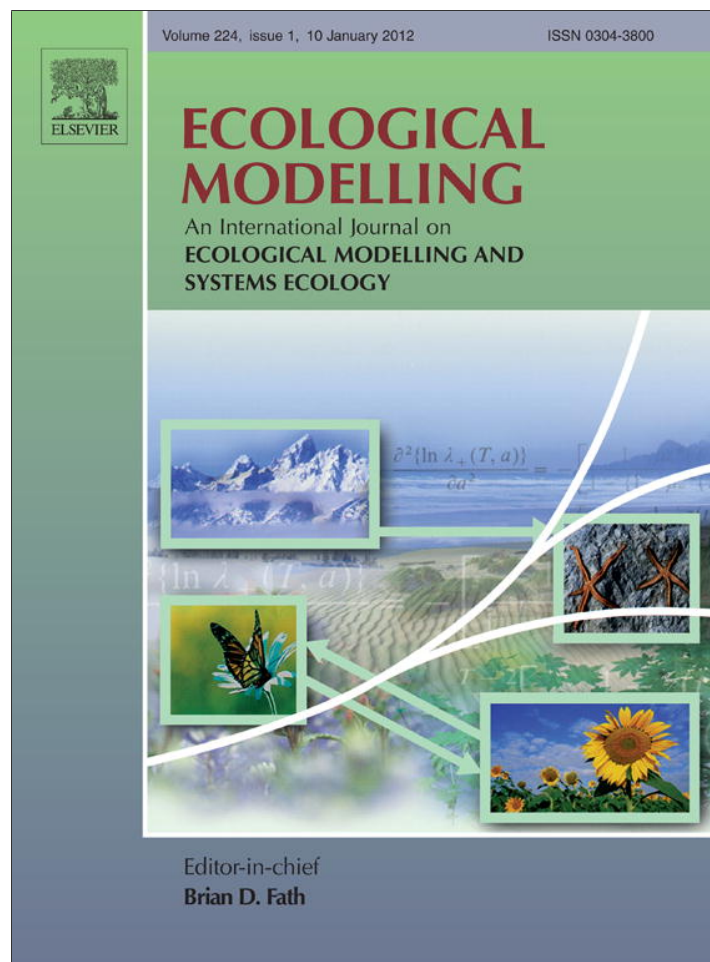


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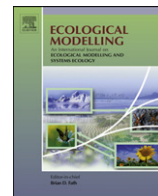
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# Ecological Modelling

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## Patch exploitation strategies of parasitoids: The role of sex ratio and forager's interference in structuring metapopulations

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### ABSTRACT

We use a mathematical model to explore the effects of parasitoid reproductive strategies and foraging behavior in response to spatio-temporal variations in the patch quality of a host–parasitoid metapopulation system. The variations of patch quality over the landscape were measured by the presence of parasitoid competitors and the density of hosts. The parasitoid responses to patch quality are given by three different foraging behaviors: (i) the decision to remain in or leave the current patch; (ii) the control of progeny's sex ratio and (iii) competitive abilities, measured by changes in the potential to attack hosts due to interference from conspecifics in the exploited patch. We study the dynamics of host and parasitoid populations characterized by different levels of density-dependent sex ratio adjustment and interference competition. Our results show that population stability increases when parasitoid growth is correlated with patch conditions. The effect of sex ratio adjustment alone does not account for qualitative changes to system dynamics or to the distribution patterns of species. In contrast, the degree of competitive interference among the parasitoids plays a crucial role in constraining the parasitoids' potential to reduce host populations and in determining the species' distribution in the landscape. We found that high levels of interference competition disrupt the population dynamics within a patch and allows hosts to completely dominate the landscape. This study shows that the inclusion of life history traits and the co-evolutionary aspects of host–parasitoid interaction can help researchers to understand species distribution patterns in the landscape.

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### 1. Introduction

Many theoretical and empirical studies have focused on the potential of a host's carrying capacity and the local demographic parameters of a parasitoid, such as sex ratio and mutual interference competition, to promote coexistence in host–parasitoid populations (Comins and Wellings, 1985; Hassell, 1978; Hassell et al., 1983; Lozano et al., 1997; Meunier and Bernstein, 2002). In addition, spatial structure has also been identified as a stabilizing factor in host–parasitoid dynamics (Hassell, 2000; Briggs and Hoopes, 2004). However, the combined effects of these demographic factors embedded in a spatial structure have yet to be considered. Demographic factors are responsible for the spatio-temporal variations of host and parasitoid populations in local patches and have important evolutionary consequences for a

species' patch selection strategies, foraging behavior and responses to local conspecific abundances (Bonsall et al., 2002; Schreiber et al., 2000; Outreman et al., 2005; Macke et al., 2011).

The host–parasitoid interaction is very complex and must be understood as an evolutionary and ecological process that is influenced not only by time but also by the distribution of species in space (Levin, 1992; Murray, 2000; Forde et al., 2004). The hosts of many parasitoids are distributed non-randomly in the environment and often occur in discrete patches (Godfray, 1994). The profitability of these patches changes over space as a result of varying levels of interference and exploitation competition and also over time as a result of resource depletion (Fauvergue et al., 2006).

The reproductive success of parasitoids is directly related to host abundance and to the way in which hosts are exploited, and insects provide excellent biological models for studying the relationship between environmental quality and foraging strategies (Godfray, 1994; Outreman et al., 2005). However, successful parasitism depends not only on host density but also on parasitoid density, given that larger numbers of parasitized hosts in an exploited patch can decrease the reproductive success of a female parasitoid. Thus, a female parasitoid's decision to exploit the current patch, as well as how it will use a host species for reproduction

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will be influenced by its ability to adopt an “optimal” foraging strategy (Fretwell and Lucas, 1970; Charnov, 1976; Outreman et al., 2005).

To maximize its chances to reproduce, a foraging female parasitoid needs to decide whether to leave its natal patch in search of more optimal conditions, and this choice is determined by the patch quality required by the species (Fretwell and Lucas, 1970; Charnov, 1976). When conspecifics are present, a female parasitoid can adopt different patch exploitation strategies, and its “optimal decision” to exploit a patch will depend on the density of conspecifics and on the host density in that patch. These conditions determine the “quality” of the exploited patch (Fauvergue et al., 2006).

Once a patch is selected, the female parasitoid must optimize its reproductive potential to ensure that its genes are passed on. Most parasitoid species exhibit a type of haplodiploid reproduction called arrhenotoky, where females are born from fertilized eggs and males from unfertilized eggs (Charnov, 1982). Commonly, arrhenotokous parasitoid species mate in isolated groups before dispersing to new host patches and frequently show female-biased sex ratios. Hamilton (1967) observed this characteristic and proposed the theory of Local Mate Competition (LMC). This theory has been the basis for many studies about adaptive sex ratio adjustment in parasitoid species (Hassell et al., 1983; Godfray, 1994; Godfray and Werren, 1996; Santolamazza-Carbone and Rivera, 2003; Shuker et al., 2006) and assumes that females have control over the sex ratio of their offspring in a haplodiploid population. Therefore, females can reduce the mating competition between their male offspring in response to foundress numbers (female that lay eggs) and the number of parasitized hosts in the patch (Hamilton, 1967; Shuker et al., 2006; Grillenberger et al., 2009). In this context, adjustment to the sex ratio of progeny can be understood as a strategy for female parasitoids to control sib-mating in patches of parasitized hosts.

