Parasitoid sex allocation affects co-evolution of patch selection and stability in host–parasitoid systems

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ABSTRACT

Previously, we have show that the co-evolution of patch selection strategies of hosts and parasitoids in heterogeneous environments can lead to contrary habitat choices in which the hosts preferentially select patches that the parasitoids avoid. Since this work did not include the variable parasitoid sex ratios that have been found in field and laboratory systems with contrary choices, we extend previous analyses to determine how parasitoid sex allocation co-evolves with host and parasitoid patch preferences. In our analysis, we assume the environment consists of two patch types: lower quality patches and higher quality patches. In the lower quality patches, hosts have a lower intrinsic rate of growth and female parasitoid larvae are less likely to survive than male parasitoid larvae. Our co-evolutionary analysis reveals that the co-evolved parasitoids preferentially search for hosts in higher quality patches, lay primarily female eggs on hosts encountered in these patches, and are more likely to lay male eggs on hosts encountered in the lower quality patches. As a co-evolutionary response, the hosts lay twice as many eggs in the poorer patches as they would if parasitoid sex ratios did not evolve. We conclude by showing that the co-evolution of parasitoid sex allocation with patch selection can stabilize host–parasitoid interactions even when co-evolution of patch selection by itself does not.

Keywords: co-evolution, host–parasitoid dynamics, parasitoid sex allocation, spatial models.

INTRODUCTION

Most species live in an inherently heterogeneous world, with patches in which their growth rates vary. For plant-feeding insects, the variability in growth and reproduction may stem from the variation in the nutritional quality of their host plants, local climate, local abundance of parasitoids and other factors. Variability in parasitoid growth and reproduction may reflect variation in the local abundance, size or quality of their hosts. Understanding how hosts and parasitoids co-evolve patch selection strategies in heterogeneous environments and the population dynamic implications of this co-evolution have been the focus of recent theoretical work (van Baalen and Sabelis, 1993, 1999; Hochberg and Holt,

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1995; Schreiber *et al.*, 2000). Under the assumption that only the life-history traits of the host vary among patches, van Baalen and Sabelis (1993) found that co-evolution of patch selection inevitably results in congruent patch choices, with parasitoids and hosts favourably selecting the same patches, and promotes ecological stability under restricted circumstances. However, if the life-history traits of the parasitoids as well as the hosts vary among patches, then co-evolved host–parasitoid populations can exhibit either contrary patch choices with hosts and parasitoids preferentially selecting different patches or congruent choices depending on the form of environmental variability (Schreiber *et al.*, 2000). Furthermore, we found that environmental variability promoting the co-evolution of contrary patch choices (e.g. the existence of patches that are of marginal quality for the host and parasitoid), coupled with the co-evolved patch preferences, can stabilize host–parasitoid interactions. Although these predictions are consistent with field and experimental observations (e.g. Fox and Eisenbach, 1992), an important biological feature of host–parasitoid interactions – namely, the ability of female parasitoids to determine the sex of the eggs they lay (Godfray, 1994; Fox *et al.*, 1996) – was not included in this analysis. The aim of this study was to incorporate this important biological detail into a co-evolutionarily stable strategy (coESS) analysis to determine how patch selection and parasitoid sex allocation co-evolve in host–parasitoid systems and the implications of this co-evolution for ecological stability.

Skewed sex ratios occur in many species of haplo-diploid Hymenoptera (Charnov, 1982; Bull, 1983; Godfray, 1994). Variable sex ratios are usually related to the haplo-diploid mechanism of sex determination: males are haploid and develop from unfertilized eggs, whereas females are diploid and develop from fertilized eggs. Eggs are fertilized at oviposition. Female wasps can control whether particular eggs are fertilized and thus determine the sex of each offspring. For both diploid and haplo-diploid species, if mating is random, a $1:1$ ratio is expected when the needs and resources for male and female progeny are equivalent (Charnov, 1982; Karlin and Lessard, 1986). But several factors can skew sex ratios. Most sex ratio theory has focused on spatially structured populations that lead to local mate competition on resources that are distributed unevenly with respect to sex and on synchrony of brood maturation and male dispersal (Charnov, 1979, 1982; Charnov *et al.*, 1981; Charnov and Skinner, 1984; Werren, 1984; Karlin and Lessard, 1986; Waage, 1986; Nunney and Luck, 1988; Kvarnemo and Ahnesjo, 1996). Such factors may lead to: (1) interspecific differences in sex ratios based on mating structure or local resources, with biases fixed by selection, as in bark beetles (Charnov, 1982) and scelionid parasitic wasps (Waage, 1982a); or to (2) species with phenotypically plastic sex ratios, such as the wasp *Diadegma insulare* (Fox *et al.*, 1990, 1996). Many parasitoids with biased sex ratios are gregarious, producing few to many offspring within a host, and they fit the local mate competition model partly because they mate locally before dispersing. However, even solitary parasitoids with panmictic breeding systems may have biased ratios (Charnov, 1982; Waage, 1982b, 1986). Sib-mating is a particularly potent mechanism for causing sex ratios to be female-biased (Getz *et al.*, 1992; Taylor and Getz, 1994).

In addition to population structure, skewed sex ratios in haplo-diploid wasps have been linked to: the size of the host (Sandlan, 1979; Charnov *et al.*, 1981; Charnov, 1982; Jones, 1982; Waage, 1982b; Werren, 1984; Wellings *et al.*, 1986; King, 1987; Fox *et al.*, 1990); the order of egg laying within hosts by gregarious species (Werren, 1980; Waage, 1982b, 1986; Waage and Ming, 1984; van den Assem, 1986; Antolin *et al.*, 1995); the availability of sperm and hence female age, since only males can be produced once all the sperm are used (van

den Assem *et al.*, 1984; Comins and Wellings, 1985; Wellings *et al.*, 1986; Ode *et al.*, 1997); the relative density of parasitoids and host (Comins and Wellings, 1985); aggregation of hosts (Hassell, 1978; Waage, 1983); abiotic factors such as extremes of temperature (Kfir and Luck, 1979; Luck and Podoler, 1985) and photoperiod (Bouletreau, 1976); and microbial infections causing sex-specific mortality (e.g. bacteria killing male eggs; Werren *et al.*, 1986). Recently, we have shown that sex ratios can also respond directly to plant quality, even in the absence of host differences (Fox *et al.*, 1990, 1996).

