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# Coevolution of Contrary Choices in Host-Parasitoid Systems

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ABSTRACT: We investigate patch selection strategies of hosts and parasitoids in heterogeneous environments. Previous theoretical work showed that when host traits vary among patches, coevolved populations of hosts and parasitoids make congruent choices (i.e., hosts and parasitoids preferentially select the same patches) and exhibit direct density dependence in the distribution of percent parasitism. However, host-parasitoid systems in the field show a range of patterns in percent parasitism, while behavioral studies indicate that hosts and parasitoids can exhibit contrary choices (i.e., hosts avoid patches favored by the parasitoid). We extend previous theory by permitting life-history traits of the parasitoid as well as the host to vary among patches. Our analysis implies that in coevolutionarily stable populations, hosts preferentially select patches that intrinsically support higher host equilibrium numbers (i.e., the equilibrium number achieved by hosts when both populations are confined to a single patch) and that parasitoids preferentially select patches that intrinsically support higher parasitoid equilibrium numbers (i.e., the equilibrium number achieved by the parasitoids when both populations are confined to a patch). Using this result, we show how variation in life-history traits among patches leads to contrary or congruent choices or leads to direct density dependence, inverse density dependence, or density independence in the distribution of percent parasitism. In addition, we determine when populations playing the coevolutionarily stable strategies are ecologically stable. Our analysis shows that heterogeneous environments containing patches where the intrinsic rate of growth of the host and the survivorship rate of the parasitoid are low result in the coevolved populations exhibiting contrary choices and, as a result, promote ecological stability.

*Keywords:* host-parasitoid interactions, coevolution, inverse density dependence, evolutionarily stable strategies, spatial models.

The effect of patchy, heterogeneous environments on the population dynamics of host-parasitoid systems has been a topic of widespread interest in ecology for several decades (Hassell and May 1973, 1974, 1988; Murdoch and Oaten 1975; May 1978; Lessells 1985; Chesson and Murdoch 1986; Stiling 1987; Reeve 1988; Walde and Murdoch 1988; Hochberg and Lawton 1990; Hassell et al. 1991; Ives 1992, 1995; Mangel and Roitberg 1992; Taylor 1993; Hochberg and Holt 1995). This work addresses the basic question of how patterns of patch selection by hosts and parasitoids contribute to ecological stability. The consensus is that a sufficient degree of variation in levels of parasitism among the patches is the essential mechanism for stability. Given that this variation results in overall persistence of hosts and parasitoids, it is important to understand what causes such variation (van Baalen and Sabelis 1993; Hochberg and Holt 1995; May 1995). One natural explanation is that the hosts and parasitoids coevolve different responses to variations in patch quality (van Baalen and Sabelis 1993; Thompson 1994).

Variability among patches arises for numerous reasons, such as variation in plant nutritional quality, plant defenses, and plant architecture. Because hosts respond to plant cues, variation in patch quality can lead to variation in host abundance. Furthermore, because parasitoids respond to cues from plants and hosts, variation in patch quality can lead to variation in parasitoid abundance and parasitism rates. Often parasitoids and hosts exhibit congruent choices with respect to patch selection, resulting in parasitoids aggregating in patches with higher host densities (Cook and Hubbard 1977; Comins and Hassell 1979; Waage 1983; Lessells 1985; Godfray 1994; DeMoraes et al. 1998). This congruence may be enhanced by chemical cues from the host and the host-damaged plants that attract parasitoids. In addition, parasitoids may learn to associate particular odors with successful searching, which further enhances the positive correlation between parasitism rates and host densities (Turlings et al. 1990; Turlings and Tumlinson 1991). However, the preferences of parasitoids and hosts with respect to patch selection are not always congruent. For example, Fox and Eisenbach (1992) showed that female diamondback moths *Plutella xylestella* and par-

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asitoids *Diadegma insulare* exhibit "contrary choices" with respect to patch selection: female diamondback moths preferentially oviposited on low-nitrogen food plants, while the parasitoid preferentially searched for hosts on high-nitrogen plants. The moth's egg-laying strategy conceivably balances the improved fitness of immature hosts developing on the high-quality food plants with the risk of these hosts being parasitized. The parasitoid's host-finding strategy conceivably balances the increased chances of finding their hosts on low-quality plants with the better performance (i.e., greater egg load, higher likelihood of emerging) of its young on the hosts found on high quality plants. Thus, a priori, tactics of the hosts and parasitoids depend on the details of the distribution of patches and the behavior of the other species and can lead to congruent or contrary choices.

Pursuing the idea that coevolutionary interactions in patchy environments may explain different patterns of patch selection by hosts and parasitoids, van Baalen and Sabelis (1993) performed an evolutionarily stable strategy (ESS) analysis of a discrete-time host-parasitoid model that permitted the intrinsic rate of growth of the host to vary among patches. In their ESS analysis, the patch selection strategies (i.e., the egg-laying preferences of the host and the searching preferences of the parasitoid) were assumed to be under selection. Van Baalen and Sabelis showed that populations playing the ESS exhibited an Ideal Free Distribution (Fretwell and Lucas 1970) in which no individual host or parasitoid can gain by moving to another patch. Furthermore, such populations always exhibited congruent choices in which host and parasitoids preferentially select the same patches.

In this article, we extend the work of van Baalen and Sabelis (1993) by studying the effects of variations in parasitoid and host life-history traits on patch selection strategies and their dynamical consequences. Our aim is to find the conditions under which environmental heterogeneity leads to coevolved populations exhibiting contrary or congruent choices.

## The Model

We consider a system consisting of a population of hosts and parasitoids that disperse among $n$ patches. To model this system, we generalize Hassell and May's (1973) model, which is based on the assumption that host and parasitoid populations have discrete and synchronized generations. Every generation, the parasitoids and hosts select patches according to fixed behavioral strategies. Hosts lay a fixed proportion $\alpha_i$ of their eggs in patch $i$, where $i = 1, \ldots, n$ and $\sum_{i=1}^{n} \alpha_i = 1$. Parasitoids spend a fixed proportion $\beta_i$ of their searching time in patch $i$, where $i = 1, \ldots, n$ and $\sum_{i=1}^{n} \beta_i = 1$. We assume that the probability of a host in patch $i$ escaping parasitism in generation $t$ is $f_i(\beta_i P_t)$, where $P_t$ is the total number of parasitoids in the environment in generation $t$. Here the $f_i$ are strictly decreasing functions that satisfy $f_i(0) = 1$ and $\lim_{x\to\infty} f_i(x) = 0$. For example, the $f_i$ can be the Poisson-distributed attack function $f_i(x) = \exp(-a_i x)$ or the negative binomial attack function $f_i(x) = (1 + a_i x/k_i)^{-k_i}$, where $a_i > 0$ is the searching efficiency of the parasitoid in patch $i$ and $k_i > 0$ is the aggregation parameter in patch $i$. We assume that intrinsic rate of growth $\lambda_i$ of a host in patch $i$ is >1 and that the expected number $\theta_i$ of parasitoids emerging from a parasitized host in patch $i$ is positive. If $N_t$ and $P_t$ denote the total number of hosts and parasitoids, respectively, in generation $t$, then we arrive at the following generalization of an $n$-patch model proposed by Hassell and May (1973) and van Baalen and Sabelis (1993):

$$N_{t+1} = \sum_{i=1}^{n} \lambda_i \alpha_i N_t f_i(\beta_i P_t)$$

$$P_{t+1} = \sum_{i=1}^{n} \theta_i \alpha_i N_t (1 - f_i(\beta_i P_t)). \tag{1}$$