In addition to inbreeding control, arrhenotoky also influences the population growth within patches. In fact, the variation of parasitoid sex ratio as a function of host and parasitoid densities clearly affects the host–parasitoid dynamics, given that only mated females are able to produce female offspring capable of parasitizing hosts. This method of population control prevents the overexploitation of hosts and consequently increases the stability of the host–parasitoid interaction (Hassell et al., 1983; Comins and Wellings, 1985; Meunier and Bernstein, 2002).

The assessment of patch quality, foraging strategies and the spatial distribution of parasitoid foragers have been analyzed using theoretical approaches (Charnov, 1976; Sutherland, 1983; Bernstein et al., 1988). Theoretical and empirical studies have found that spatial heterogeneity promotes persistence and stability in a population, allowing host clusters of different sizes to have different probabilities to be parasitized (Nicholson and Bailey, 1935; Hassell et al., 1991; Lozano et al., 1997; Bonsall et al., 2002). Heterogeneity and dispersal range can also limit parasitism by promoting different dynamic and spatial patterns of species distribution (Hassell et al., 1991; Maionchi et al., 2006).

Previous studies have focused on the mechanisms that these insects use to adjust their fitness to maximize their reproductive potential in response to spatial structure (Charnov, 1976; Outreman et al., 2005). In contrast, mathematical models have shown how host–parasitoid metapopulation dynamics determine the spatial pattern of species distribution. However, most of these models have assumed that the characteristics of parasitoid progeny depend only on host densities and that the makeup of a parasitoid population is determined only by females (Nicholson and Bailey, 1935; Hassell, 2000).

In this study, we propose a spatial host–parasitoid model to investigate how the different foraging strategies adopted by the parasitoids affect the coexistence and spatial distribution of the interacting species. We model the responsiveness of parasitoid

populations to patch quality, taking the number of conspecific foragers and host density into account. The profitability of the patches can change over space and time, and the parasitoid's response to patch quality is based on three different foraging behaviors: (i) the decision to remain in or leave the current patch; (ii) the control of progeny's sex ratio in response to spatio-temporal fluctuations of the host in the landscape and (iii) competitive abilities resulting in delays to successive ovipositions (decrease in the potential to attack hosts) due to interference from conspecifics in the exploited patch.

## 2. Modeling framework

In this section, we present a model of the metapopulation that allows us to understand how variations in patch quality (measured by the number of conspecific foragers and host abundance), its consequences for the parasitoid sex allocation and interference competition among female parasitoids can influence coexistence in host–parasitoid interaction and patterns of species distribution. Thus, we analyzed the consequences of the different foraging strategies adopted by parasitoid populations in response to competition from foragers in exploited patches. The parasitoids were assumed to be arrhenotokous gregarious species that exhibit a female-biased sex ratio under optimal patch conditions (Hamilton, 1967).

The foraging responses of parasitoids will be defined by their competitive abilities, i.e., their efficiency in recognizing parasitized hosts and laying their eggs on healthy hosts (interference competition) and also by changes in the sex ratio of progeny according to variations in patch quality (sex ratio adjustment). As previously mentioned, the density of female parasitoids has direct consequences for the density of hosts. Thus, the variation of the female population in response to hosts' spatio-temporal fluctuations has important implications for host–parasitoid dynamics. Therefore, we will consider parasitoid populations with three different levels of competitive ability and three degrees of sex ratio variations.

We consider low, medium and high levels of interference among conspecifics. A low degree of interference characterizes parasitoid populations that can detect healthy hosts in a parasitoid-crowded patch efficiently, consequently causing higher host mortality than parasitoid populations with medium and high levels of response to conspecifics (Fig. 2). The degree of interference competition among conspecific is given by the parameter  $\beta$  in our model (Table 1) and will be discussed in detail in the model presentation.

The adjustment to the sex ratio of offspring is given by the optimal proportion of hosts per parasitoid needed to favor female parasitoid offspring and is represented by the parameter  $\gamma$  in our model (Table 1). Parasitoid populations can exhibit three different responses to fluctuations in patch quality: low, medium and high variations in the sex ratio. Thus, patches that have parasitoid populations with a low sex ratio variation are expected to have a high density of females (Fig. 3).

The overall habitat is modeled by a large number of patches where host resources are limited by a carrying capacity. Only hosts and female parasitoids are allowed to disperse into other patches. Because male parasitoids are unable to disperse, mating occurs only in their native patch. The foraging strategy adopted by female parasitoids occurs at two moments: (i) the pre-dispersal period, where the decision to leave a patch is based on the density of female competitors and the host abundance at the current patch, and (ii) the post-dispersal period, where changes in the sex ratio of progeny are based on patch quality. Part of a new host generation originating from non-parasitized hosts disperses to adjacent patches. The new parasitoid generation disperses according to its responsiveness to patch conditions, and this response will determine the number of

**Table 1**

List of all parameters involved in the model with values used in the simulations and a short description.

Parameter	Values	Short meaning
$\lambda$	1.5	Hosts' intrinsic growth rate
$k$	1600	Host carrying capacity
$c$	20	Average number of adult parasitoids emerging from each host
$\alpha$	0.15	Parasitoid attack rate
$\beta$	$\beta = \{0.01, 0.03, 0.05\}$ (low, medium, high)	Competitive interference in the host attack
$\gamma$	$\gamma = \{0.1, 0.5, 0.9\}$ (low, medium, high)	Degree of sex ratio adjustment
$\mu_H$	$\mu_H = \{0.2, 0.5, 0.8\}$	Maximum dispersal rate of hosts
$\mu_F$	$\mu_F = \{0.2, 0.5, 0.8\}$	Maximum dispersal rate of parasitoids
$R_H^a$	3.61	Maximum host dispersal reach
$R_F$	3	Maximum parasite dispersal reach
$h^0$	$k/16 = 100$	Host tolerance to conspecifics
$H^0$	$k/5.3 \sim 300$	Number of hosts needed to keep the parasitoid from dispersing.
$f^0$	$H^0/3 \sim 100$	Female parasitoids' tolerance to conspecifics

<sup>a</sup> This is not a parameter; it is a consequence of Eq. (5).

dispersers. Fig. 1 shows a brief conceptual diagram of the studied host–parasitoid dynamic.

We divide the host–parasitoid metapopulation dynamics into two phases: (1) interaction within a patch, and (2) the dispersal of a fraction of emerging adult hosts and female parasitoids. Values for the host's intrinsic growth rate, carrying capacity of a patch, size of parasitoid offspring, parasitoid attack rate and the definition of the dispersal functions were obtained from demographic data for a pre-existent experimental host–parasitoid system (Reigada and de Aguiar, 2012). The values and definition of parameters used in the model are summarized in Table 1.