THE MODEL

To understand how parasitoid sex allocation and host and parasitoid patch selection evolve in a patchy environment, we model a population of hosts and parasitoids that disperse between two patches (patch 1 and 2). This model is based on the following assumptions. Host and parasitoids have synchronized generations. Hosts lay a fixed proportion α_i of their eggs in patch i, where $i = 1, 2$ and $\alpha_1 + \alpha_2 = 1$. Female parasitoids spend a fixed proportion β_i of their searching time in patch i, where $i = 1, 2$ and $\beta_1 + \beta_2 = 1$. The probability of a host in patch i escaping parasitism in generation t is $f_i(\beta_i P_t)$, where $\beta_i P_t$ is the total number of female parasitoids in patch i in generation t. The f_i are strictly decreasing functions that approach zero [e.g. Poisson distributed attacks $f_i(x) = \exp(-a_i x)$ or negative binomial distributed attacks $f_i(x) = (1 + a_i x/k_i)^{-k_i}$, where k_i is a clumping parameter and $a_i > 0$ is the searching efficiency of the parasitoid] and that do not depend on the α_i. The intrinsic rates of growth λ_i of the hosts in patch i ($i = 1, 2$) are greater than 1. The parameters θ_i (or ψ_i) are the expected number of female (or male) parasitoids emerging from a host parasitized with a female (or male) egg in patch i. In the case of solitary parasitoids, the θ_i (or ψ_i) represent the probability that a female (or male) parasitoid emerges from a host parasitized with a female (or male) egg in patch i. Upon encountering a host on patch i, a female parasitoid parasitizes the host with a female egg with probability q_i and with a male egg with probability $1 - q_i$. If N_t denotes the total number of hosts in generation t, then we arrive at the following two-patch model:

$$N_{t+1} = \lambda_1 \alpha_1 N_t f_1(\beta_1 P_t) + \lambda_2 \alpha_2 N_t f_2(\beta_2 P_t)$$
$$P_{t+1} = q_1 \theta_1 \alpha_1 N_t (1 - f_1(\beta_1 P_t)) + q_2 \theta_2 \alpha_2 N_t (1 - f_2(\beta_2 P_t)) \tag{1}$$

THE ANALYSIS

To understand how the behaviours of the hosts and the parasitoids co-evolve in a heterogeneous environment, we perform an evolutionarily stable strategy (ESS) and a co-evolutionarily stable strategy (coESS) analysis of equation (1) with respect to the sex-allocation parameters q_i of the parasitoid and the patch selection strategies α_i and β_i of the hosts and parasitoids, respectively. The analysis consists of three parts. First, we analyse the ESS for parasitoid sex allocation when the population dynamics of both host and parasitoid are at equilibrium. Second, we find the coESS for sex allocation and patch selection. This analysis combines our earlier work on patch selection co-evolution (Schreiber *et al.*, 2000) with the ESS analysis for sex allocation. Finally, since the preceding analysis is predicated upon equilibrium population dynamics, we analyse the stability of the unique feasible equilibrium of (1) when the populations play the coESS for parasitoid sex allocation and patch selection.

Throughout our analysis, we assume that the female parasitoid larvae benefit more from hosts on patch 1 than the male parasitoid larvae (i.e. $\theta_1/\theta_2 > \psi_1/\psi_2$). The analysis in the complementary case (i.e. $\theta_1/\theta_2 < \psi_1/\psi_2$) gives the expected complementary results.

Evolutionarily stable parasitoid sex allocation

In this subsection, we analyse the optimal sex allocation strategies for a parasitoid. The analysis assumes that the host and parasitoid populations are at equilibrium and π_i of the parasitized hosts are found in patch i. In the next section, when we perform the coESS analysis for patch selection, the proportions π_i are given (cf. equation 1) by

$$\pi_i = \frac{\alpha_i(1 - f_i(\beta_i P))}{\alpha_1(1 - f_1(\beta_1 P)) + \alpha_2(1 - f_2(\beta_2 P))} \tag{2}$$

where (N, P) denotes the equilibrium of (1). Following Fisher (1930), we assume that the fitness of a female equals the number of daughters she produces plus the number of females inseminated by her sons. This fitness measure is valid if (cf. Godfray, 1994: section 4.2.2): (1) mating is panmictic; (2) both sexes benefit equally from increased investments; and (3) mothers are equally related to their sons and daughters. We remark that (3) holds for diploid populations. In outbred haplo-diploid populations, our fitness measure also holds because the same 50% chance exists for a gene in the mother to be passed on to either daughters or sons.

Consider a population of parasitoids at equilibrium playing the sex allocation strategy $\mathbf{q} = (q_1, q_2)$. In Appendix 1, we show that the relative fitness of a small population of parasitoids playing a 'mutant' strategy $\mathbf{q}' = (q'_1, q'_2)$ is given by

$$\Phi(\mathbf{q}, \mathbf{q}') = \frac{\Sigma_i \theta_i \pi_i q'_i}{2\Sigma_i \theta_i \pi_i q_i} + \frac{\Sigma_i \psi_i \pi_i (1 - q'_i)}{2\Sigma_i \psi_i \pi_i (1 - q_i)}$$

The strategy $\mathbf{q}^* = (q_1^*, q_2^*)$ is an ESS for sex allocation provided that the relative fitness of all other strategies is less than 1; that is, $\Phi(\mathbf{q}^*, \mathbf{q}') \leq 1$ for all strategies $\mathbf{q}'$. In Appendix 1, the ESS strategy for sex allocation is shown to depend on the distribution (π_1, π_2) of hosts as follows (see Fig. 1):

$$q_1^* = \begin{cases} 1 & \text{if } \pi_1\psi_1 \leq \pi_2\psi_2 \\ \dfrac{\pi_1\psi_1 + \pi_2\psi_2}{2\pi_1\psi_1} & \text{if } \pi_1\psi_1 \geq \pi_2\psi_2 \end{cases}$$

$$\tag{3}$$

$$q_2^* = \begin{cases} \dfrac{\pi_2\theta_2 - \pi_1\theta_1}{2\theta_2\pi_2} & \text{if } \pi_1\theta_1 \leq \pi_2\theta_2 \\ 0 & \text{if } \pi_1\theta_1 \geq \pi_2\theta_2 \end{cases}$$

In addition to being the unique ESS for sex allocation, the analysis in Appendix 1 implies that this strategy is *evolutionarily convergent*: for any initial parasitoid sex allocation strategy, repeated invasions of nearby mutant strategies result in the resident strategy converging to $\mathbf{q}^*$.

From the expressions in equation (3), we get two predictions independent of the host distribution. First, whenever a female playing the ESS for sex allocation encounters a host developing on patch 1, the probability that she lays a female egg in this host is at least 50%.
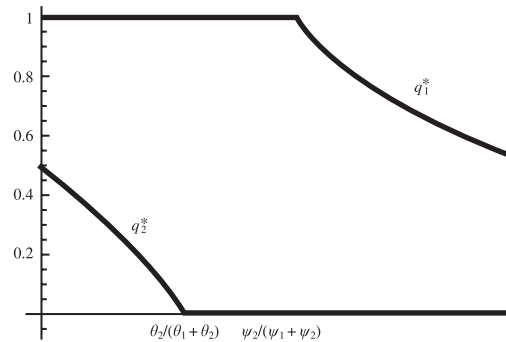
Fig. 1. Graphs of the ESS for sex allocation q_i^* as functions of the proportion π_1 of parasitized hosts in patch 1. *Note*: The inequality $\pi_1\theta_1 \leq \pi_2\theta_2$ (or $\pi_1\psi_1 \leq \pi_2\psi_2$) is equivalent to the inequality $\pi_1 \leq \theta_2/(\theta_1 + \theta_2)$ (or $\pi_1 \leq \psi_2/(\psi_1 + \psi_2)$).