## The Analysis

To understand how the host and parasitoid may coevolve their patterns of egg laying and searching across patches of varying quality, we employ the dynamical theory of evolutionarily stable strategies (see, e.g., Vincent and Brown 1988; Rand et al. 1994). For simplicity and tractability, we focus on ESSs that occur under equilibrial conditions. We break the ESS analysis into three parts. First, we consider the case where the host is the species able to evolve and the egg laying distribution $\alpha = (\alpha_1, \ldots, \alpha_n)$ is the trait under selection. Second, we consider the case where the parasitoid is the species able to evolve and the parasitoid's distribution of searching time $\beta = (\beta_1, \ldots, \beta_n)$ is the trait under selection. Finally, we consider the case where the host and parasitoid coevolve (i.e., both $\alpha$ and $\beta$ are under selection). The details of the analysis are presented in appendixes A, B, and C.

In our analysis, the quantities $\hat{N}_i$ and $\hat{P}_i$ represent the abundances of the host and parasitoid when the populations are at equilibrium in an environment consisting of a single patch of type $i$. Quantities $\hat{N}_i$ and $\hat{P}_i$ correspond to the nonzero equilibrium of

$$N_{t+1} = N_t \lambda_i f_i(P_t)$$

$$P_{t+1} = \theta_i N_t (1 - f_i(P_t)). \tag{2}$$

Because the attack functions $f_i$ are strictly decreasing,

$f_i(0) = 1$ and $\lambda_i > 1$, equation (2) implies that $\hat{N}_i$ and $\hat{P}_i$ exist and are given by

$$\hat{N}_i = \frac{f_i^{-1}(1/\lambda_i)}{\theta_i(1 - 1/\lambda_i)} \qquad \hat{P}_i = f_i^{-1}(1/\lambda_i). \tag{3}$$

### Evolution of the Host

Suppose the host's strategy $\alpha$ evolves, while the strategy $\beta$ of the parasitoids remains fixed throughout evolutionary time. When $\beta_i = 0$ for one or more patches, one can easily verify that the ESS for the host is to lay all of its eggs in these "enemy-free" patches. Consequently, we restrict our attention to the case where the parasitoid is actively searching all of the patches (i.e., $\beta_i > 0$ for all patches $i$). In this case, equation (1) always has a unique equilibrium at which both populations have a positive density (see app. A).

Imagine that there are "resident" populations of hosts and parasitoids playing the strategies $\alpha$ and $\beta$, respectively, and that these populations are at the feasible equilibrium, $(\hat{N}, \hat{P})$, of equation (1). If a "mutation" in the host population occurs, leading to a small population of new phenotypes playing the strategy $\alpha'$, then the invasion rate of the mutant population is given by

$$I_M(\alpha, \beta, \alpha') = \sum_{i=1}^{n} \lambda_i \alpha'_i f_i(\beta_i \hat{P}). \tag{4}$$

The mutant population is able to invade the resident population at a geometric rate if $I_M(\alpha, \beta, \alpha') > 1$. In appendix A, we show that the ESS $\alpha^*(\beta)$ for the host is to lay all of its eggs in the patch or patches, where $\hat{P}_i/\beta_i$ is the largest. This host ESS corresponds to laying eggs in patches that result in the maximal equilibrium parasitoid abundance, $\hat{P}$.

### Evolution of the Parasitoid

Consider the case where the parasitoid strategy $\beta$ evolves, while the host strategy $\alpha$ remains fixed throughout evolutionary time. To determine the invasion rate for a population of "mutant" parasitoids, we need to augment equation (1) with a mutant parasitoid population $Q_t$ playing a mutant strategy $\beta'$. If we assume that the proportion of the total parasitized hosts $\alpha_i N_t[1 - f_i(\beta_i P_t) f_i(\beta'_i Q_t)]$ in patch $i$ successfully parasitized by the mutant parasitoids equals the proportion of searching parasitoids that are mutant parasitoids in patch $i$, then we get the following model:

$$N_{t+1} = \sum_{i=1}^{n} \lambda_i \alpha_i N_t f_i(\beta_i P_t) f_i(\beta'_i Q_t)$$

$$P_{t+1} = \sum_{i=1}^{n} \theta_i \alpha_i N_t \frac{\beta_i P_t}{\beta_i P_t + \beta'_i Q_t}[1 - f_i(\beta_i P_t) f_i(\beta'_i Q_t)]$$

$$Q_{t+1} = \sum_{i=1}^{n} \theta_i \alpha_i N_t \frac{\beta'_i Q_t}{\beta_i P_t + \beta'_i Q_t}[1 - f_i(\beta_i P_t) f_i(\beta'_i Q_t)].$$

If the mutation population is small in size and the resident population at the equilibrium $(\hat{N}, \hat{P})$ of equation (1), then the invasion rate of the mutant population is given by

$$I_Q(\alpha, \beta, \beta') = \sum_{i=1}^{n} \theta_i \alpha_i \hat{N} \frac{\beta'_i}{\beta_i \hat{P}}[1 - f_i(\beta_i \hat{P})].$$

In the case of Poisson-distributed attacks and no variation in $\theta_i$ and $f_i$, this invasion rate coincides with the invasion rate used by van Baalen and Sabelis (1993). Unlike the host case, the ESS $\beta^*(\alpha)$ for the parasitoids is a continuous function of $\alpha$ that cannot be solved explicitly for the general attack function $f_i$. However, it is easy to verify that the parasitoid playing the ESS spends no time searching in host-free patches (i.e., $\beta^*_i(\alpha) = 0$ whenever $\alpha_i = 0$).