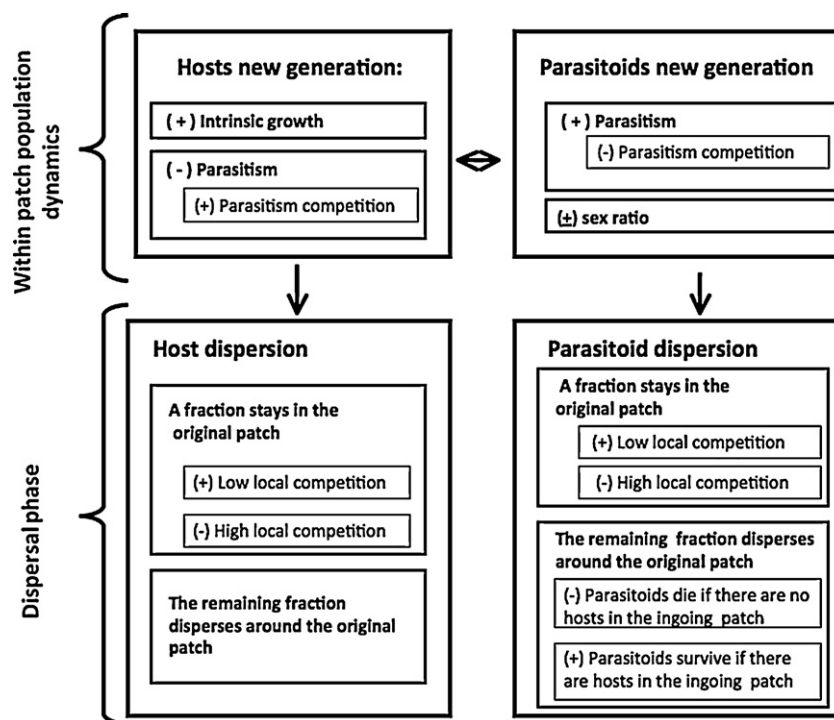
### 2.1. Population dynamics within a patch

Let  $H_{i,t}$ ,  $F_{i,t}$  and  $M_{i,t}$  represent the populations of hosts, female and male parasitoids on patch  $i$  and time  $t$ , respectively. Although the proportion of males and females has important consequences to the genetic variation of local populations, in this study we do not consider the consequences of sib-mating in the parasitoid population. The total parasitoid population is denoted as  $P_{it} = M_{it} + F_{it}$ ; however, we will focus on the female population because of its direct effects on the host population. The population dynamics of the male parasitoids will not be presented here, but the fluctuations in the density of males can be considered to be negatively correlated with the fluctuations of the females. Time is discrete and measured by the number of generations. The local dynamics in each patch consists of hosts laying eggs, their larvae feeding and becoming pupae and adult female parasitoids searching for pupa hosts to parasitize. Both hosts and parasitoids are assumed to have discrete generations, and the parasitoid life cycle is synchronous with that of the host.

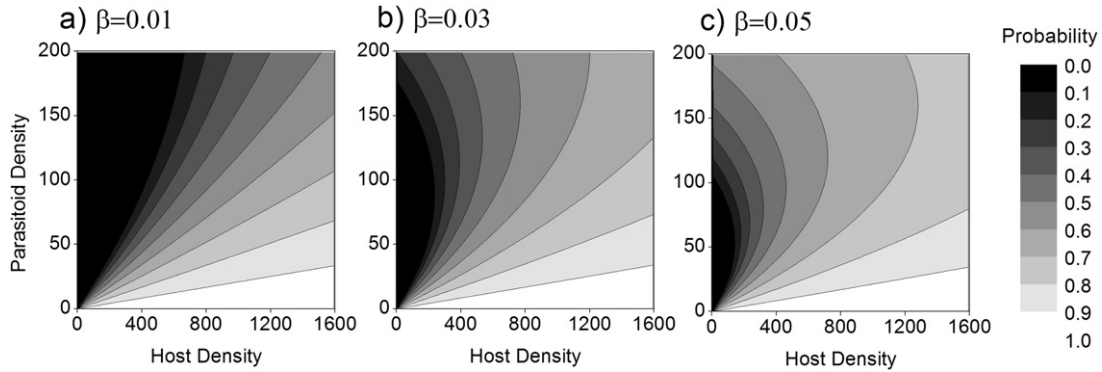
The equations describing the in-patch interactions are given below. We use small letters for the populations at generation  $t + 1$  because these are not yet the final populations. We switch back to capital letters after parasitoid dispersal in phase 2.

$$\begin{aligned}
 h_{i,t+1} &= H_{i,t} \left( \frac{\lambda k}{H_{i,t}(\lambda - 1) + k} \right) [1 - p(H_{i,t}, F_{i,t})], \\
 f_{i,t+1} &= cH_{i,t}p(H_{i,t}, F_{i,t})s(H_{i,t}, F_{i,t}), \\
 m_{i,t+1} &= cH_{i,t}p(H_{i,t}, F_{i,t})[1 - s(H_{i,t}, F_{i,t})].
 \end{aligned}
 \tag{1}$$

The population of hosts increases with the intrinsic growth rate  $\lambda$  and reaches the carrying capacity  $k$  when parasitoids are absent. The effect of parasitism is included in the function  $1 - p(H, F)$ , that is, the proportion of hosts surviving parasitism, as discussed below. The population of female parasitoids in the next generation is proportional to the number of parasitized hosts:  $H_{i,t} p(H, F)$  is multiplied by  $c$ , the average number of adult parasitoids emerging from each host (assumed to be gregarious parasitoids). The function  $s(H, F)$  defines the proportion of female parasitoids that emerge



**Fig. 1.** Conceptual diagram of host–parasitoid dynamics showing the effects of patch quality on a population in two instances: the pre- and post-dispersal phases.



**Fig. 2.** Probability of survival for host populations interacting with a parasitoid population under different levels of interference competition in a patch. The contour plots are drawn for (a) low effect ( $\beta=0.01$ ), (b) medium effect ( $\beta=0.03$ ) and (c) high effect ( $\beta=0.05$ ) of interference competition.

and is controlled by adjustments to the sex ratio of progeny ( $\gamma$ ). The population of male parasitoids is similar but multiplies by  $1 - s(H, F)$ .

The model assumes that superparasitism (one host parasitized by more than one parasitoid) does not occur (female parasitoids are capable of discriminating between parasitized and healthy hosts, although their competitive ability differs according to  $\beta$ ). The functional response  $p(H, F)$  defines the fraction of parasitized hosts and is defined as

$$p(H_{i,t}, F_{i,t}) = \begin{cases} 1 & \text{if } v(H_{i,t}, F_{i,t}) > 1 \\ v(H_{i,t}, F_{i,t}) & \text{if } v(H_{i,t}, F_{i,t}) \leq 1 \end{cases}$$

where

$$v(H_{i,t}, F_{i,t}) = \frac{32\alpha F_{i,t}}{H_{i,t} + \beta F_{i,t}^2}, \tag{2}$$

and  $\alpha$  is the parasitoid attack rate. The term  $32\alpha$  represents the maximum number of hosts that one parasitoid can parasitize if there is no competition for hosts among conspecifics. We assume  $\alpha=0.15$ , which reduces the maximum number of hosts that one parasitoid can parasitize to 4.8. This is an average value that we obtained in a previous study (Reigada and de Aguiar, 2012). The parameter  $\beta$  represents the degree of interference competition among conspecifics and reduces the female's potential to attack hosts in depleted patches. This is caused by the delay between successive female ovipositions due to the female encountering high rates of parasitized hosts, i.e., cost of discriminating between healthy and parasitized hosts. The effects of this interference competition increase with the density of females (foundresses) found in a patch.

