

Ecological Archives E092-133-A1

Sebastian J. Schreiber, Reinhard Bürger, and Daniel I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92:1582–1593.

Appendix A: Conditions for persistence of predator and prey species.

The purpose of this appendix is develop conditions for persistence of predator and the prey species. We begin with conditions for persistence of the predator which turn out to be surprisingly subtle due to the evolutionary dynamics. Under the assumption that the predator persists, we develop a general persistence condition for the prey.

A.1. Conditions for predator persistence

When there is only a single prey species present, $\frac{e_i K_i \alpha_i \tau_i}{d \sqrt{\sigma^2 + \tau_i^2}} > 1$ is necessary for the persistence of the predator as discussed in the main text. When both prey species are present, a characterization of persistence of the predator becomes more subtle. Predator persistence depends on whether the predator can invade the equilibrium at which both prey are at their carrying capacity: $(N_1, N_2) = (K_1, K_2)$. At (K_1, K_2) , the phenotype dynamics of the predator equilibrate at the local extrema of the fitness function $\bar{W}(\bar{x}, K_1, K_2) = \sum_i e_i \bar{a}_i(\bar{x}) K_i - d$. There are two cases to consider: $\bar{W}(\bar{x}, K_1, K_2)$ has a unique maximum or there exist two maxima separated by a minimum. We say that the predator persists in the sense of permanence (Hofbauer and Sigmund 1998) if there exists $\eta > 0$ such that $P(t) \geq \eta$ whenever t is sufficiently large and $\min\{N_1(0), N_2(0), P(0)\} > 0$.

When there is a unique maximum at $\bar{x} = \hat{x}$, the predator persists in the sense of permanence if $\bar{W}(\hat{x}, K_1, K_2) > 0$. Alternatively, if $\bar{W}(\hat{x}, K_1, K_2) < 0$, then the predator can go extinct for all initial values of \bar{x} . Since $\bar{W}(\hat{x}, K_1, K_2)$ is greater than $\bar{W}(\theta_1, K_1, 0)$ and $\bar{W}(\theta_2, 0, K_2)$, persistence on a single prey is sufficient for predator persistence on both prey. In the case of three extrema, this no longer need hold.

Assume there are three extrema for $\bar{W}(\bar{x}, K_1, K_2)$. Let $\hat{x}_1 < \hat{x}_2$ be the local maxima and $\hat{x}_{\min} \in (\hat{x}_1, \hat{x}_2)$ be the local minimum. Generically, there are four scenarios to consider. First, if $\bar{W}(\hat{x}_i, K_1, K_2) < 0$ for $i = 1, 2$, then the predator can go extinct for all initial values of \bar{x} . Second, if $\bar{W}(\hat{x}_{\min}, K_1, K_2) > 0$, then $\bar{W}(\hat{x}_i, K_1, K_2) > 0$ for $i = 1, 2$ and the predator persists in the sense of permanence. Third, if $\bar{W}(\hat{x}_1, K_1, K_2) \bar{W}(\hat{x}_2, K_1, K_2) < 0$, then the invading predator goes extinct when its initial mean phenotype is near the \hat{x}_i at which $\bar{W} < 0$ or its invasion succeeds (possibly resulting in persistence) if its mean phenotype is near the other local maximizer of

fitness. Hence, in this third scenario, the predator at best, exhibits persistence that is contingent on initial conditions. Finally, if $\bar{W}(\hat{x}_i, K_1, K_2) > 0$ for $i = 1, 2$ and $\bar{W}(\hat{x}_{\min}, K_1, K_2) < 0$, then the predator can invade for $\bar{x} \neq \hat{x}_{\min}$. However, the predator does not persist in the sense of permanence as there is at least a one-dimensional set of initial conditions with $P(0) > 0$, $N_1(0) > 0$, and $N_2(0) > 0$ that lead to predator extinction.