### Coevolution of Hosts and Parasitoids

To study coevolution of the host egg-laying and parasitoid searching strategies, we define $(\alpha^{**}, \beta^{**})$ to be a (strong) coevolutionarily stable strategy (Co-ESS) for equation (1) if any small population playing any other strategy is driven to extinction at a geometric rate (i.e., $I_M(\alpha^{**}, \beta^{**}, \alpha') < 1$ and $I_Q(\alpha^{**}, \beta^{**}, \beta') < 1$ for all $\alpha' \neq \alpha^{**}$, and $\beta' \neq \beta^{**}$). We define $(\alpha^{**}, \beta^{**})$ to be a weak Co-ESS for equation (1) if a small population playing another strategy is unable to grow at a geometric rate, and, hence, its invasion fails (i.e., $I_M(\alpha^{**}, \beta^{**}, \alpha') \leq 1$ and $I_Q(\alpha^{**}, \beta^{**}, \beta') \leq 1$ for all $\alpha'$ and $\beta'$). In appendix B, we show that a unique weak Co-ESS exists for equation (1). It is given by

$$\alpha^{**}_i = \frac{\hat{N}_i}{\hat{N}_1 + \hat{N}_2 + \ldots + \hat{N}_n} \tag{5}$$

$$\beta^{**}_i = \frac{\hat{P}_i}{\hat{P}_1 + \hat{P}_2 + \ldots + \hat{P}_n}. \tag{6}$$

Equations (5) and (6) determine a weak Co-ESS and not a strong Co-ESS because the invasion rate of any mutant population is exactly one whenever the resident populations play the strategies $\alpha^{**}$ and $\beta^{**}$.

Equations (5) and (6) have the following interpretation:

the Co-ESS corresponds to hosts laying eggs preferentially in patch types that intrinsically support higher host numbers and parasitoids spending more time searching in patches that intrinsically support higher parasitoid numbers. Solving for the equilibrium values of $\hat{N}$ and $\hat{P}$ in equation (1) when $\alpha = \alpha^{**}$ and $\beta = \beta^{**}$, we get

$$\hat{N} = \hat{N}_1 + \hat{N}_2 + \dots + \hat{N}_n \quad (7)$$

$$\hat{P} = \hat{P}_1 + \hat{P}_2 + \dots + \hat{P}_n. \quad (8)$$

Combining equations (5)–(8), it follows that the number $\alpha_i^{**}\hat{N}$ of coevolved hosts in patch $i$ equals the number $\hat{N}_i$ of hosts supported by an environment consisting of a single patch of type $i$. Similarly, the number $\beta_i^{**}\hat{P}$ of coevolved parasitoids in patch $i$ equals the number $\hat{P}_i$ of parasitoids supported by an environment consisting of a single patch of type $i$. Consequently, the parasitism rate is $1 - f_i(\beta_i^{**}\hat{P})$ in patch $i$ when the coevolved populations are at equilibrium equals $1 - 1/\lambda_i$. While some of these statements may appear tautological at first reading, we emphasize that the population numbers $\hat{N}_i$ and $\hat{P}_i$ are determined in the absence of choices. Hence, there is no reason to believe a priori that they determine the host and parasitoid abundance in a patchy environment or have anything to do with the behavior of the hosts and parasitoids in a patchy environment.

### *Coevolution in Environmental Gradients and Environments with Marginal Patches*

To extract some additional information about the Co-ESS and how it depends on environmental heterogeneity, we assume that the escape functions $f_i$ are of the form $f_i(x) = g(a_i x)$, where $g(x)$ is a decreasing, convex function satisfying $g(0) = 1$ and $\lim_{x\to\infty} g(x) = 0$ (e.g., $g(x) = \exp(-x)$ or $g(x) = (1 + x/k)^{-k}$ with $k > 0$) and where we interpret $a_i > 0$ to be the searching efficiency of the parasitoid in patch $i$. If we define $h(x) = g^{-1}(x)/(1 - x)$, then we can write

$$\hat{N}_i = \frac{h(1/\lambda_i)}{a_i\theta_i} \quad (9)$$

$$\hat{P} = \frac{g^{-1}(1/\lambda_i)}{a_i} \quad (10)$$

Note that $g$ is a decreasing function implies that $g^{-1}$ is decreasing. In appendix B we demonstrate that $h$ also is a decreasing function. A patchy environment is an environmental gradient with respect to all of the life-history traits of the populations provided that we can order the patches such that $\lambda_1 \geq \dots \geq \lambda_n$, $\theta_1 \geq \dots \geq \theta_n$, and $a_1 \geq \dots \geq a_n$.

*Variation in Parasitoid Searching Efficiency.* Suppose only parasitoid searching efficiency varies among patches ($\lambda_1 = \dots = \lambda_n$, $\theta_1 = \dots = \theta_n$, and $a_1 > a_2 > \dots > a_n$). This might occur, for example, if the physical and chemical structure provided by different plants effects the ability of the hosts to hide from parasitoids (i.e., a refuge effect) or the ability of parasitoids to cue in on hosts (Atsatt and O'Dowd 1976; Price et al. 1980; Godfray 1994). Equations (9) and (10) imply that $\hat{N}_1 < \hat{N}_2 < \dots < \hat{N}_n$ and $\hat{P}_1 < \hat{P}_2 < \dots < \hat{P}_n$. Hence, the hosts and parasitoids playing the Co-ESS $(\alpha^{**}, \beta^{**})$ preferentially select patches where the parasitoid searching efficiency is low. Since the parasitism rate at equilibrium is $1 - f_i(\beta^{**}\hat{P}) = 1 - 1/\lambda_i$ and the intrinsic rate of growth for the hosts does not vary among patches, parasitism rates do not vary from patch to patch. Therefore, if only the searching efficiency of the parasitoid varies among the patches, then the coevolved populations exhibit congruent choices at equilibrium but the distribution of parasitoid attacks is density independent (i.e., there is no correlation between percent parasitism and host density in a patch).

*Variation in Parasitoid Survivorship Rate.* Suppose only parasitoid survivorship rates vary among patches ($\lambda_1 = \dots = \lambda_n$, $\theta_1 > \theta_2 > \dots > \theta_n$, and $a_1 = \dots = a_n$). This may occur for systems where plants produce chemical compounds that are sequestered by the host resulting in reduced parasitoid survivorship rates (Price et al. 1980). Equations (9) and (10) imply that $\hat{P}_1 = \dots = \hat{P}_n$ and $\hat{N}_1 < \hat{N}_2 < \dots < \hat{N}_n$. Consequently, the hosts preferentially select patches where the parasitoid has a low survivorship rate and the parasitoids spend equal amounts of time searching all patches. Since $\lambda_i$ does not vary from patch to patch, as noted above, the parasitoid attack rate is the same in all patches. Hence, if only the parasitoid survivorship rates varies among patches, then the parasitoids exhibit no patch preference and the distribution of parasitoid attacks is density independent.