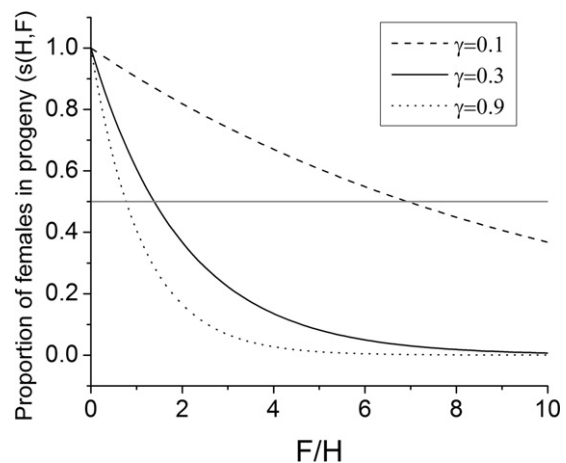
In this study, we considered parasitoid populations to be characterized by three levels of interference: (i)  $\beta=0.01$  (low), (ii)  $\beta=0.03$  (medium) and (iii)  $\beta=0.05$  (high). The range of variation in  $\beta$  is sufficient to generate different scenarios. The probability of hosts surviving an attack by parasitoids under these different levels interference is illustrated in Fig. 2. For example, consider that 200 hosts interact with 200 parasitoids in a patch (see Fig. 2): under conditions of low competitive interference from parasitoids, all hosts will be parasitized; under conditions of medium interference, approximately 30% of the hosts survive; and under high interference, 60% of the hosts survive the attack.

The function  $s(H, F)$  defines the proportion of female parasitoids emerging from the pupae and controls adjustments to the sex ratio of progeny. The proportion of male parasitoids (i.e., sex ratio) is

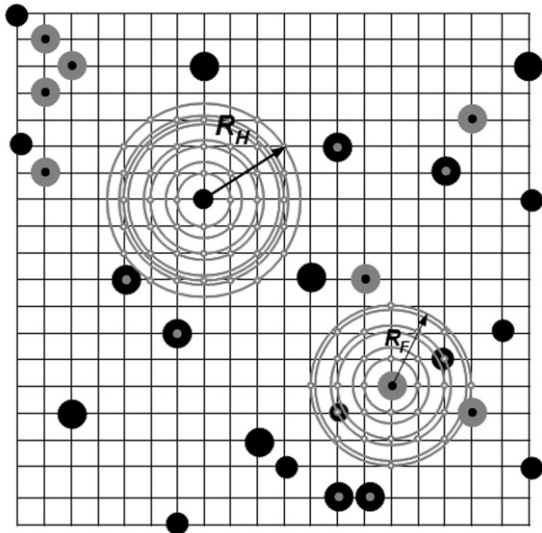
therefore  $1 - s(H, F)$ . Thus, a high sex ratio indicates a small number of females among parasitoid offspring. We used

$$s(H_{i,t}, F_{i,t}) = \exp\left(\frac{-\gamma F_{i,t}}{H_{i,t}}\right), \tag{3}$$

where  $\gamma$  represents the degree of adjustment to sex ratio. In the simulations,  $\gamma$  was set to 0.1, 0.5 and 0.9, respectively indicating low, medium and high variation in the sex ratio in response to changes in patch quality. The adjustment of sex ratio in the parasitoid population reflects the proportion  $F/H$  (quality of patch) necessary to provoke changes in the sex ratio of progeny by a female parasitoid. In other words, this proportion allows a female to determine the ratio of males in its offspring, thus increasing the chance that its male progeny will mate with female progeny from other females (Hamilton, 1967). Thus, parasitoid populations generated by females with a value of  $\gamma=0.1$  are less responsive to variations in  $F/H$  in an exploited patch. Therefore, for a given patch quality, the ratio of males to females is expected to be larger under large values of  $\gamma$  (Fig. 3).



**Fig. 3.** Proportion of female offspring (decrease in the sex ratio) in parasitoid populations with different levels of sex ratio adjustment as a function of changes in the quality of local conditions ( $F/H$ ). The adjustment of sex ratio in the parasitoid population can be translated as the proportion  $F/H$  (quality of patch) necessary to provoke changes in the ratio of a female parasitoid's progeny. The dashed line represents low ( $\gamma=0.1$ ), the solid line medium ( $\gamma=0.3$ ) and the dotted line high ( $\gamma=0.9$ ) degrees of sex ratio adjustment. Note that more than 50% of the offspring will be female for the following patch qualities:  $F/H < 6.93$  for  $\gamma=0.1$ ;  $F/H < 1.39$  for  $\gamma=0.5$  and  $F/H < 0.77$  for  $\gamma=0.9$ .



**Fig. 4.** Scheme of the  $20 \times 20$  grid of patches. In each patch, populations of hosts (black cycle) and parasitoids (gray cycle) can be present. The small white circle inside of the species' dispersal radius ( $r_{ij}$ ) represents the patches that can be chosen. Host dispersers tend to spread over longer distance than parasitoids ( $R_H$  and  $R_F$ , represent host and parasitoid spread over the spatial arena, respectively). Host and parasitoid population dispersal is given long to increase the distance of the radius ( $r_{ij}$ ) from the current patch until reaching the dispersal limit ( $R_H$  and  $R_F$ , respectively). Patches located inside each  $r_{ij}$  value are chosen randomly by dispersers according to the following rules: (1) the host and parasitoid dispersal fraction for each  $r_{ij}$  are defined by Eqs. (4) and (7), respectively; (2) the number of patches for a specific  $r_{ij}$  value represents the number of dispersal events that will occur for a given  $r_{ij}$ , (3) for each dispersal event, one of those patches is chosen at random to receive one fraction of dispersers. The events are independent, and thus, one patch can receive more dispersers than others. This increment is the only random rule imposed on the model and allows us to verify the robustness of our model under conditions of heterogeneous dispersion.