Conversely, whenever she encounters a host developing on patch 2, she lays a male egg in this host with a probability of at least 50%. The ESS for sex allocation also implies that three distinct levels of heterogeneity exist. When a small proportion of encountered hosts are in patch 1 (i.e. $\pi_1\theta_1 \leq \pi_2\theta_2$), only female eggs are laid on hosts from patch 1, whereas both male and female eggs are laid on hosts from patch 2. Conversely, when the proportion of hosts encountered in patch 1 is sufficiently high (i.e. $\pi_1\psi_1 \geq \pi_2\psi_2$), only male eggs are laid on hosts from patch 2, whereas both male and female eggs are laid on hosts from patch 1. Finally, when the proportion of hosts encountered in patch 1 is intermediate (i.e. $\theta_2/\theta_1 \leq \pi_1/\pi_2 \leq \psi_2/\psi_1$), only male eggs are laid in hosts encountered in patch 2 and only female eggs are laid in hosts encountered in patch 1.

Co-evolution of patch selection and sex allocation

The analysis in this subsection draws upon the analysis of the previous subsection and the analysis of Schreiber *et al.* (2000). For the sake of completeness, we review how to determine co-evolutionarily stable patch selection strategies and describe them explicitly for the case when parasitoids lay male and female eggs with equal likelihood on all encountered hosts. After this review, we analyse the co-evolution of patch selection with parasitoid sex allocation. To describe these strategies concisely, we introduce the equilibrium densities of the hosts and parasitoids in single patch environments. For an environment that only consists of one patch, say patch i, and parasitoids laying females and males with equal likelihood on all encountered hosts, the dynamics of the hosts and parasitoids are given by

$$N_{t+1} = \lambda_i N_t f_i(P_t)$$
$$P_{t+1} = \frac{\theta_i}{2} N_t (1 - f_i(P_t)) \tag{4}$$

The non-trivial equilibrium of hosts $\hat{N}_i$ and parasitoids $\hat{P}_i$ of equation (4) is given by

$$\hat{N}_i = \frac{2f_i^{-1}(1/\lambda_i)}{\theta_i(1 - 1/\lambda_i)} \qquad \hat{P}_i = f_i^{-1}(1/\lambda_i)$$

   To understand how hosts and parasitoids may co-evolve their patterns of patch selection, we use the dynamical theory of evolutionarily stable strategies (Hines, 1987; Rand *et al.*, 1994). Following this approach, we consider a population of hosts and parasitoids at the equilibrium $(\hat{N}, \hat{P})$ that play the patch selection strategies $\boldsymbol{\alpha} = (\alpha_1, \alpha_2)$ and $\boldsymbol{\beta} = (\beta_1, \beta_2)$. If a small population of hosts M playing the 'mutant' patch selection strategy $\boldsymbol{\alpha'} = (\alpha'_1, \alpha'_2)$ is introduced, then the invasion rate of the mutant hosts is given by

$$I_M(\boldsymbol{\alpha'}) = \sum_i \alpha'_i \lambda_i f_i(\beta_i \hat{P})$$

Alternatively, if a small population of parasitoids Q playing the 'mutant' patch selection strategy $\boldsymbol{\beta'} = (\beta'_1, \beta'_2)$ is introduced, then the invasion rate of the mutant parasitoids is given by

$$I_Q(\boldsymbol{\beta'}) = \hat{N} \sum_i \frac{q_i \theta_i \alpha_i \beta'_i}{\beta_i \hat{P}} (1 - f_i(\beta_i \hat{P}))$$

The patch selection strategies $(\tilde{\boldsymbol{\alpha}}, \tilde{\boldsymbol{\beta}})$ are a coESS if no population of hosts or parasitoids playing a different strategy is able to invade (i.e. if $\boldsymbol{\alpha} = \tilde{\boldsymbol{\alpha}}$ and $\boldsymbol{\beta} = \tilde{\boldsymbol{\beta}}$, then $I_M(\boldsymbol{\alpha'}) \leq 1$ and $I_Q(\boldsymbol{\beta'}) \leq 1$ for all strategies $\boldsymbol{\alpha'}$ and $\boldsymbol{\beta'}$).
   Schreiber *et al.* (2000) found explicit expressions for the coESS for patch selection. When parasitoids lay female and male eggs with equal likelihood, this coESS is given by

$$\tilde{\alpha}_i = \frac{\hat{N}_i}{\hat{N}_1 + \hat{N}_2} \qquad \tilde{\beta}_i = \frac{\hat{P}_i}{\hat{P}_1 + \hat{P}_2} \qquad i = 1, 2$$

Hence, parasitoids and hosts preferentially select patches in which they achieve a higher equilibrium abundance in the absence of choices. Furthermore, the co-evolved equilibrium $(\tilde{N}, \tilde{P})$ satisfies an additive principle: $(\tilde{N}, \tilde{P}) = (\hat{N}_1, \hat{P}_1) + (\hat{N}_2, \hat{P}_2)$. Equivalently, the abundance of the co-evolved hosts and parasitoids in each patch equals the abundance they achieve in the absence of choices (i.e. $\tilde{\alpha}_i \tilde{N} = \hat{N}_i$ and $\tilde{\beta}_i \tilde{P} = \hat{P}_i$).
   Now, we consider the co-evolution of patch selection and parasitoid sex allocation. Recall q_i is the probability that a parasitoid lays a female egg on a host encountered in patch i, $\mathbf{q} = (q_1, q_2)$ and $\Phi(\mathbf{q}, \mathbf{q'})$ is the relative fitness of a small mutant parasitoid population playing the strategy $\mathbf{q'}$ in a parasitoid population playing primarily the strategy $\mathbf{q}$. The strategies $(\boldsymbol{\alpha}^*, \boldsymbol{\beta}^*, \mathbf{q}^*)$ are co-evolutionarily stable provided that all other strategies cannot invade (i.e. if $\boldsymbol{\alpha} = \boldsymbol{\alpha}^*$, $\boldsymbol{\beta} = \boldsymbol{\beta}^*$ and $\mathbf{q} = \mathbf{q}^*$, then $I_M(\boldsymbol{\alpha'}) \leq 1$, $I_Q(\boldsymbol{\beta'}) \leq 1$ and $\Phi(\mathbf{q}^*, \mathbf{q'}) \leq 1$ for all $\boldsymbol{\alpha'}$, $\boldsymbol{\beta'}$ and $\mathbf{q'}$). In Appendix 2, we show that the coESS for parasitoid sex allocation when both patch selection and sex allocation co-evolve is given by

