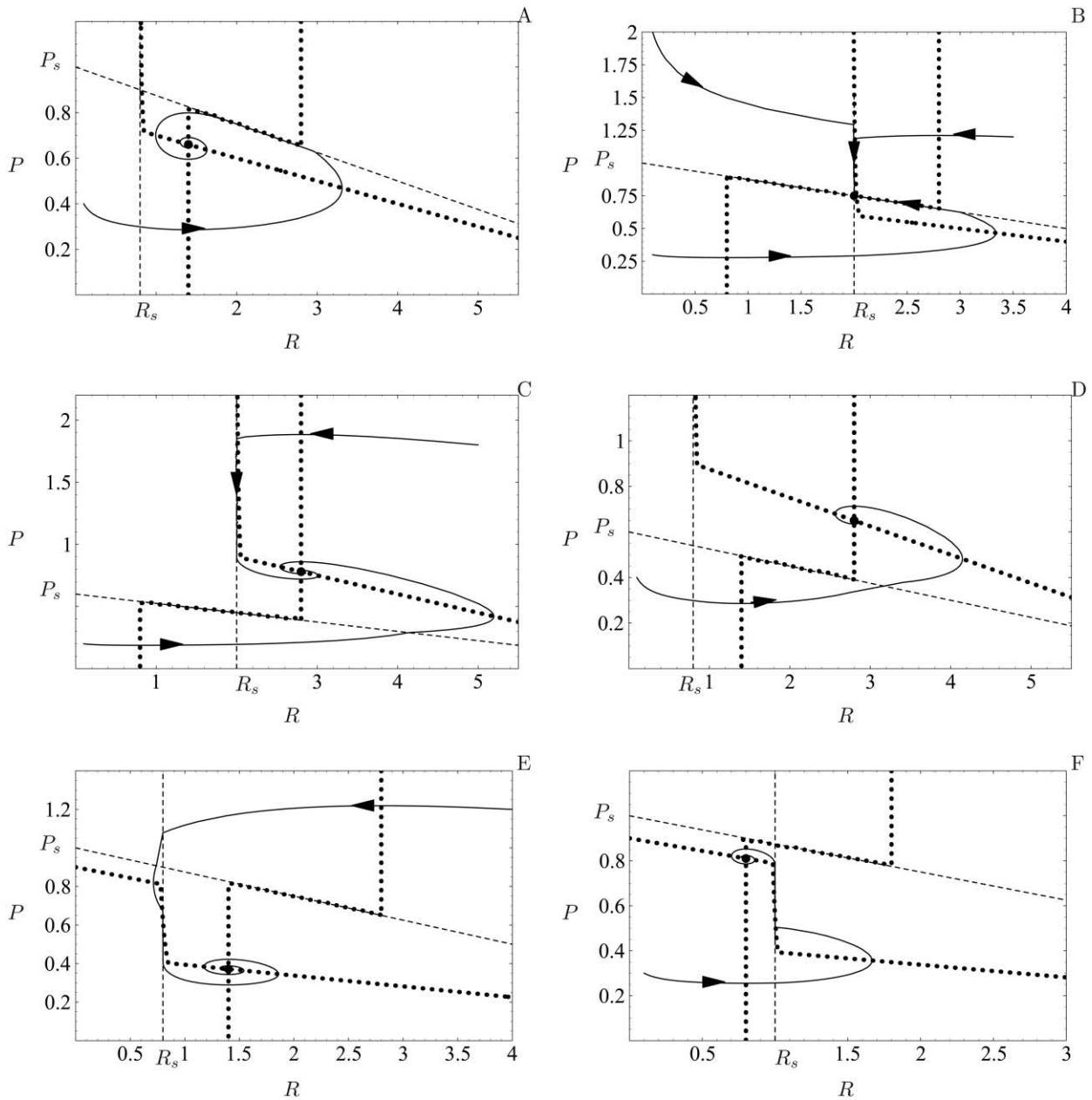

Figure 6: Solutions of model (5) where prey growth is negatively density dependent and both prey and predators are adaptive. The dotted lines are isoclines, the dashed lines correspond to prey ($R_s = m_2/e\lambda_2$) and predator ($P_s = r_1/\lambda_1(1 - R/K)$) switching densities. Parameter r_2 is positive in *A–D* and negative in *E* and *F*. Parameters for each panel are the same as those used in the corresponding panels of figure 3, with $K = 8$.