## 2.2. Dispersal phase

In our model, space is represented by a two-dimensional square grid of  $20 \times 20$  cells, with each cell representing a habitat for local subpopulations governed by the local interactions described by Eq. (1). The grid has reflective boundaries, and the subpopulations are coupled by a distance-dependent dispersal. Our choice of grid size is based on the observation that larger arenas produced qualitatively similar results for co-existence and spatial patterns. In contrast, smaller arenas affected the probability of coexistence; for instance, parasitoids always became extinct in a  $10 \times 10$  grid. After phase 1, adult hosts emerged from unparasitized pupae, and female parasitoids emerged from parasitized hosts and remained in or left their current patch, depending on the local conditions. The dispersion among patches occurs within a distance  $R$  from the original patch such that the dispersal area is approximately  $\pi R^2$ . The fraction of hosts that leave the current patch ( $h_{i,t+1}^{out}$ ) is given by

$$h_{i,t+1}^{out} = \frac{\mu_H h_{i,t+1}^2}{h_{i,t+1} + h^0}, \quad (4)$$

where  $\mu_H$  is the maximum dispersal rate of hosts in a patch with a high density of hosts (density-dependent dispersion), and  $h^0 = k/16 = 100$  is the hosts' tolerance to conspecifics.  $k$  is the host carrying capacity of the patch and is fixed at 1600 host individuals for all patches in these simulations. However, if the host density in the current patch is low, a higher fraction of hosts will stay in the patch. The  $h_{i,t+1}^{out}$  host population will disperse among neighboring patches inside of the dispersal area  $R_H$  (Fig. 4). Thus, each patch  $j$  ( $j \neq i$ ) will receive a fraction of these host individuals given by

$$h_{j,t+1}^{in} = \frac{0.05}{r_{ij}} h_{i,t+1}^{out}. \quad (5)$$

The number of dispersing hosts arriving at patch  $j$  is inversely proportional to  $r_{ij}$ , the distance between the current patch  $i$  and the destination patch  $j$  ( $r_{ij}$  is set to 1 for the adjacent patches). The factor 0.05 ensures that the hosts spread over several patches of the spatial arena and might populate patches located farther from the native patch (Fig. 4). To avoid directional preferences, whenever more than one patch is available at a given distance  $r_{ij}$ , they are populated randomly (Fig. 4).

Therefore, 20% of the dispersers will settle in the nearest four patches ( $r_{ij} = 1$ ; each patch can receive 5% of the dispersers), 14% will disperse among the second nearest four patches ( $r_{ij} = 1.42$ ), and so on until  $R_H = 3.61$ , where the last 11% of the hosts will settle. After the dispersal phase, the distribution of the new generation of hosts in each patch is given by

$$H_{i,t+1} = h_{i,t+1} - h_{i,t+1}^{out} + \sum_{r_{ij} \leq R_H} h_{i,t+1}^{in}. \quad (6)$$

The dispersal of the parasitoids occurs after that of the hosts. This is due to the longer period of maturation generally required for parasitoids to reach the adult stage. The number of dispersing female parasitoids is given by a slightly more complicated expression and depends on the density of hosts in the originating patch:

$$f_{i,t+1}^{out} = \mu_F \frac{H^0}{H^0 + H_{i,t+1}} \frac{f_{i,t+1}^2}{f_{i,t+1} + f^0} \quad \text{if } H_{i,t+1} > 0, \quad (7)$$

$$f_{i,t+1}^{out} = f_{i,t+1} \quad \text{if } H_{i,t+1} = 0$$

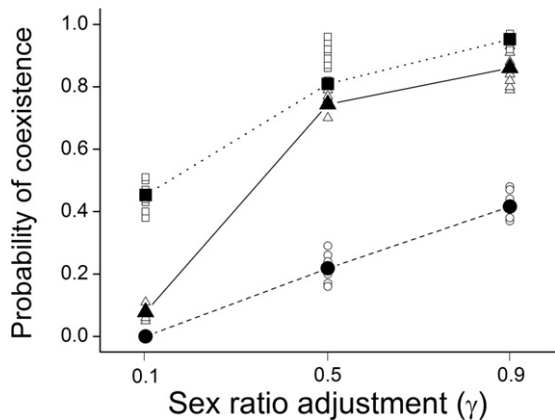
Here  $f_{i,t+1}^{out}$  is the female parasitoid population that will disperse among neighboring patches in the dispersal area  $R_F$ .  $\mu_F$  is the maximum parasitoid dispersal rate when few hosts are present or when the quality of patch is not ideal (high proportion of  $F/H$ ). The constant factors are  $H^0 = k/5.3 \sim 300$  (the number of hosts needed to keep the female parasitoids from dispersing) and  $f^0 = H^0/3 = 100$  (tolerance to conspecifics, i.e., the number of females that can stay in the patch without dispersing). Female parasitoids  $f_{i,t+1}^{out}$  disperse from patch  $i$  to neighboring patches within a distance  $r_{ij} \leq R_F$  but only colonize new patches  $j$  that are already occupied by hosts:

$$f_{j,t+1}^{in} = \frac{0.25}{r_{ij}} f_{i,t+1}^{out} \quad \text{if } H_{j,t+1} > 0$$

$$f_{j,t+1}^{in} = 0 \quad \text{if } H_{j,t+1} = 0 \quad (8)$$

The number of dispersing female parasitoids is inversely proportional to  $r_{ij}$ . The factor 0.25 ensures that when  $r_{ij} = 1$ , each of the four nearest neighbors can receive 25% of the dispersing parasitoids, thereby exhibiting a tendency to aggregate (Fig. 4). If any of the four nearest patches are empty, the parasitoids continue to disperse to other patches inside the dispersal area. However, given that we set  $R_F = 3$ , only 33% of the dispersing individuals can reach this distance (each of the four sites at  $r_{ij} = 3$  can receive up to  $0.25/3\%$  of the parasitoids). Larger values of  $r_{ij}$  imply a higher mortality factor for parasitoid dispersal when hosts are scarce in the nearest patches. This model accounts for the poor long-distance dispersal abilities of the parasitoids relative to the hosts, and this dynamic was based on observations in the field (Tscharntke et al., 2005). Patches at a given distance are also chosen randomly by the dispersing parasitoids, as described in Fig. 4. The absence of sufficient suitable patches in this area leads the remaining  $f_{i,t+1}^{out}$  to die without reproducing. Afterward, the parasitoid population in each patch is given by

$$F_{i,t+1} = f_{i,t+1} - f_{i,t+1}^{out} + \sum_{r_{ij} \leq R_F} f_{i,t+1}^{in}. \quad (9)$$



**Fig. 5.** Coexistence probabilities of host–parasitoid metapopulations as a function of the parasitoid sex ratio index ( $\gamma$ ) for different values of the competitive interference parameter ( $\beta$ ) after 5000 time-steps ( $\lambda = 1.5$ ;  $\alpha = 0.15$ ). Open symbols represent the coexistence probability obtained from simulations with several combinations of host ( $\mu_H$ ) and parasitoid ( $\mu_P$ ) dispersal rates, with  $0.1 \leq \mu_H \leq 1.0$  and  $0.1 \leq \mu_P \leq 1.0$ . Full symbols represent the average over 5 replicates of these simulations. Circles and dashed lines, triangles and solid lines, and squares and dotted lines represent the results for low ( $\beta = 0.01$ ), medium ( $\beta = 0.03$ ) and high ( $\beta = 0.05$ ) parasitoid interference competition, respectively.

### 3. Results

In the absence of migration ( $R_H = R_P = 0$ ), any initial condition drives the host–parasitoid populations to extinction. Coexistence is possible only when the spatial structure is considered. To ensure that the parasitoids do not parasitize all hosts in the first few generations, we started our simulations with 300 hosts and 4 parasitoids at a single patch located in the center of the landscape. We observed that any initial condition that allows the hosts to spread in the initial time-steps leads to similar long-term results. Because of the randomness in the choice of patches at a given distance during dispersal, we ran ten sets of simulations for each set of parameters to ensure the robustness of the results.