*Variation in Host Intrinsic Rate of Growth.* Suppose that only the host intrinsic rate of growth varies among the patches ($\lambda_1 > \lambda_2 > \dots > \lambda_n$, $\theta_1 = \dots = \theta_n$, and $a_1 = \dots = a_n$). This case was considered by van Baalen and Sabelis (1993) and may occur when variation in plant quality affects the intrinsic rate of growth the host (Lawton and McNeil 1979; van Emden 1986). Equations (9) and (10) now imply that $\hat{N}_1 > \hat{N}_2 > \dots > \hat{N}_n$ and $\hat{P}_1 > \hat{P}_2 > \dots > \hat{P}_n$. The gradient in the $\lambda_i$ implies that parasitism rate is higher in the patches where the host has the higher intrinsic rate of growth. Consequently, when the host's intrinsic rates

**Table 1:** Consequences of life-history variation for coevolved behavior, form of density dependence, and stabilizing properties of the Co-ESS

| Type of environment | Behavior | Distribution of parasitoid attacks | Stabilizing? |
|---|---|---|---|
| Environmental gradients: | | | |
| Case 1: | | | |
| $a_1 > \dots > a_n$<br>$\theta_1 = \dots = \theta_n$<br>$\lambda_1 = \dots = \lambda_n$ | Congruent choices | Density independence | Never |
| Case 2: | | | |
| $a_1 = \dots = a_n$<br>$\theta_1 > \dots > \theta_n$<br>$\lambda_1 = \dots = \lambda_n$ | Parasitoids have no patch preference | Density independence | Never |
| Case 3: | | | |
| $a_1 = \dots = a_n$<br>$\theta_1 = \dots = \theta_n$<br>$\lambda_1 > \dots > \lambda_n$ | Congruent choices | Density dependence | Sometimes |
| Case 4: | | | |
| $a_1 = \dots = a_n$<br>$\theta_1 \gg \dots \gg \theta_n$<br>$\lambda_1 > \dots > \lambda_n$ | Contrary choices | Inverse density dependence | Sometimes |
| Case 5: | | | |
| $a_1 = \dots = a_n$<br>$\theta_1 > \dots > \theta_n$<br>$\lambda_1 \gg \dots \gg \lambda_n$ | Congruent choices | Density dependence | Sometimes |
| Marginal patch: | | | |
| Case 6: | | | |
| $0 \approx \theta_1 \ll \theta_2 \le \dots \le \theta_n$ | Host has strong preference for patch 1 | ... | Sometimes |
| Case 7: | | | |
| $1 \approx \lambda_1 \ll \lambda_2 \le \dots \le \lambda_n$ | Parasitoids avoid patch 1 | ... | Sometimes |
| Case 8: | | | |
| $0 \approx a_1 \ll a_2 \le \dots \le a_n$ | Strong congruent choices | Density dependence | Never |
| Case 9: | | | |
| $0 \approx \theta_1 \ll \theta_2 \le \dots \le \theta_n$<br>$1 \approx \lambda_1 \ll \lambda_2, \dots, \lambda_1 \ll \lambda_n$ | Strong contrary choices | Inverse density dependence | Always |

of growth varies among patches, the populations playing the Co-ESS exhibit congruent choices and direct density dependence in the distribution of parasitoid attacks (i.e., there is a positive correlation between percent parasitism and host density in a patch).

*Variation in Host Intrinsic Rate of Growth and Parasitoid Survivorship.* We consider two cases in which the parasitoid survivorship rates and the hosts intrinsic rate of growth co-vary among patches. First, suppose the differences in patches form a gradient for the host ($\lambda_1 > \lambda_2 > \dots > \lambda_n$) and a stronger gradient for the parasitoid ($\theta_1 \gg \theta_2 \gg \dots \gg \theta_n$). Equations (9) and (10) imply $\hat{N}_1 < \dots < \hat{N}_n$ and $\hat{P}_1 > \hat{P}_2 > \dots > \hat{P}_n$. Therefore, the populations playing the Co-ESS exhibit contrary choices and inverse density dependence in the distribution of parasitoid attacks (i.e., a negative correlation exists between percent parasitism and host density in a patch). In the reverse case where the differences in the patches form a gradient for the parasitoid ($\theta_1 > \dots > \theta_n$) and a stronger gradient for the host ($\lambda_1 \gg \dots \gg \lambda_n$), it follows that $\hat{N}_1 > \dots > \hat{N}_n$ and $\hat{P}_1 > \dots > \hat{P}_n$. Therefore, the coevolved populations exhibit congruent choices and direct density dependence in the distribution of parasitoid attacks. A summary of these results are presented in table 1.

*Strong Choices in Environments with Marginal Patches.* It is natural to ask what conditions result in hosts or parasitoids avoiding a given patch, hosts laying most of their eggs in a given patch or parasitoids spending most of their searching time in a given patch? Equations (9) and (10) suggest that such extreme behaviors occur when the environment contains at least one patch (say, patch 1) of marginal quality. When the parasitoid searching efficiency is marginal in patch 1 ($a_1 \approx 0$), equations (9) and (10) imply that $\hat{N}_1$ and $\hat{P}_1$ become extremely large. Consequently, the coevolved populations exhibit "strong congruent choices" in which the hosts lay almost all of their eggs in the marginal patch ($\alpha_1^{**} \approx 1$) and parasitoids spend almost all their searching time in the marginal patch ($\beta_1^{**} \approx 1$). Next, consider the case that the host intrinsic rate of growth is marginal in patch 1 ($\lambda_1 \approx 1$). Because $f_1(0) = 1$, equation (10) implies that $\hat{P}_1 \approx 0$, and, therefore, the parasitoids playing the Co-ESS spend almost no time searching in the marginal patch ($\beta_1^{**} \approx 0$). Alternatively, when the parasitoid survivorship is marginal in patch 1 ($\theta_1 \approx 0$), equation (9) implies that hosts playing the Co-ESS will lay almost all their eggs in the marginal patch ($\alpha_1^{**} \approx 1$). Finally, if patch 1 is marginal for the host's intrinsic rate of growth and the parasitoid's survivorship ($\lambda_1 \approx 1$ and $\theta_1 \approx 0$), then the coevolved populations exhibit "strong contrary choices" in which almost all of the host eggs are laid in the marginal patch while the parasitoids spend almost no time searching in the marginal patch ($\alpha_1^{**} \approx 1$ and $\beta_1^{**} \approx 0$). We summarize these conclusions in table 1.