$$q_1^* = 1 \qquad q_2^* = \frac{\hat{P}_2}{2\hat{P}_2 + \hat{P}_1}$$

Hence, the co-evolved female parasitoids lay only female eggs upon encountering a host in patch 1, and lay a female egg with a probability less than 0.5 upon encountering a host in patch 2.
   In Appendix 2, we show that the coESS for patch selection for the parasitoids when both patch selection and sex allocation co-evolve is given by

$$\beta_i^* = \frac{\hat{P}_i}{\hat{P}_1 + \hat{P}_2} \qquad i = 1, 2$$

Furthermore, the parasitoid equilibrium for the co-evolved populations is $P^* = \hat{P}_1 + \hat{P}_2$. Hence, the parasitoid coESS for patch selection when patch selection and sex allocation co-evolve is the same as the parasitoid coESS for patch selection when only patch selection co-evolves and female parasitoids lay male and female eggs with equal likelihood.

The host coESS for patch selection when patch selection and parasitoid sex allocation co-evolve is given by

$$\alpha_1^* = \frac{\hat{N}_1}{2N^*} \qquad \alpha_2^* = \frac{\hat{N}_2}{N^*}\left(1 + \frac{\hat{P}_1}{2\hat{P}_2}\right)$$

where

$$N^* = \frac{\hat{N}_1}{2} + \hat{N}_2\left(1 + \frac{\hat{P}_1}{2\hat{P}_2}\right)$$

From these equations, we draw two conclusions. First, the equilibrium abundance of the co-evolved hosts in patch 1 is one-half of the abundance they achieve in patch 1 without choices (i.e. $\alpha_1^* N^* = \hat{N}_1/2$), while in patch 2 their abundance is greater than what they achieve in the absence of choices (i.e. $\alpha_2^* N^* = \hat{N}_2(1 + \hat{P}_1/(2\hat{P}_2))$). Second, the co-evolved hosts preferentially lay more eggs in patch 2 when parasitoids play the coESS for patch selection and sex allocation than when parasitoids only play the coESS for patch selection. The reason behind this shift of the host towards patch 2 is that parasitoids playing the ESS for sex allocation are less likely to lay female eggs on patch 2 than on patch 1. Consequently, by shifting to patch 2, the hosts reduce the production of female parasitoids.

Ecological stability of the coESS equilibrium

The analysis in the preceding subsections is based on the assumption that the populations are in equilibrium. Therefore, to determine when the previous analysis is relevant, we need to find under what conditions the feasible equilibrium (i.e. the equilibrium for which both host and parasitoid densities are positive) of equation (1) is stable. Schreiber *et al.* (2000) showed that the equilibrium $(\hat{N}, \hat{P})$ for equation (1) is stable if, and only if,

$$-\sum_i f_i'(\beta_i \hat{P}) (\lambda_i \alpha_i \beta_i \hat{P} + q_i \theta_i \beta_i \alpha_i \hat{N}) < 1 \qquad (5)$$

If the populations play the coESS for patch selection and the female parasitoids lay male and female eggs with equal likelihood (i.e. $q_1 = q_2 = 1/2$), the co-evolved equilibrium with $\alpha_i = \tilde{\alpha}_i$ and $\beta_i = \tilde{\beta}_i$ is stable if, and only if,

$$-\sum_i f_i'(\hat{P}_i)(\lambda_i \hat{P}_i \tilde{\alpha}_i + \theta_i \hat{N}_i \tilde{\beta}_i/2) < 1 \qquad (6)$$

In Appendix 3, we show that the coESS equilibrium (N^*, P^*) when the populations have co-evolved patch selection and parasitoid sex allocation strategies (i.e. $\alpha_i = \alpha_i^*$, $\beta_i = \beta_i^*$ and $q_i = q_i^*$) is stable if, and only if,

$$-\sum_i f_i'(\hat{P}_i)(\lambda_i \hat{P}_i \alpha_i^* + \theta_i \hat{N}_i \beta_i^*/2) < 1 \qquad (7)$$

Because the host patch selection strategies differ between populations that have only co-evolved patch selection and populations that have co-evolved patch selection and sex allocation, these stability criteria are not the same. More precisely, since $\beta_i^* = \tilde{\beta}_i$ for $i = 1, 2$, $\alpha_1^* < \tilde{\alpha}_1$ and $\alpha_2^* < \tilde{\alpha}_2$, the left-hand side of equation (7) is strictly less than the left-hand side of equation (6) whenever $\lambda_1 > \lambda_2$. Hence, the co-evolution of sex allocation with patch selection is stabilizing whenever the host rate of increase is greater in patch 1 (see Fig. 2). Conversely, the co-evolution of sex allocation with patch selection is destabilizing whenever the host rate of increase is greater in patch 2.

DISCUSSION

Our analysis extends previous work (van Baalen and Sabelis, 1993; Schreiber *et al.*, 2000) by evaluating how parasitoid sex allocation co-evolves with patch preferences of the hosts and parasitoids. Our analysis is based on seven assumptions: (1) hosts and parasitoids have synchronized generations; (2) the hosts in the absence of parasitoids exhibit geometric growth; (3) the parasitoids are search limited but not egg limited; (4) the environment consists of two patch types; (5) the fitness of a female parasitoid with respect to sex allocation equals the number of daughters produced plus the number of females inseminated by her sons; (6) the population dynamics are near or approaching a steady state; and (7) the co-evolving traits (patch selection and sex allocation) are density independent. Under these assumptions, our analysis determines the co-evolutionarily stable strategies for both species and indicates when these co-evolved strategies stabilize host–parasitoid interactions.