#### 3.1. Coexistence in host–parasitoid interaction

Fig. 5 shows the probability of host–parasitoid coexistence under different combinations of sex ratio adjustment ( $\gamma$ ) and interference competition ( $\beta$ ) for parasitoid populations with different responsiveness to variations in patch quality. Full symbols represent the average probability over sets of simulations with different values for host and parasitoid dispersal rates, and these are represented by open symbols. Coexistence was absent or very low for low values of interference competition ( $\beta = 0.01$ , circles) and also for low degrees of adjustment in sex ratio ( $\gamma = 0.1$ ). These results indicate that female parasitoid populations that are less responsive to variations in patch quality ( $F/H$ ) and thus have large numbers of females in poor-quality patches do not persist in the landscape. This dynamic also occurs in parasitoid populations that are very efficient in exploiting hosts in patches with a large density of conspecifics. Because we are most interested in situations where coexistence is possible, the next analysis focuses only on medium and high levels of conspecific interference during patch exploitation.

Extinction was a frequent outcome for parasitoid populations with a low variation in sex ratio ( $\gamma = 0.1$ , Fig. 6a). However, in the cases where coexistence was reached, a long transient phase with large oscillations was observed until host and parasitoid metapopulations eventually reached a stable abundance distribution (Fig. 6d). For higher levels of sex ratio control ( $\gamma = 0.9$ ), the fluctuations in population density were much smaller and extinction was a much less likely outcome. The results showed that female parasitoids that

are more responsive to patch conditions require higher patch quality to favor female offspring, restrict parasitism in poor-quality patches, decrease fluctuations in the population and present a higher probability of coexistence (Fig. 6c and f).

Considering the effects of foraging on reproduction success, we analyzed parasitoid populations under two degrees of conspecific interferences. In parasitoid populations with a high degree of interference among foragers ( $\beta = 0.05$ ), the increase of  $F/H$  in patches (poor-quality patches) reduces the efficiency of oviposition when compared with parasitoid populations with a medium degree of interference competition ( $\beta = 0.03$ ). When competitive interference was high ( $\beta = 0.05$ ), the population of hosts and parasitoids exhibited much smaller oscillations (Fig. 6d–f). In these cases, host and parasitoid populations oscillated around two abundance distributions. This dynamic behavior was more expressive for medium levels of sex ratio adjustment (Fig. 6e). This tendency for a stable average abundance in host and parasitoid population sizes was not observed for ( $\beta = 0.03$ ) (Fig. 6a–c).

Considering the combined results from the sex ratio adjustment and the degrees of interference competition, we can conclude that host–parasitoid populations that are highly constrained by demographic factors (i.e., population growth is strongly correlated with patch conditions) are more stable.

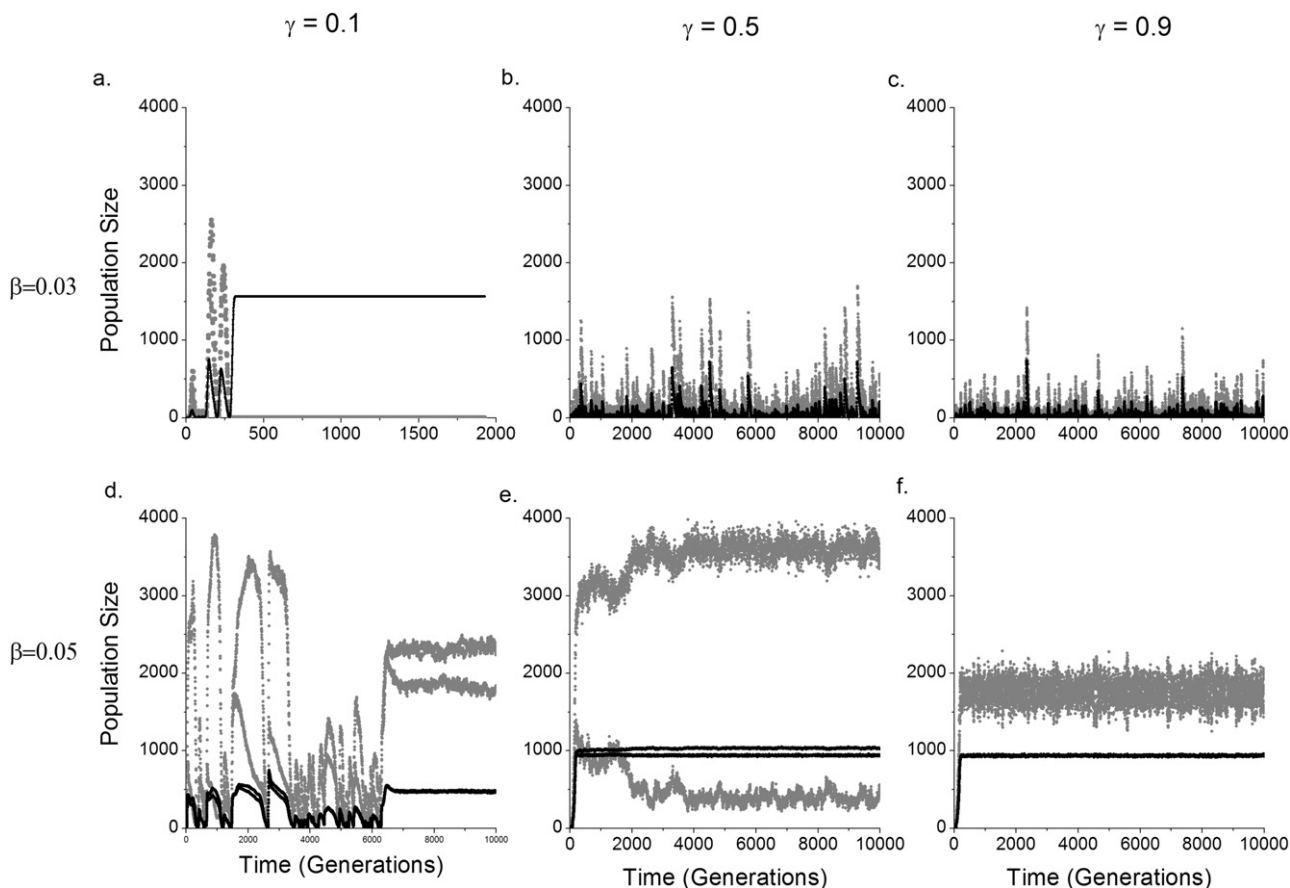
#### 3.2. Host–parasitoid patch occupancy

Snapshots of the host and parasitoid (under high degree of sex ratio adjustment) patch occupancy are shown in Fig. 7 for three instances of time separated by 5 steps. Under conditions of intermediate competitive interference ( $\beta = 0.03$ ), we found traveling waves of host and parasitoid abundances within the metapopulation arena. Host and parasitoid abundances fluctuated from patch to patch, with originating waves of abundance that persisted briefly before leaving patches empty (Fig. 7Aa–c). This behavior was observed in intermediary and high values of sex ratio adjustment (when  $\gamma = 0.1$ , the parasitoids went extinct) and for different combinations of host and parasitoid dispersal rates.