### Stability of the Equilibrium Co-ESS

*General Attack Rates.* The preceding analysis was based on the assumption that the resident populations are at an equilibrium of equation (1). Therefore, to determine when the previous analysis is relevant, we need to find under what conditions this equilibrium is stable. When this occurs and the populations are playing their Co-ESSs, the equilibrium for equation (1) is an evolutionarily stable attractor (Rand et al. 1994). As mentioned earlier, when the populations are playing the Co-ESS ($\alpha^{**}$, $\beta^{**}$), the equilibrium of equation (1) at which both populations have positive densities is given by equations (7) and (8). In appendix C, we show that this equilibrium is stable if and only if the inequality

$$-\sum_{i=1}^{n} f_i'(\hat{P}_i)(\hat{P}_i\alpha_i^{**}\lambda_i + \hat{N}_i\beta_i^{**}\theta_i) < 1 \tag{11}$$

holds. A particularly appealing aspect of inequality (11) is that it can be explicitly written down in terms of the parameters $\lambda_i$ and $\theta_i$ whenever the inverse of the attack functions $f_i$ can be explicitly written down (e.g., $f_i(x) = \exp(-a_i x)$ and $f_i(x) = (1 + a_i x/k_i)^{-k_i}$).

*Poisson Attack Rates.* To understand when the coevolutionary process actually stabilizes a system whose within-patch dynamics are inherently unstable, we assume that the parasitoid attack functions are Poisson distributed, $f_i(x) = \exp(-a_i x)$ with $a_i > 0$. Under this assumption, the stability condition in inequality (11) is equivalent to

$$\sum_{i=1}^{n}\left(\beta_i^{**}\frac{\ln\lambda_i}{\lambda_i - 1} + \alpha_i^{**}\ln\lambda_i\right) < 1. \tag{12}$$

An immediate implication of equation (12) is that, if the hosts have a high intrinsic rate of growth in all of the patches (e.g., $\lambda_i > e$ for all patches $i$), then the Co-ESS equilibrium is never stable.

Van Baalen and Sabelis (1993) considered the effect of variation only in the host intrinsic rate of growth among patches and showed that this could be stabilizing for the coevolved populations as long as sufficiently many patches of marginal quality for the host exist (fig. 1). Alternatively, suppose the only variation in the system is in the life-history traits of the parasitoid ($\lambda_1 = \ldots = \lambda_n$ but $a_i$ and $\theta_i$ vary). In appendix C, we prove that the stability inequality (12) never holds in this case, and, hence, variation in parasitoid life-history traits alone is not stabilizing. Contrary choices in conjunction with marginal patches can be a strong stabilizing factor even when there are only a few marginal patches (fig. 1). One can get a sense of this from equation (12) as follows: for any $\lambda_i > 1$, $\ln\lambda_i/(\lambda_i - 1)$ is strictly <1, while $\ln\lambda_i + (\ln\lambda_i)/(\lambda_i - 1)$ is strictly >1. However, $\ln\lambda_i$ is <1 only when $\lambda_i$ is sufficiently close to 1. Therefore, if the parameters of the model are such that the $\lambda_i$ are close to 1 for some patches and the hosts preferentially select those patches while the parasitoids avoid those patches, then stability is ensured. For example, when one patch (say, patch 1) is marginal with respect to host intrinsic rate of growth and parasitoid survivorship ($\theta_1 \approx 0$ and $\lambda_1 \approx 1$), the populations playing the Co-ESS exhibit strong contrary choices and the left-hand side of inequality (12) is well approximated by $\sum_{i=2}^{n}\beta_i^{**}\ln\lambda_i/(\lambda_i - 1)$, which is always strictly <1. Hence, strong contrary choices ensure stability.

### On the Nature of the Co-ESS

In this section, we discuss the relationship between the Co-ESS and the single species ESSs, and how the Co-ESS may be approached over time. When the hosts are playing the Co-ESS (i.e., $\alpha = \alpha^{**}$), the single species parasitoid ESS is given by the parasitoid Co-ESS (i.e., $\beta^{*}[\alpha^{**}] = \beta^{**}$). On the other hand, when the parasitoids are playing the Co-ESS (i.e., $\beta = \beta^{**}$), the single species ESS analysis implies that any host strategy is a weak ESS, as the overall equilibrial parasitoid abundance is independent of the host strategy. While these observations imply that populations playing strategies different from the Co-ESS are susceptible to invasion, it does not explain how the Co-ESS would be approached over time. To formally address this issue, it is necessary to augment the population dynamics with the

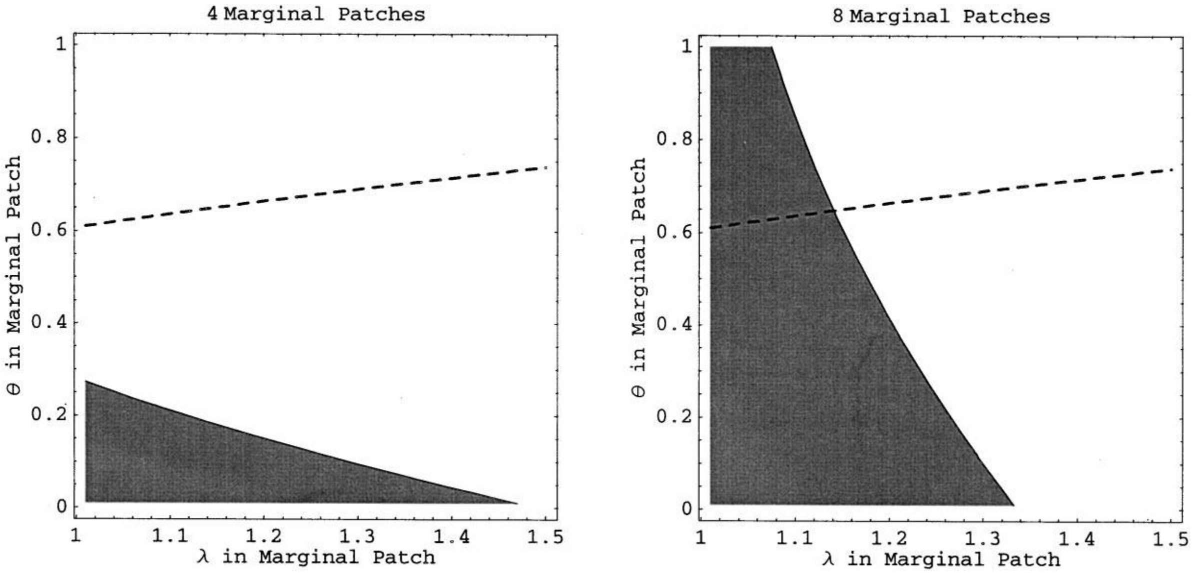

**Figure 1:** Ecological stability diagrams for coevolved hosts and parasitoids in a 10-patch environment. Parasitoid attacks in all patches are Poisson distributed with searching efficiency $a_i = 1$. The environment consists of two types of patches: "nonmarginal" patches ($\lambda_i = 3.0$ and $\theta_i = 1.0$) and "marginal" patches ($\lambda_i = \lambda$ and $\theta_i = \theta$ allowed to vary as shown in the diagrams). The left-hand and right-hand panels correspond to having four and and marginal patches, respectively. The shaded region corresponds to combinations of λ and θ for which the coevolved equilibrium is ecologically stable. The unshaded region corresponds to combinations of λ and θ for which the coevolved equilibrium is ecologically unstable. The dashed line corresponds to combinations of λ and θ for which the host selects all patches with equal preference. Since the parasitoid always preferentially selects the nonmarginal patches and the host preferentially selects the marginal patches for λ and θ values below the dashed line, the region below the dashed line corresponds to contrary choices and the region above the dashed line corresponds to congruent choices.