2006). In models, rapid switching occurs when animal fitness is a linear function of animal strategies, which is the case considered in this article. This, then, leads to population models with prey (predator) isoclines that have a vertical (horizontal) part. Rosenzweig and MacArthur (1963) recognized that such isoclines limit the oscillatory amplitude by inducing a maximum oscillation, although they did not provide any explicit model where this can occur. The model presented in this article leads to isoclines exactly like those predicted by Rosenzweig and MacArthur (1963). Moreover, Rosenzweig and MacArthur also realized that behaviorally responsive prey lead to positively sloped predator isocline (see also Brown et al. 1999), which has a strong stabilizing effect. This is fully consistent with

the results of the present model, where the predator isocline is an increasing function of the prey density. In this model, the particular shape of isoclines is due to rapid prey and/or predator switching. A more realistic gradual switching would lead to nonlinear isoclines without sharp corners (van Baalen et al. 2001). However, such models can be difficult to analyze because of strong nonlinearities, and it can even be difficult to obtain analytical expressions for the equilibrium population densities. In fact, Gause (1934) was perhaps the first who used discontinuous predator-prey models to describe his empirical observations. It is interesting that, although very useful in other biological disciplines (e.g., in gene regulatory networks; Thomas and D'Ari 1990; Edwards 2000; Casey et al. 2006), this approach has not been more widely used in theoretical ecology (but see, e.g., Křivan 1996, 1997; van Baalen et al. 2001; Meza et al. 2005; Cressman and Křivan 2006; Dercole et al. 2007).

Because the Lotka-Volterra model (without prey and/or predator switching) is neutrally stable, one can ask what happens if we start with a more realistic, structurally stable model. The first step in this direction is to replace the unlimited prey growth in model (1) with a negative density-dependent growth, which is often modeled by logistic growth. This, then, leads to the following model:

$$\frac{dR}{dt} = \left[\left(r_1 u + r_2\right)\left(1 - \frac{R}{K}\right) - (\lambda_1 u + \lambda_2 v)P\right]R,$$
$$\frac{dP}{dt} = [e(\lambda_1 u + \lambda_2 v)R - (m_1 + m_2 v)]P. \tag{5}$$

This model can by analyzed along exactly the same lines as model (1). The prey isocline, which was piecewise constant in model (1), becomes piecewise linear with a negative slope (fig. 6), which stabilizes population dynamics at an equilibrium.

This article also shows that predictions based on a short-term behavioral experiments where population numbers are approximately constant may be of little use on a longer population timescale. Indeed, at the short timescale, behavior depends on population numbers. For example, a prediction based on a short timescale can be that increased predation risk decreases prey activity. This can be based on a series of experiments that manipulate the number of predators present and observe corresponding prey activity. However, as shown in this article, this prediction can be of little use when population dynamics are considered because, depending on the environmental characteristics, predator population numbers can be depressed to low levels, where prey do not perceive predators as a risk and can be active. For example, this happens in figure 2*A* and figure 3*A*, 3*E*, and 3*F*. Thus, projection of short-term behavioral experiments on a population timescale calls for more modeling effort and more long-term population experiments.

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APPENDIX A

Flexible Predators

I consider the case where only predators are flexible foragers and prey activity is at its maximum level ($u = 1$). For prey densities above the switching threshold ($R > R_s = m_2/e\lambda_2$), predators are active ($v = 1$), and population dynamics are

$$\frac{dR}{dt} = [r_1 + r_2 - (\lambda_1 + \lambda_2)P]R,$$
$$\frac{dP}{dt} = [e(\lambda_1 + \lambda_2)R - (m_1 + m_2)]P. \tag{A1}$$

These are the classical Lotka-Volterra equations, with equilibrium

$$E_1 = \left[\frac{m_1 + m_2}{e(\lambda_1 + \lambda_2)}, \frac{r_1 + r_2}{\lambda_1 + \lambda_2}\right].$$

The resource equilibrium is higher than the switching threshold R_s if

$$\frac{\lambda_2}{m_2} > \frac{\lambda_1}{m_1}. \tag{A2}$$

Similarly, when prey density is below the threshold ($R < R_s = m_2/e\lambda_2$), predators are inactive ($v = 0$), and population dynamics are

$$\frac{dR}{dt} = (r_1 + r_2 - \lambda_1 P)R,$$
$$\frac{dP}{dt} = (e\lambda_1 R - m_1)P, \tag{A3}$$

with equilibrium

$$E_2 = \left(\frac{m_1}{e\lambda_1}, \frac{r_1 + r_2}{\lambda_1}\right).$$

This resource equilibrium density is lower than the threshold resource level R_s if the inequality in equation (A2) is reversed.