When interference competition was large ( $\beta = 0.05$ ), the host population displayed an approximately uniform distribution over space and time (Fig. 7Ad–f). The hosts were always present in all patches, although parasitoid populations displayed a traveling wave pattern. This pattern was observed in intermediary and high values of sex ratio adjustment and different combinations of host and parasitoid dispersal rates. Changes in the dispersal rates of species increased or decreased the spatial intensity of the traveling waves.

The results suggest that the effects of the sex ratio alone are not substantial enough to cause changes in the distribution of a species across a landscape. However, under a fixed condition of sex ratio adjustment, an increase in the degree of interference competition changes the host distribution patterns from that of a traveling wave to a uniform pattern of occupied patches.

Spatial patterns are also sensitive to species dispersal rates, particularly in parasitoid populations with a low variation in the sex ratio ( $\gamma = 0.1$ ). Fig. 7B shows the effects of dispersal under a high degree of interference competition and low levels of adjustment to the sex ratio. When hosts are less dispersive than parasitoids, we observed host subpopulations grouped in a few clusters or one large group. These clusters evolve over space and time, changing in shape and number. These changes occur over a time scale in the order of 100 generations. Parasitoid subpopulations spread throughout all of the host clusters; however, they organized themselves in subgroups where their subpopulation abundances oscillated synchronously. Fig. 7Ba–c shows a large host cluster and tree parasitoid subgroups that collectively covered all of the host sites. When hosts were more dispersive than parasitoids, both hosts and parasitoids



**Fig. 6.** Representative numerical simulations showing the mean populations of host (black) and parasitoids (gray) over a grid of  $20 \times 20$  patches as a function of time. In panels (a)–(c),  $\beta = 0.03$  and in panels (d)–(f),  $\beta = 0.05$ . For both values, the degree of sex ratio adjustment varies from  $\gamma = 0.1$  to  $\gamma = 0.9$ . The simulations were performed with  $\lambda = 1.5$ ,  $\alpha = 0.15$ ,  $\mu_H = \mu_F = 0.5$ .

spread throughout the arena. Fig. 7Bd–f shows two parasitoid subgroups whose abundances oscillated synchronously.

### 3.3. Metapopulation dynamics – persistence time of extinction for parasitoid subpopulations

For the sets of parameters where coexistence was observed ( $\beta = 0.03$  and  $\beta = 0.05$ ), we computed the average time that each patch remained empty and/or with parasitoid population densities lower than 10% of the mean field of population density – the so-called persistence time of extinction. Fig. 8 shows the spatial demography of the persistence time of extinction for parasitoid subpopulations under three combinations of species dispersal rates. For parasitoid populations that exhibit intermediary degrees of interference competition ( $\beta = 0.03$ ), some patches remained empty and/or with low densities for relatively long periods of time before being recolonized (Fig. 8a and b) compared with instances of high degrees of competition ( $\beta = 0.05$ ). In those cases, the time of recolonization for empty patches was influenced by the species dispersal rates. In general, the lower the parasitoid dispersal rate was, the longer the average time was that the borders of the metapopulation arena remained empty after extinction. Variations in the adjustment of the sex ratio of parasitoid populations significantly changed the time of colonization under fixed conditions of interference competition (compare Fig. 8a and b).

When competition among parasitoids foragers was greater ( $\beta = 0.05$ ), the recolonization of empty patches decreased to one time-step for all values of sex ratio adjustment, except for parasitoid populations with low variation in the sex ratio ( $\gamma = 0.1$ ).

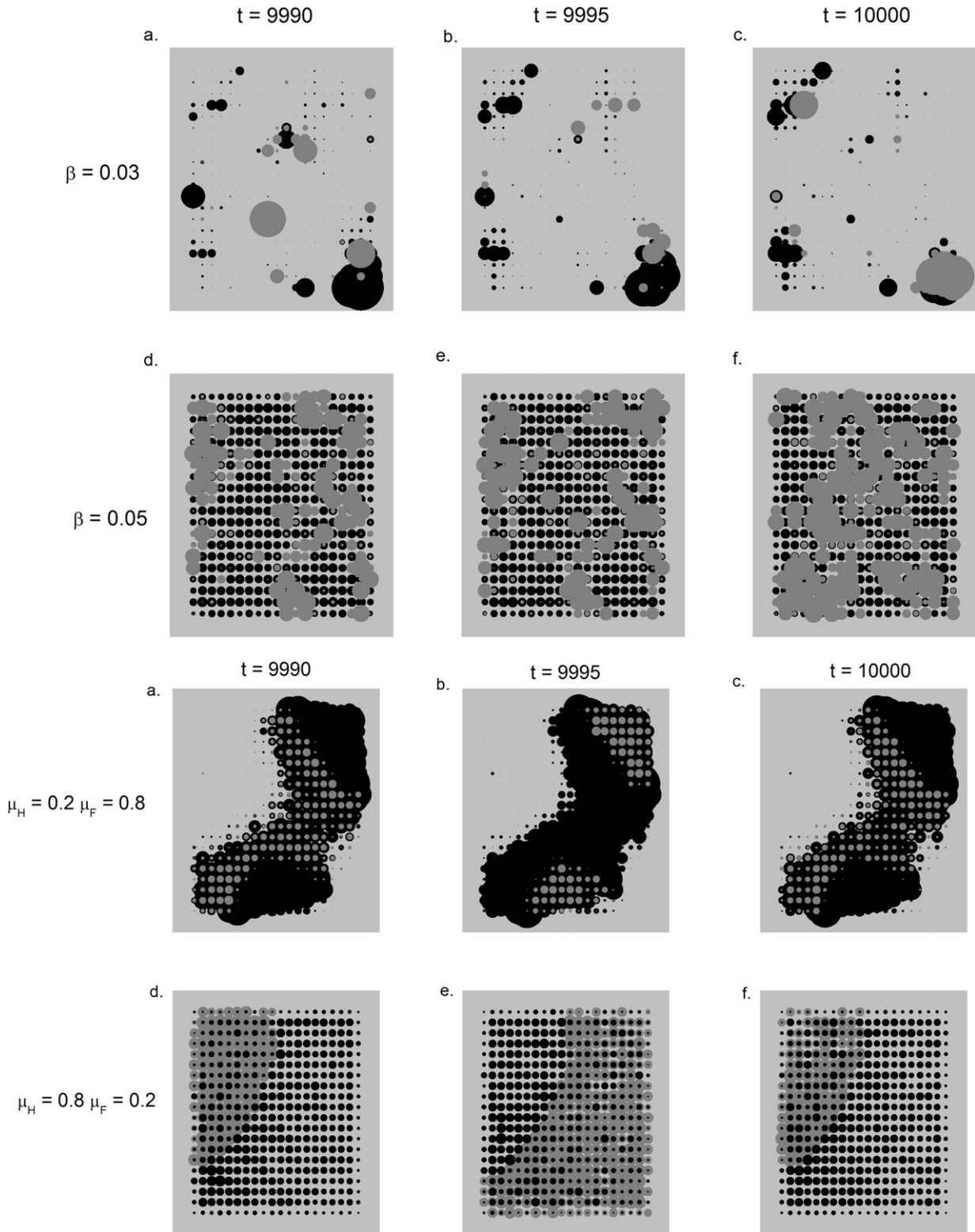
For these simulations some local parasitoid populations remained empty for long periods during the period of analyses. This is a consequence of the clustering occupation pattern of hosts that limited the parasitoid occupation to the host cluster area. In general, the species dispersal rates did not influence the results for medium and high sex ratio adjustment.