strategy dynamics (Vincent et al. 1993) and evaluate whether the Co-ESS in the augmented system is globally stable. Although such an analysis is beyond the scope of this article, our single species analysis provides some arguments that make an approach to the Co-ESS seem plausible. For illustrative purposes, consider a two-patch environment, say, patch A and patch B, with a Co-ESS for which hosts preferentially select patch B and parasitoids preferentially select patch A. Suppose hosts and parasitoids initially both only select patch A, and evolutionary changes in behavior occur sufficiently slowly so that population dynamics constantly remain near equilibrium. The single species host ESS predicts that the hosts' preferences will shift toward patch B. The single species parasitoid ESS predicts that once the host distribution is sufficiently skewed, the parasitoids should spend some time searching in patch B. The single species ESS analysis implies that these evolutionary shifts by hosts and parasitoids toward patch B will decelerate until both species settle upon the Co-ESS at which there in no further evolutionary pressure for the hosts or parasitoids to shift their patch preferences.

## Discussion

Our model adds the realistic complexity of variation in patch quality with respect to host and parasitoid life-history traits to previous host-parasitoid models considered by Hassell and May (1973, 1974) and van Baalen and Sabelis (1993). Our model and its analysis include the following four assumptions. First, the hosts and parasitoids have coupled and synchronized interactions with discrete host and parasitoid generations. Second, the parasitoids are search limited, not egg limited. Third, both hosts and parasitoids have density-independent searching and egg-laying behaviors, and these behaviors can evolve in response to changes in population abundance and patch qualities. Fourth, in the absence of parasitism, the host population grows at a geometric rate.

Our analysis considers the evolution of a single species as well as coevolution of both the host and parasitoid. When only the host evolves in response to a population of parasitoids playing a fixed searching strategy, the ESS for the host is to lay all of its eggs in patches that act as a refuge from the parasitoid (i.e., patches where the parasitoid does not search) or in the absence of refuges to lay all of its eggs in patches that maximize the parasitoid abundance at equilibrium. These predictions are consistent with Hochberg and Holt's (1995) work on refuge evolution and Holt and Lawton's (1993) work on apparent competition in host-parasitoid communities. When the host and parasitoid coevolve, our analysis shows that the Co-

ESS for both populations can be predicted based on the equilibrium abundance of the host and parasitoid confined to a single patch. Namely, when playing the Co-ESS, the hosts and parasitoids preferentially select patches in which their populations intrinsically attain higher equilibrium densities. This prediction corresponds to an ideal free distribution of host and parasitoids and concurs with many previous theoretical treatments of patch selection (Fretwell and Lucas 1970; Comins and Hassell 1979; Sutherland 1983; van Baalen and Sabelis 1993) or life-history evolution (Kaitala and Getz 1995). From this we deduce that environmental variation in the life-history traits of only one species may lead to coevolved populations exhibiting congruent choices with direct density dependence or density independence in the distribution of percent parasitism, but does not lead to the coevolution of contrary choices or inverse density dependence in the distribution of percent parasitism. However, if the life-history traits of both species co-vary among patches, then populations playing the Co-ESS can exhibit contrary choices and inverse-density dependence in the distribution of percent parasitism.

Theoretical studies have shown that patchy environments may stabilize host-parasitoid interactions provided that there is sufficient variation in the distribution of percent parasitism (Hassell and May 1973; Murdoch and Oaten 1975; Hassell 1984; Chesson and Murdoch 1986; Hassell and May 1988; Walde and Murdoch 1988; Pacala et al. 1990; Hassell et al. 1991). These studies assumed that life-history traits do not vary among patches, and that the heterogeneity manifests itself via heterogeneous patch selection strategies of both populations. As pointed out by van Baalen and Sabelis (1993), in the absence of variation in life-history traits, populations playing the Co-ESS for patch selection visit all patches with equal frequency. Consequently, such populations would exhibit no variation in percent parasitism rates and host-parasitoid interactions would not be stabilized. Van Baalen and Sabelis (1993) showed, however, that the inherently unstable Nicholson-Bailey dynamics could be stabilized by populations playing the Co-ESS for patch selection when sufficiently many patches for which the host intrinsic rate of growth is low exist. Hence, variation in host life-history traits can stabilize host-parasitoid interactions. Alternatively, our analysis implies that variation in parasitoid life-history traits is not stabilizing by itself. We show, however, that variation in both host and parasitoid life-history traits leading to contrary choices can be extremely stabilizing. In particular, if there exist patches for which the host has a low intrinsic rate of growth and the parasitoid has a low survivorship rate, then the populations playing the Co-ESS exhibit strong contrary choices and coexist at a stable equilibrium.

Many field studies have examined percent parasitism rates as a function of host density, but only a few behavioral studies have investigated parasitoid and host preferences in the context of heterogeneous environments. Our model provides testable hypotheses regarding what heterogeneities in life-history parameters lead to these different host egg laying and parasitoid searching patterns. Below we discuss our results in the context of existing experimental and field data.

### *Contrary Choices and Enemy-Free Space*

Our coevolutionary analysis implies that patch heterogeneity may lead to contrary choices in which parasitoid and host prefer different patch types. When contrary choices occur, both species can appear to be making “inappropriate” choices (Fox and Eisenbach 1992). For instance, herbivores may have intrinsically higher growth and survival rates in the better quality patch in the absence of parasitoids, yet prefer to lay their eggs on poorer quality plants. On the other hand, the parasitoids may prefer searching patches with fewer hosts. This paradoxical behavior only occurs when the poorer quality patches for the host are also poorer quality patches for the parasitoids. In this light, hosts are effectively shifting to “enemy-free space” (Jeffries and Lawton 1984; Holt and Lawton 1993).