Co-evolution of patch selection and parasitoid sex allocation

Although our analysis applies to various scenarios, the most relevant one occurs when the environment consists of lower and higher quality patches: the hosts growing in the lower quality patch have a lower intrinsic rate of growth than the hosts growing in the higher quality patches. Under the assumptions that the parasitoid searches equally effectively in either patch type [e.g. $f_1(\cdot) = f_2(\cdot) = \exp(-a\cdot)$, where $a > 0$] and that the female parasitoid larvae benefit more from hosts on higher quality patches than the male parasitoid larvae (i.e. $\theta_1/\theta_2 > \psi_1/\psi_2$), the co-evolution of patch selection and parasitoid sex allocation results in parasitoids preferentially searching for hosts in higher quality patches (i.e. monotonicity of $f_1(\cdot) = f_2(\cdot)$ implies $\hat{P}_1 = f_1^{-1}(1/\lambda_1) > f_1^{-1}(1/\lambda_2) = \hat{P}_2$ whenever $\lambda_1 > \lambda_2$) and primarily laying female eggs on hosts encountered in higher quality patches. Upon encountering hosts in lower quality patches, the co-evolved parasitoids are more likely to lay male eggs than female eggs. In response to these parasitoid behaviours, the hosts lay twice as many eggs in the lower quality patches than if the parasitoid laid female and male eggs with equal likelihood on all patches. Thus, our analysis implies that the co-evolution of patch preference with parasitoid sex allocation can increase the likelihood of hosts and parasitoids exhibiting contrary patch preferences. However, if patches affect the performance of the host or parasitoid in different ways (e.g. the female parasitoid larvae benefit less
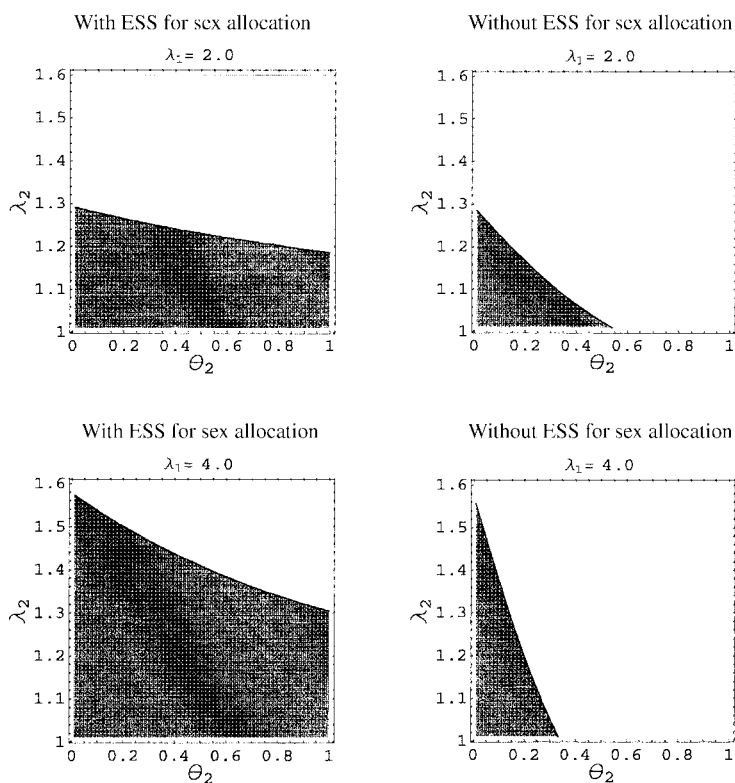
Fig. 2. In all bifurcation diagrams, $\theta_1 = 1$, $\lambda_1 = 2$ and $f_1(x) = f_2(x) = \exp(-0.1x)$. The values of λ_2 and θ_2 are allowed to vary as shown. The shaded region corresponds to parameter values for which the coESS equilibrium is ecologically stable. In the left-hand diagrams, parasitoid sex allocation co-evolves with patch preference. In the right-hand diagrams, only patch preferences co-evolve and parasitoids lay female and male eggs with equal likelihood on all hosts.

than the male parasitoid larvae from hosts on higher quality patches, the parasitoids search more efficiently on lower quality patches than higher quality patches, or the parastioids' life-history traits are patch independent), then the co-evolved patch preferences can be congruent (i.e. hosts and parasitoids preferentially search the same patches) (van Baleen and Sabelis, 1993; Schreiber *et al.*, 2000).

Evidence from Nature

Few field or laboratory studies have provided the combination of host preferences and performance with parasitoid preferences, fitness and sex allocation strategies to test our results. However, studies on interactions of the diamondback moth (*Plutella xylostella*), an ichneumonid parasitoid (*Diadegma insulare*) and food-plants of varying quality are relevant to these ideas (Fox *et al.*, 1990, 1996; Fox and Eisenbach, 1992). In both laboratory and field studies, *Plutella* females preferred to search poorer quality food-plants, even though survival and growth of their offspring were intrinsically lower on those plants, compared

to available high-quality plants. On the other hand, *Diadegma* preferentially searched for hosts on high-fertilized plants (see Schreiber *et al.*, 2000, for further discussion). The results on *Diadegma* sex ratios agree qualitatively with our predictions, although quantitative agreement with the sex ratio predictions is weaker. For instance, in one field experiment, 93% of wasps emerging from *Plutella xylostella* larvae on high nitrogen collards were female, compared to 58% on low nitrogen plants in a nearby patch. However, in a second, smaller-scale field experiment, only 53% of emerging wasps were female on high nitrogen versus 29% on low nitrogen plants. Finally, in laboratory experiments in which wasps were offered hosts on plants of different qualities, 78% and 7% females emerged from hosts on high and low nitrogen plants, respectively. These experiments differed in scale and the complexity of the environment, which might have affected search behaviour and perceived patch distinctiveness for ovipositing wasps. The results from a separate study on *Plutella xylostella* and *Diadegma* sp. (unknown) in South Africa are equivocal, although the sample sizes were low: *Diadegma* sp. sex ratios varied among several crop plants, and was lower on several plants of poorer quality for *Plutella xylostella*, although the average percentage of emerging females was 67% on poorer quality plants versus 78% on higher quality plants (Charleston and Kfir, 2000; D.S. Charleston, personal communication). In other systems, *Aphytis melinus* wasps lay more female eggs in hosts (*Aonidiella aurantii*; California red scale) on the best food-plant for the scale, but the difference in sex ratio is only 37% versus 18% females on other varieties (Hare and Luck, 1991). At the other extreme, while caterpillars (*Lymnaecia phragmitella*) and parasitic wasps appeared to have contrary food-plant preferences (fewer caterpillars were on the hybrid *Typha × glauca* than either parental genotype, *T. latiforlia* or *T. angustifolia*, and a higher proportion of the caterpillars on the hybrid plants were parasitized), all emerging wasps were female (Eisenbach, 1996 and personal communication). In this case, it is unknown whether the parasitoids only produce female offspring via parthenogenesis (thelotoky) (J. Eisenbach, personal communication). To better understand the ecology and evolution of host–parasitoid systems in heterogeneous environments, our analysis highlights the need for more studies comparing preference and performance, of both hosts and parasitoids, on an array of plants.