APPENDIX B

Flexible Prey

I consider the case where prey only are flexible and predator activity is at its maximum ($v = 1$). For predator densities that are lower than the switching threshold ($P < P_s = r_1/\lambda_1$), prey are active ($u = 1$), and population dynamics are given by equation (A1). The corresponding equilibrium E_1 is in the region of the predator-prey density phase space where $P < P_s$ if

$$\frac{r_2}{\lambda_2} < \frac{r_1}{\lambda_1}. \tag{B1}$$

For predator densities that are higher than the switching threshold ($P > P_s = r_1/\lambda_1$), prey are inactive ($u = 0$), and population dynamics are

$$\frac{dR}{dt} = (r_2 - \lambda_2 P)R,$$

$$\frac{dP}{dt} = [e\lambda_2 R - (m_1 + m_2)]P. \tag{B2}$$

These population dynamics have equilibrium

$$E_3 = \left(\frac{m_1 + m_2}{e\lambda_2}, \frac{r_2}{\lambda_2}\right),$$

which is in the region where $P > P_s$ when the inequality in equation (B1) is reversed.

APPENDIX C

Both Species Are Flexible

I consider the case where both predators and prey are flexible. The two switching lines divide the prey-predator density phase space into four regions. When predator density is low ($P < P_s$) and prey density is high ($R > R_s$), both prey and predators are active, and population dynamics are described by equation (A1). The corresponding equilibrium E_1 is in this part of the prey-predator density phase space if

$$\frac{r_2}{\lambda_2} < \frac{r_1}{\lambda_1},$$

$$\frac{\lambda_1}{m_1} < \frac{\lambda_2}{m_2}; \tag{C1}$$

see figure 3*A*.

When both predator and prey densities are low ($P < P_s$, $R < R_s$), prey are active, predators are inactive, and population dynamics are described by equation (A3). There are two possibilities. If $r_2 > 0$, the point E_2 is outside of this region, and no interior equilibrium exists in this region. If $r_2 < 0$, then E_2 is in this region of the prey-predator density phase space, provided that

$$\frac{\lambda_1}{m_1} > \frac{\lambda_2}{m_2}. \tag{C2}$$

When both predator and prey densities are high ($P > P_s$, $R > R_s$), prey are inactive, predators are active, and population dynamics are described by equation (B2). Equilibrium E_3 is in this part of the prey-predator phase space, provided that

$$\frac{r_2}{\lambda_2} > \frac{r_1}{\lambda_1}. \tag{C3}$$

The above inequality can be satisfied only if $r_2 > 0$.

When predator density is high ($P > P_s$) and prey density is low ($R < R_s$), both species are inactive, and population dynamics are described by

$$\frac{dR}{dt} = r_2 R,$$

$$\frac{dP}{dt} = -m_1 P. \tag{C4}$$

This model has no interior equilibrium.

Let us consider the case where $r_2 > 0$. If equation (C1) holds, then prey and predator isoclines look qualitatively like those shown in figure 3*A*. They intersect at the equilibrium E_1. If

$$\frac{r_2}{\lambda_2} < \frac{r_1}{\lambda_1} \tag{C5a}$$

and

$$\frac{\lambda_1}{m_1} > \frac{\lambda_2}{m_2}, \tag{C5b}$$

then neither E_1 nor E_3 is an equilibrium of model (1). In

this case, the prey and predator isoclines intersect at the point (R_s, P_s) (fig. 3*B*), which is the interior equilibrium of model (1). Inspection of the vector field shows that this equilibrium is stable. If inequality (C3) holds, then prey and predator isoclines intersect at E_3 irrespective of whether inequality (B1) or (C2) holds. Analysis of the case where $r_2 < 0$ is similar, and it is graphically presented in figure 3*E*, 3*F*.

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