A.2 Conditions for prey coexistence

Here, we develop the general prey coexistence criterion under the assumption that the predator can persist in the presence of one or both prey species. We begin by examining the invasion rates of the missing prey species at the equilibria determined by a predator-prey pair. If prey species j is the missing resource species, then its invasion rate at the predator-prey i ($\neq j$) equilibrium, (3), is

$$r_j - \bar{a}_j(\theta_i) \frac{r_i}{\bar{a}_i(\theta_i)} \left(1 - \frac{\hat{N}_i}{K_i} \right),$$

where $\hat{N}_i = \frac{d}{e_i \bar{a}_i(\theta_i)}$. Hence, prey species j can invade provided that

$$\frac{r_j}{\bar{a}_j(\theta_i)} > \frac{r_i}{\bar{a}_i(\theta_i)} \left(1 - \frac{\hat{N}_i}{K_i} \right), \quad j \neq i. \quad (\text{A.1})$$

When (A.1) holds for both prey species, i.e., the prey species exhibit mutual invasability, all three species coexist in the sense of permanence (Hofbauer and Sigmund 1998). When the opposite inequality of (A.1) holds, the equilibrium supporting only prey species i is stable and prey species j can be displaced. Since $0 < 1 - \frac{\hat{N}_i}{K_i} < 1$ and $\bar{a}_j(\theta_i) \leq \bar{a}_j(\theta_j)$, (A.1) always hold for the species j such that $\frac{r_j}{\bar{a}_j(\theta_j)} > \frac{r_i}{\bar{a}_i(\theta_i)}$, i.e., the superior apparent competitor. When $\tau_1 = \tau_2$ (as assumed in the main text), this condition for superiority simplifies to $r_j/a_j > r_i/a_i$.

The fact that the sign of the invasion rate of the missing prey species determines stability follows from the block diagonal form of the derivative matrix at these boundary equilibria. For example, if we use the coordinate system (N_1, P, x, N_2) and linearize the system of differential equations at the equilibrium $(N_1, P, x, N_2) = (\hat{N}_1, \hat{P}_1, \theta_1, 0)$, we get a block diagonal matrix of the form

$$\begin{pmatrix} A & B \\ 0 & c \end{pmatrix}$$

where A is a 3×3 matrix corresponding to linearizing the N_1 - P - x subsystem, B is a 3×1 matrix, and c is the per-capita growth rate of prey 2 evaluated at this equilibrium. Since the eigenvalues of A have negative real parts (i.e., the boundary equilibrium is stable in the N_1 - P - x subsystem), it is the sign of c that determines whether the equilibrium is stable or not in the full state space.

These conditions for prey coexistence imply permanence for all species (i.e., there exists $\eta > 0$ such that $\min\{N_1(t), N_2(t), P(t)\} \geq \eta$ whenever t is sufficiently large and $\min\{N_1(0), N_2(0), P(0)\} > 0$) if the predator is permanent as discussed in the previous section. A proof of this statement follows from (i) the observation that all solutions on the boundary converge to equilibria, (ii) there are no heteroclinic cycles amongst these equilibria, (iii) the Stable Manifold Theorem (Perko 1996), and (iv) the topological characterization of permanence (Hofbauer and So 1989; Garay 1989).

REFERENCES

- B. M. Garay. Uniform persistence and chain recurrence. *J. Math. Anal. Appl.*, 139:372–382, 1989.
- J. Hofbauer and K. Sigmund. *Evolutionary games and population dynamics*. Cambridge University Press, 1998.
- J. Hofbauer and J. W. H. So. Uniform persistence and repellers for maps. *Proceedings of the American Mathematical Society*, 107:1137–1142, 1989.
- L. Perko. *Differential Equations and Dynamical Systems*, volume 7 of *Texts in Applied Mathematics*. Springer Verlag, New York, 1996.
- Y. Takeuchi and N. Adachi. Existence and bifurcation of stable equilibrium in two-prey, one-predator communities. *Bulletin of Mathematical Biology*, 45(6):877–900, 1983.