Ecological stability

Provided that female parasitoid larvae benefit more from hosts with a higher rate of increase than male parasitoid larvae, our analysis shows that the co-evolution of patch preference and parasitoid sex allocation can stabilize host–parasitoid interactions even when co-evolution of patch preference in itself does not. This enhancement of ecological stability can be explained using the CV^2 rule, which roughly states that host–parasitoid interactions are stabilized provided that the distribution of searching parasitoids per host is sufficiently heterogeneous (Hassell and May, 1988; Hassell *et al.*, 1991). Specifically, the square of the coefficient of variation (CV^2) of the searching parasitoids (at equilibrium) per host must exceed unity for stability (see, however, Getz and Mills, 1996, for the case of egg-limited parasitoids). The explanation follows from two observations. First, the co-evolution of parasitoid sex allocation with patch selection leads to more hosts occupying lower quality patches and fewer hosts occupying higher quality patches than the co-evolution of patch selection alone. In contrast, the equilibrium abundance of searching parasitoids in all patches is unaffected by the inclusion of parasitoid sex allocation. Second, this change in the distribution and abundance of the host results in the number of searching

parasitoids per host doubling in the higher quality patches and decreasing in the lower quality patches. Consequently (see Appendix 4), the inclusion of parasitoid sex allocation increases the CV^2 of the searching parasitoids per host and, thereby, enhances ecological stability.

Previous work of parasitoid sex allocation found that density-dependent parasitoid sex ratios are rarely the sole cause of stability of host–parasitoid interactions (Hassell *et al.*, 1983). However, when combined with a contagion in the distribution of parasitism (i.e. the escape function is given by the negative binomial; Hassell *et al.*, 1983) or host density dependence (Comins and Wellings, 1985; Getz *et al.*, 1992; Kaitala and Getz, 1992; Taylor and Getz, 1994), the parameter values that enhance stability broaden considerably. Alternatively, our analysis implies that co-evolution in spatially heterogeneous environments selects patch choices and parasitoid sex allocation strategies that stabilize locally unstable interactions over a broad range of parameter values. Previously, the evolutionary selection of stable equilibrium dynamics has been observed in single-species models when there is sufficient flexibility (or biological complexity) in the model to permit the growth rate, carrying capacity and dynamical complexity to appear as essentially independent parameters (Doebeli and Koella, 1995; Getz, 1996; Schoombie and Getz, 1998). Similarly, we find that, as the complexity of host–parasitoid models increases with respect to diversity of behaviour among patches, co-evolution selects with greater likelihood behavioural choices that stabilize host–parasitoid interactions. This is seen by comparing the stability of host–parasitoid models when only the life-history traits of the host vary among patches (van Baleen and Sabelis, 1993) with the case when both the host and parasitoid life-history traits covary among patches (Schreiber *et al.*, 2000) and, finally, with the case considered here that includes parasitoid sex allocation among patches.

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APPENDIX 1

To analyse how the fitness of a female parasitoid varies as a function of the probability q_i that she lays a female egg on a host of type i, we consider a population of parasitoids consisting of individuals playing one of two sex allocation strategies. Call these strategies $\mathbf{q} = (q_1, q_2)$ and $\mathbf{q}' = (q'_1, q'_2)$. Let p denote the proportion of the population playing strategy $\mathbf{q}$. Let H denote the average number of hosts available per female parasitoid, P the total number of female parasitoids, and π_i the proportion of parasitized hosts that are in patch i. If P denotes the total number of female parasitoids in the population, then the total number of female progeny produced by the population equals

$$T_{\text{females}} = (1 - p)HP \sum_i \theta_i q'_i \pi_i + pHP \sum_i \theta_i q_i \pi_i$$

and the total number of male progeny produced by the population equals

$$T_{\text{males}} = (1 - p)HP \sum_i \psi_i(1 - q'_i)\pi_i + pHP \sum_i \psi_i(1 - q_i)\pi_i$$

Our assumption that the fitness of a female equals the number of female progeny plus the number of females inseminated by her sons implies that the fitness of a female playing the strategy $\mathbf{q}'$ equals

$$F_{\mathbf{q}'}(p) = H \sum_i \theta_i q'_i \pi_i + HT_{\text{females}} \frac{\Sigma_i \psi_i \pi_i (1 - q'_i)}{T_{\text{males}}}$$

where the second term of the sum equals the number of female progeny inseminated by her sons. Similarly, the fitness of an individual playing the strategy $\mathbf{q}$ is given by

$$F_{\mathbf{q}}(p) = H \sum_i \theta_i q_i \pi_i + HT_{\text{females}} \frac{\Sigma_i \psi_i \pi_i (1 - q_i)}{T_{\text{males}}}$$

If the population of parasitoids playing the sex allocation strategy $\mathbf{q}'$ is small (i.e. $p \approx 1$), then we can view the population of individuals playing the strategy $\mathbf{q}$ as the 'resident' population and the population of individuals playing the strategy $\mathbf{q}'$ as the 'invading' or 'mutant' population. In this case, the fitness of an invading female simplifies to

$$F_{\mathbf{q}'}(1) = H \sum_i \theta_i q'_i \pi_i + H \sum_i \pi_i \theta_i q_i \frac{\Sigma_i \psi_i \pi_i (1 - q'_i)\pi_i}{\Sigma_i \psi_i \pi_i (1 - q_i)\pi_i}$$

The fitness of a resident female simplifies to $F_{\mathbf{q}}(1) = 2H\Sigma_i \pi_i \theta_i q_i$. Therefore, the relative fitness of an invading female is

$$\Phi(\mathbf{q}, \mathbf{q}') = F_{\mathbf{q}'}(1)/F_{\mathbf{q}}(1) = \frac{\Sigma_i \theta_i \pi_i q'_i}{2\Sigma_i \theta_i \pi_i q_i} + \frac{\Sigma_i \psi_i \pi_i (1 - q'_i)}{2\Sigma_i \psi_i \pi_i (1 - q_i)}$$

while the relative fitness of a resident female is $\Phi(\mathbf{q}, \mathbf{q}) = F_{\mathbf{q}}(1)/F_{\mathbf{q}}(1) = 1$.

An evolutionarily stable strategy $\mathbf{q} = \mathbf{q}^*$ for sex allocation is a strategy such that the relative fitness $\Phi(\mathbf{q}, \mathbf{q}')$ of all other strategies $\mathbf{q}'$ is less than 1. This statement corresponds to the fact that no other strategy can invade a resident population that plays the ESS for sex allocation. A necessary condition for $\mathbf{q}^*$ to be an ESS is that for each $i = 1, 2$, either $(\partial\Phi/\partial q'_i)(\mathbf{q}^*, \mathbf{q}^*) = 0$, $q_i^* = 0$ and $(\partial\Phi/\partial q'_i)(\mathbf{q}^*, \mathbf{q}^*) < 0$, or $q_i^* = 1$ and $(\partial\Phi/\partial q'_i)(\mathbf{q}^*, \mathbf{q}^*) > 0$. It follows from the form of Φ that the cases $q_1^* = q_2^* = 0$ and $q_1^* = q_2^* = 1$ are impossible. The remaining cases we need to consider are: (i) $(\partial\Phi/\partial q'_1)(\mathbf{q}^*, \mathbf{q}^*) = 0$, (ii) $(\partial\Phi/\partial q'_2)(\mathbf{q}^*, \mathbf{q}^*) = 0$, (iii) $q_1^* = 0$ and $q_2^* = 1$, and (iv) $q_1^* = 1$ and $q_2^* = 0$. We discuss these cases under the assumption that $0 < \pi_1 < 1$.