Fox and Eisenbach (1992) found contrary choices in preference for searching plants used by the moth *Plutella xylostella* and its specialist solitary parasitoid *Diadegma insulare* when comparing ovipositional and searching preferences in collard and red cabbage crops that were grown at high and low fertilizer levels. *Diadegma* preferentially searched for hosts on high-fertilized plants, while *Putella* preferentially laid eggs on low-fertilized plants. In choices between high-fertilized plants of both collards and red cabbage, wasps preferentially searched for hosts on collards, while hosts preferentially laid eggs on red cabbage. As predicted by our theory, additional experiments on host growth, reproduction, parasitism rates and sex ratios (Fox et al. 1990, 1996; Fox and Eisenbach 1992) suggest that the parasitoids preferentially searched the plants that were of higher quality for the host, while the host laid more eggs on plants that were of lower quality for the parasitoid.

We know of no other study that explicitly examines the behavioral choices of both hosts and their parasitoids. However, there are many examples of herbivores that are attacked by parasitoids on one food plant but not on another (Shepard and Dahlman 1988). Most of these examples involve hosts that switch from a native plant to a cultivated plant without a corresponding switch in the parasitoids’ behavior (Shepard and Dahlman 1988). Selection on herbivores may be particularly high in agricultural situations because of higher parasitoid pressures, and shifts in plant preferences of agricultural pests may be rapid (Tabashnik 1983; Via 1986*a*, 1986*b*).

### Distribution of Parasitoid Attacks

Walde and Murdoch (1988) in their statistical analysis of results from 75 studies on spatial density dependence of parasitism in the field found that 28% exhibited inverse density dependence, 23% exhibited direct density dependence, and the remaining 49% exhibited density independence. In a similar analysis, Lessells (1985) found that 66% of 43 field studies showed a relationship between host density and distribution of parasitoid attacks, and in half of these the correlation was negative. These studies clearly show that all three patterns of parasitism occur in the field. Regarding inverse density dependence, Walde and Murdoch (1988, p. 456) state, “In most cases, the mechanisms are unknown, but are likely to include egg limitation and handling time.” Our analyses suggests that inverse density dependence may be the product of coevolutionary interactions in a heterogeneous environment.

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## APPENDIX A

### The Host ESS When the Parasitoid Strategy Remains Fixed

In this appendix, we derive the ESS for the host strategy $\alpha$ when the parasitoid strategy $\beta$ is fixed. We assume that $\beta$ satisfies $\beta_i > 0$ for all patches $i$. Under this assumption, equation (1) has a unique equilibrium $(\hat{N}, \hat{P})$ such that $\hat{N} > 0$ and $\hat{P} > 0$. To see why this is the case, define $H(P) = \sum_{i=1}^{n} \alpha_i \lambda_i f_i(\beta_i P)$ and notice that any equilibrium $(\hat{N}, \hat{P})$ of equation (1) with $\hat{N} > 0$ must satisfy $1 = H(\hat{P})$. Because we have assumed that $\lambda_i > 1$ and $f_i(0) = 1$ for all $i$, we have $H(0) > 1$. Also, because we have assumed $\beta_i > 0$ for all $i$, $f_i$ is strictly decreasing, and $f_i$ satisfies $\lim_{P\to\infty} f_i(P) = 0$ for all $i$, we have that $H$ is strictly decreasing and satisfies $\lim_{P\to\infty} H(P) = 0$. Hence, there is a unique $\hat{P} > 0$, which satisfies $1 = H(\hat{P})$. Equation (1) implies $\hat{N} = \hat{P} / \sum_{i=1}^{n} \theta_i \alpha_i [1 - f_i(\beta_i \hat{P})]$.

We perform the ESS analysis for the host in the generic case when a patch $j$ exists such that

$$\hat{P}_j \big/ \beta_j > \hat{P}_i \big/ \beta_i \qquad \text{for all } i \neq j. \tag{A1}$$

By permuting the indices if necessary, we may assume that $j = 1$. Let $\alpha^*$ be the strategy defined by $\alpha^* = (1, 0, 0, \dots, 0)$. We will show that a population playing this strategy cannot be invaded by a mutant host population playing a different strategy. We begin with two observations. First, equation (3) implies that $\lambda_i f_i(\hat{P}_i) = 1$ for all $i \geq 1$. Equation (A1) and the strictly decreasing property of $f_i$ imply that $\hat{P}_i < \beta_i \hat{P}_1 / \beta_1$ and $f_i(\hat{P}_i) > f_i(\beta_i \hat{P}_1 / \beta_1)$ for all $i \geq 2$. Hence,

$$1 = \lambda_1 f_1(\hat{P}_1) \text{ and } 1 > \lambda_i f_i(\beta_i \hat{P}_1 \big/ \beta_1) \text{ for all } i \geq 2. \tag{A2}$$

Our second observation is that the equilibrium density $\hat{P}(\alpha^*)$ of the parasitoid in equation (1), when $\alpha = (1, 0, \dots, 0)$, is given by $\hat{P}(\alpha^*) = \hat{P}_1 / \beta_1$. Now, consider any other host strategy $\alpha' \neq \alpha^*$. The invasion rate of this strategy is given by (cf. eq. [4] and our two observations) $I_M(\alpha^*, \beta, \alpha') = \sum_{i=1}^{n} \alpha_i' \lambda_i f_i(\beta_i \hat{P}_1 / \beta_1)$. Since $\alpha' \neq \alpha^*$, there exists an $i \geq 2$ such that $\alpha_i' > 0$. Therefore, equation (A2) implies that $I_M(\alpha^*, \beta, \alpha') < 1$. Thus, a mutant host population playing $\alpha'$ is driven to extinction at a geometric rate. To see that this host strategy $\alpha^* = (1, 0, \dots, 0)$ results in the maximal parasitoid abundance in equation (1), let $\hat{P}(\alpha')$ correspond to the equilibrium of equation (1) when $\alpha = \alpha'$. Since $I_M(\alpha^*, \beta, \alpha') = \sum_{i=1}^{n} \alpha_i' f_i(\beta_i \hat{P}(\alpha^*)] < 1$, the $f_i$ are decreasing and $\sum_{i=1}^{n} \alpha_i' f_i[\beta_i \hat{P}(\alpha')] = 1$, it follows that $\hat{P}(\alpha') < \hat{P}(\alpha^*)$.