Suppose that $(\partial\Phi/\partial q'_1)(\mathbf{q}^*, \mathbf{q}^*) = 0$. Then

$$0 = \frac{\theta_1 \pi_1}{2\Sigma \theta_i \pi_i q_i^*} - \frac{\psi_1 \pi_1}{2\Sigma \psi_i \pi_i (1 - q_i^*)}$$

Hence,

$$\frac{\theta_1}{\psi_1} = \frac{\Sigma\,\theta_i\pi_i q_i^*}{\Sigma\,\psi_i(1-q_i^*)\pi_i} \tag{A1}$$

On the other hand,

$$\frac{\partial\Phi}{\partial q_2'}(\mathbf{q}^*,\mathbf{q}^*) = \frac{\theta_2\pi_2}{2\Sigma\,\theta_i\pi_i q_i^*} - \frac{\psi_2\pi_2}{2\Sigma\,\psi_i\pi_i(1-q_i^*)}$$

Equation (A1) implies

$$\frac{\partial\Phi}{\partial q_2'}(\mathbf{q}^*,\mathbf{q}^*)\,\frac{2\Sigma\,\theta_i\pi_i q_i^*}{\pi_2\psi_2} = \frac{\theta_2}{\psi_2} - \frac{\theta_1}{\psi_1}$$

Since we have assumed that $\theta_1/\psi_1 > \theta_2/\psi_2$, it follows that $(\partial\Phi/\partial q_2')(\mathbf{q}^*,\mathbf{q}^*) < 0$. Hence, the ESS for sex allocation in this case must satisfy $q_2^* = 0$. Plugging $q_2^* = 0$ into equation (A1) and solving for q_1^*, we get $q_1^* = (\psi_1\pi_1 + \psi_2\pi_2)/(2\psi_1\pi_1)$. This expression for q_1^* makes sense (i.e. satisfies $0 \le q_1^* \le 1$) if, and only if, $\pi_2\psi_2 \le \pi_1\psi_1$.

Next, we consider case (ii). Suppose that $(\partial\Phi/\partial q_2')(\mathbf{q}^*,\mathbf{q}^*) = 0$. Then

$$0 = \frac{\theta_2\pi_2}{2\Sigma\,\theta_i\pi_i q_i^*} - \frac{\psi_2\pi_2}{2\Sigma\,\psi_i\pi_i(1-q_i^*)}$$

Hence,

$$\frac{\theta_2}{\psi_2} = \frac{\Sigma\,\theta_i\pi_i q_i^*}{\Sigma\,\psi_i(1-q_i^*)\pi_i} \tag{A2}$$

On the other hand,

$$\frac{\partial\Phi}{\partial q_1'}(\mathbf{q}^*,\mathbf{q}^*) = \frac{\theta_1\pi_1}{2\Sigma\,\theta_i\pi_i q_i^*} - \frac{\psi_1\pi_1}{2\Sigma\,\psi_i\pi_i(1-q_i^*)}$$

Equation (A2) implies

$$\frac{\partial\Phi}{\partial q_1'}(\mathbf{q}^*,\mathbf{q}^*)\,\frac{2\Sigma\,\theta_i\pi_i q_i^*}{\pi_1\psi_1} = \frac{\theta_1}{\psi_1} - \frac{\theta_2}{\psi_2}$$

Since we have assumed that $\theta_1/\psi_1 > \theta_2/\psi_2$, it follows that $(\partial\Phi/\partial q_1')(\mathbf{q}^*,\mathbf{q}^*) > 0$. Hence, the ESS for sex allocation in this case must satisfy $q_1^* = 1$. Plugging $q_1^* = 1$ into equation (A2) and solving for q_2^*, we get $q_2^* = (\theta_2\pi_2 - \theta_1\pi_1)/(2\theta_2\pi_2)$. This expression for q_2^* only makes sense (i.e. satisfies $0 \le q_2^* \le 1$) if, and only if, $\pi_1\theta_1 \le \pi_2\theta_2$. The work from cases (i) and (ii) implies that $(\partial\Phi/\partial q_1')(\mathbf{q}^*,\mathbf{q}^*) \ge 0$ and $(\partial\Phi/\partial q_2')(\mathbf{q}^*,\mathbf{q}^*) \le 0$, with $\mathbf{q}^* = (1, 0)$ if, and only if, $\psi_2/\psi_1 \ge \pi_1/\pi_2 \ge \theta_2/\theta_1$. Finally, consider case (iv) in which $\mathbf{q}^* = (0, 1)$. On the one hand,

$$\frac{\partial\Phi}{\partial q_1'}(\mathbf{q}^*,\mathbf{q}^*) = \frac{\pi_1\theta_1}{2\pi_2\theta_2} - \frac{1}{2} \tag{A3}$$

On the other hand,

$$\frac{\partial \Phi}{\partial q'_2}(\mathbf{q}^*, \mathbf{q}^*) = \frac{1}{2} - \frac{\pi_2 \psi_2}{2\pi_1 \psi_1} \tag{A4}$$

Equation (A3) is non-positive if, and only if, $\pi_1\theta_1/\pi_2\theta_2 \leq 1$, while equation (A4) is non-negative if, and only if, $\pi_2\psi_2/\pi_1\psi_1 \leq 1$. Our assumption that $\theta_1/\psi_1 > \theta_2/\psi_2$ implies that both inequalities cannot be simultaneously satisfied. Hence, $\mathbf{q}^* = (0, 1)$ is not an ESS. The analysis of the cases implies that the only candidate for the ESS for sex allocation is given by cases (i), (ii) and (iii) as shown in equation (3).

APPENDIX 2

To find the coESS for patch selection and sex allocation, we need to find $\boldsymbol{\alpha} = \boldsymbol{\alpha}^*$, $\boldsymbol{\beta} = \boldsymbol{\beta}^*$ and $\mathbf{q} = \mathbf{q}^*$ such that $I_M(\boldsymbol{\alpha}') \leq 1$, $I_Q(\boldsymbol{\beta}') \leq 1$ and $\Phi(\mathbf{q}^*, \mathbf{q}') \leq 1$ for all $\boldsymbol{\alpha}'$, $\boldsymbol{\beta}'$ and $\mathbf{q}'$, where the proportion π_i of hosts encountered on patch i is given by (2). Let (N^*, P^*) be the non-zero equilibrium of (1) with $\boldsymbol{\alpha} = \boldsymbol{\alpha}^*$ and $\boldsymbol{\beta} = \boldsymbol{\beta}^*$. In Appendix 1, we found that $\Phi(\mathbf{q}^*, \mathbf{q}') \leq 1$ for all $\mathbf{q}'$ if, and only if, $\mathbf{q} = \mathbf{q}^*$ is given by (3). On the other hand, using the method of Lagrange multipliers and assuming the populations are at equilibrium, Schreiber *et al.* (2000) showed that $I_M(\boldsymbol{\alpha}') \leq 1$ and $I_Q(\boldsymbol{\beta}') \leq 1$ if, and only if,

$$\lambda_i f_i (\beta_i^* P^*) = 1$$
$$\frac{\theta_i q_i^* \alpha_i^* N^*}{\beta_i^* P^*}(1 - 1/\lambda_i) = 1 \qquad i = 1, 2 \tag{B1}$$

The first line in (B1) implies that $\beta_i^* = \hat{P}_i/(\hat{P}_1 + \hat{P}_2)$ and $P^* = \hat{P}_1 + \hat{P}_2$. Since equation (3) implies that $q_2^* = 0$ for $\theta_1\pi_1 \geq \theta_2\pi_2$, the second line of (B1) can only hold if $\theta_1\pi_1 < \theta_2\pi_2$. Since we have assumed that $\theta_1/\theta_2 > \psi_1/\psi_2$, it follows that $\psi_1\pi_1 < \psi_2\pi_2$. Hence at the coESS, $q_1^* = 1$ and $q_2^* = (\theta_2\pi_2 - \pi_1\theta_1)/(2\theta_2\pi_2)$. The second line of (B1) with $i = 1$ implies that $\alpha_1^* N^* = \hat{P}_1/(\theta_1(1 - 1/\lambda_1)) = \hat{N}_1/2$. Alternatively, substituting q_2^* into the second line of (B1) with $i = 2$, we get

$$\frac{\theta_2\pi_2 - \pi_1\theta_1}{2\pi_2}\alpha_2^* N^*(1 - 1/\lambda_2) = \beta_2^* P^* = \hat{P}_2 \tag{B2}$$

Since we have $\beta_i^* P^* = \hat{P}_i$, we get

$$\pi_i = \frac{\alpha_i^*(1 - 1/\lambda_i)}{\alpha_1^*(1 - 1/\lambda_1) + \alpha_2^*(1 - 1/\lambda_2)}$$

Plugging π_i into (B2) and simplifying we get

$$\theta_2\alpha_2^* N^*(1 - 1/\lambda_2)/2 - \theta_1\alpha_1^* N^*(1 - 1/\lambda_1)/2 = \hat{P}_2 \tag{B3}$$

Since $\alpha_1^* N^* = \hat{P}_1/(\theta_1(1 - 1/\lambda_1))$, equation (B3) is equivalent to

$$\theta_2\alpha_2^* N^*(1 - 1/\lambda_2) = 2\hat{P}_2 + \hat{P}_1$$

Dividing both sides by $\theta_2(1 - 1/\lambda_2)$ and recalling the definition of $\hat{N}_2$, we get $\alpha_2^* N^* = \hat{N}_2(1 + \hat{P}_1/(2\hat{P}_2))$.

Now that we have an explicit expression for $\alpha_i^* N^*$, we can find an explicit expression for q_2^*. Since $f_i(\beta_i P^*) = 1/\lambda_i$,

$$q_2^* = \frac{\theta_2\alpha_2^* N^*(1 - 1/\lambda_2) - \theta_1\alpha_1^* N^*(1 - 1/\lambda_1)}{2\theta_2\alpha_2^* N^*(1 - 1/\lambda_2)}$$

Substituting the expressions $\alpha_1^* N_1^* \theta_1(1 - 1/\lambda_1) = \hat{P}_1$ and $\alpha_2^* N_2^* \theta_2(1 - 1/\lambda_2) = 2\hat{P}_2 + \hat{P}_1$ into the previous equation, we get $q_2^* = \hat{P}_2/(2\hat{P}_2 + \hat{P}_1)$.

APPENDIX 3

Here, we show how equation (5) reduces to equation (7) when the populations have co-evolved their patch selection and sex allocation strategies. Plugging α_i^*, β_i^* and q_i^* into (5), we get

$$-\sum_i f_i'(\hat{P}_i)(\lambda_i \alpha_i^* \hat{P}_i + q_i^* \theta_i \alpha_i^* N^* \beta_i^*)$$

It remains to be shown that $q_i^* \alpha_i^* N^* = \hat{N}_i/2$ for $i = 1, 2$. Since $q_1^* = 1$ when the co-evolved populations are at equilibrium and $\alpha_1^* N^* = \hat{N}_1/2$, $q_1^* \alpha_1^* N^* = \hat{N}_1/2$. Since $q_2^* = \hat{P}_2/(2\hat{P}_2 + \hat{P}_1)$ when the co-evolved populations are at equilibrium and $\alpha_2^* N^* = \hat{N}_2(1 + \hat{P}_1/(2\hat{P}_2))$, $q_2^* \alpha_2^* N^* = \hat{N}_2/2$.

APPENDIX 4

Here, we show how the inclusion of parasitoid sex allocation increases the squared coefficient of variation (CV^2) of the number of searching parasitoids per host. For parasitoids that lay males and females with equal likelihood on all hosts, let $a = \hat{P}_1/\hat{N}_1$ and $b = \hat{P}_2/\hat{N}_2$ denote the number of searching parasitoids per host in the higher quality and lower quality patches, respectively. Under the assumptions outlined in the body of the text, we have $a > b$. For parasitoids and hosts playing the coESS for parasitoid sex allocation and patch selection, the number of searching parasitoids per host equals $2a$ in higher quality patches and equals ca in lower quality patches, where $c = 1/(1 + (\hat{P}_1/2\hat{P}_2)) < 1$. CV^2 for $\{a, b\}$ equals

$$\frac{(a - b)^2}{(a + b)^2}$$

and CV^2 for $\{2a, ca\}$ equals

$$\frac{(2a - bc)^2}{(2a + bc)^2}$$

Setting $x = b/a$, we find that the ratio of the CV^2 for $\{2a, cb\}$ to the CV^2 for $\{a, b\}$ equals

$$h(x) = \left(\frac{1 + x}{1 - x}\right)^2 \left(\frac{2 - cx}{2 + cx}\right)^2$$

Because $0 < c < 1$, $h'(x)$ can be shown to have only complex roots. Therefore, $h'(x)$ does not change sign. As $h'(0) = 2 - c > 0$ and $h(0) = 1$, it follows that $h(x) > 1$ for all $0 < x < 1$.