## APPENDIX B

### Coevolution of the Hosts and Parasitoids

A necessary condition for $(\alpha^{**}, \beta^{**})$ to be the Co-ESS solution for the dynamical system in equation (1) is that the function $A(\alpha') = I_M(\alpha^{**}, \beta^{**}, \alpha')$ is maximized at $\alpha' = \alpha^{**}$ and the function and $B(\beta') = I_Q(\alpha^{**}, \beta^{**}, \beta')$ is maximized at $\beta' = \beta^{**}$ (Vincent et al. 1996). Because $\alpha'$ and $\beta'$ are constrained by the relationships $\sum_{i=1}^{n} \alpha_i' = 1$ and $\sum_{i=1}^{n} \beta_i' = 1$, the solution to this optimization problem occurs either at the boundary of the $(2n - 2)$ simplex (i.e., $\beta_i = 0$ or $\alpha_i = 0$ for some patch $i$) or the interior of the $(2n - 2)$ simplex (i.e., $\beta_i > 0$ and $\alpha_i > 0$ for all patches $i$). In the latter case, this maximization problem is equivalent to the statement that there exists Lagrange multipliers $\mu_1$ and $\mu_2$ such that for all $1 \leq i \leq n$,

$$\frac{\partial A}{\partial \alpha_i'}(\alpha^{**}) = \mu_1 \qquad \frac{\partial B}{\partial \beta_i'}(\beta^{**}) = \mu_2. \tag{B1}$$

From the definition of $A(\alpha')$ and $B(\beta')$, equation (B1) implies that for all $1 \leq i \leq n$,

$$\lambda_i f_i(\beta_i^{**}\hat{P}) = \mu_1 \qquad \frac{\theta_i \alpha_i^{**}\hat{N}}{\beta_i^{**}\hat{P}}[1 - f_i(\beta_i^{**}\hat{P})] = \mu_2. \tag{B2}$$

Summing the left-hand equation in (B2) over the index $i$ with respect to the weighting $\alpha_i^{**}$, we obtain $\sum_{i=1}^{n} \alpha_i^{**}\lambda_i f_i(\beta_i^{**}\hat{P}) = \mu_1$. This equality in conjunction with the equilibrium condition for (1) implies that $\mu_1 = 1$. Hence, equation (B2) implies $\beta_i^{**}\hat{P} = f_i^{-1}(1/\lambda_i) = \hat{P}_i$ and $\hat{P} = \hat{P}_1 + \ldots + \hat{P}_n$. Summing the right-hand side of (B2) over the index $i$ and weighting each entry by $\beta_i^{**}$, we obtain

$$\sum_{i=1}^{n} \frac{\theta_i \alpha_i^{**}\hat{N}}{\hat{P}}[1 - f_i(\beta_i^{**}\hat{P})] = \mu_2. \tag{B3}$$

The equilibrium condition for equation (1) with $(\alpha, \beta) = (\alpha^{**}, \beta^{**})$ and (B3) imply that $\mu_2 = 1$. Hence, $\alpha_i^{**}\hat{N} = f_i^{-1}(1/\lambda_i)/\theta_i(1 - 1/\lambda_i) = \hat{N}_i$ and $\hat{N} = \hat{N}_1 + \ldots + \hat{N}_n$.

Now suppose that $g(x)$ is strictly decreasing and convex function such that $g(0) = 1$ and $\lim_{x\to\infty} g(x) = 0$. In the main text, we define a function $h(x) = g^{-1}(x)/(1 - x)$ and claim that it is a strictly decreasing function. To see that $h(x)$ is decreasing for $0 \leq x < 1$, notice that

$$h'(x) = \frac{g^{-1'}(x)(1 - x) + g^{-1}(x)}{(1 - x)^2}. \tag{B4}$$

Our assumption that $g(x)$ is decreasing and convex for $x \geq 0$ implies that $g^{-1}(x)$ is decreasing and convex for $0 < x \leq 1$. Convexity of $g^{-1}(x)$ implies that $g^{-1'}(x)(1 - x) + g^{-1}(x) < 0$ for $0 < x < 1$. Hence, (B4) implies that $h(x)$ is a strictly decreasing function for $0 < x \leq 1$.

## APPENDIX C

### Stability of the Co-ESS Equilibrium

To determine the stability of the equilibrium $(\hat{N}, \hat{P})$ when the populations are playing any strategy $(\alpha, \beta)$, we evaluate the Jacobian matrix $\mathbf{J}$ of (1) at the equilibrium density $(\hat{N}, \hat{P})$ and get

$$\mathbf{J} = \begin{pmatrix} 1 & \hat{N}\sum_{i=1}^{n} f_i'(\beta_i\hat{P})\alpha_i\beta_i\lambda_i \\ \dfrac{\hat{P}}{\hat{N}} & -\hat{N}\sum_{i=1}^{n} f_i'(\beta_i\hat{P})\alpha_i\beta_i\theta_i \end{pmatrix}.$$

Matrix $\mathbf{J}$ has eigenvalues of modulus <1 if, and only if, $2 > 1 + \det\mathbf{J} > |\text{trace } \mathbf{J}|$ (see, e.g., sec. 2.8 in Edelstein-Keshet 1988). Notice that

$$\det\mathbf{J} = -\sum_{i=1}^{n} f_i'(\beta_i\hat{P})\alpha_i\beta_i\left(\hat{P}\lambda_i + \hat{N}\theta_i\right)$$

and

$$\text{trace } \mathbf{J} = 1 - \hat{N}\sum_{i=1}^{n} f_i'(\beta_i\hat{P})\alpha_i\beta_i\theta_i.$$

Since $f_i' < 0$, the inequality $1 + \det\mathbf{J} > |\text{trace } \mathbf{J}|$ always holds. Hence $(\hat{N}, \hat{P})$ is stable if and only if $\det\mathbf{J} < 1$. When $(\alpha, \beta)$ equals the Co-ESS $(\alpha^{**}, \beta^{**})$,

$$\det \mathbf{J} = -\sum_{i=1}^{n} f_i'(\hat{P}_i)\left(\hat{P}_i\alpha_i^{**}\lambda_i + \hat{N}_i\beta_i^{**}\theta_i\right). \tag{C1}$$

Consider the case when $f_i(x) = \exp(-a_i x)$ with $a_i > 0$, and the hosts and parasitoids are playing the Co-ESS $(\alpha^{**}, \beta^{**})$. In this case, $f_i^{-1}(x) = (1/a_i)\ln(1/x)$ and $f_i'(x) = -a_i f_i(x)$. Consequently, $\hat{P}_i = (1/a_i)\ln\lambda_i$ and $\hat{N}_i = \ln\lambda_i/[\theta_i a_i(1 - 1/\lambda_i)]$. Evaluating and simplifying the expression for $\det\mathbf{J}$, we get

$$\det\mathbf{J} = \sum_{i=1}^{n} \beta_i^{**}\frac{\ln\lambda_i}{\lambda_i - 1} + \alpha_i^{**}\ln\lambda_i.$$

To see that no variation in host life-history traits implies that $\det \mathbf{J} > 1$, assume that $\lambda_1 = \ldots = \lambda_n$. Under this assumption, $\det \mathbf{J} = \lambda_1\ln\lambda_1/(\lambda_1 - 1)$, which is strictly greater than 1 whenever $\lambda_1 > 1$. Thus, if only the parasitoids life-history traits vary among the patches, then the coevolved populations with Poisson distributed attack rates is unstable.

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