## 4. Discussion

The foraging behavior and reproductive success of parasitoids are strictly related to the quality and density of hosts, which are explored using an optimal strategy. Because of this dependence, interesting ecological and co-evolutionary aspects arise from this interaction, resulting in complex adaptive behaviors of interacting species (Perry and Pianka, 1997; Schreiber et al., 2000). However, female parasitoid species can differ in relation to their tolerance to patch quality, foraging rules adopted to explore a patch and the way to maximize their rate of progeny production (Bernstein and Driessen, 1996; van Alphen et al., 2003; Wajnberg, 2006; van Alphen and Bernstein, 2008; Amat et al., 2009; Macke et al., 2011). Motivated by these differences among parasitoid species, we explored some of the reproductive and foraging adaptive behaviors associated with parasitoid populations, characterized by different degrees of sex ratio control and competitive ability in response to fluctuations in host density in a patchy structured landscape.

We found that systems with parasitoid populations that are more responsive to patch quality variation were more stable. Parasitoid populations with low variation in the sex ratio (low sex ratio adjustment) among patches of different quality ( $F/H$ )

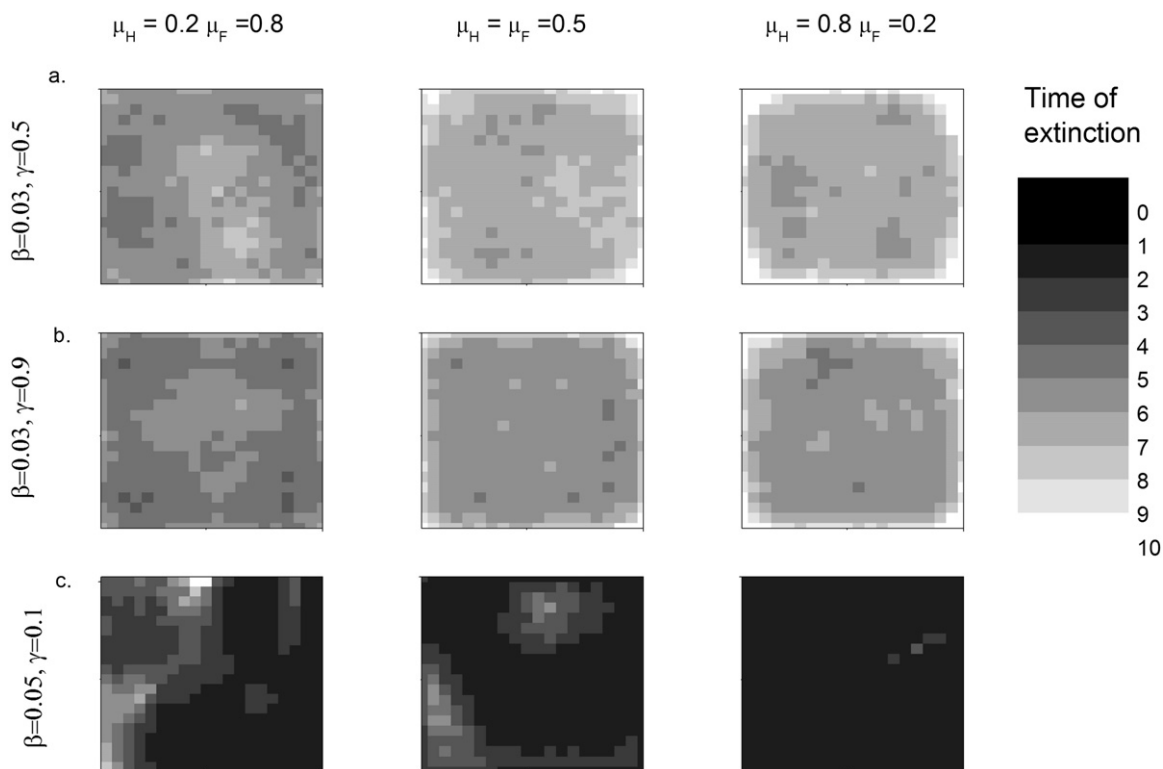




**Fig. 7.** Snapshots of host and parasitoid spatial occupancy for  $t=9990, 9995$  and  $10,000$ . Black and dark gray symbols represent host and parasitoid abundance within each patch ( $\lambda=1.5, \alpha=0.15$ ), respectively. The size of the dots is proportional to the population at the site. In Fig. 6A, we compared the effects of different levels of competitive interference for  $\gamma=0.9, \mu_H=0.2, \mu_F=0.8$ .  $\beta=0.03$  in panels (a)–(c), and  $\beta=0.05$  in (d)–(f). In Fig. 6B, we compared the effects of host and parasitoid dispersal rates for populations exhibiting a low level of sex ratio adjustment ( $\gamma=0.1$ ) and large competitive interference ( $\beta=0.05$ ) for (a)–(c)  $\mu_H=0.2, \mu_F=0.8$  and (d)–(f)  $\mu_H=0.8, \mu_F=0.2$ .

exhibited high density of females and consequently higher rates of parasitism on patches with low density of hosts. Under these conditions, parasitoid populations tended to go extinct. The probability of coexistence dropped drastically for parasitoid populations

in which in association with low sex ratio adjustment, females were very efficient in attacking the hosts (low interference competition). In this case, for all sets of simulations we found parasitoid global extinction because the increase in the number of females



**Fig. 8.** Diagram showing the mean persistence time of parasitoid subpopulations for different values of parasitoid sex ratio adjustment ( $\gamma$ ) after 8000 time-steps (out of a total of 10,000 time-steps) for  $\lambda = 1.5$  and  $\alpha = 0.15$ . For each column, the persistence time is given for different host and parasitoid dispersal rate combinations: (a)  $\beta = 0.03$ ,  $\gamma = 0.5$ ; (b)  $\beta = 0.03$ ,  $\gamma = 0.9$ ; (c)  $\beta = 0.05$ ,  $\gamma = 0.1$ . The black areas represent host subpopulations that were not extinct during the 2000 time-steps analyzed. The white areas represent host subpopulations that remained extinct and/or with low densities for at least 10 time-steps. The gray colors represent intermediate average persistence times at 1-time-step intervals.

was positively correlated with the increase of parasitism rates, resulting in overexploitation of hosts, jeopardizing the survival of the future generations.

Local mate competition is a widespread phenomenon in parasitoids that exploit and mate on patchily distributed hosts (Hassell et al., 1983). Experimental and theoretical works have studied the potential effects of the sex ratio to the stability of host–parasitoid systems and noted several mechanisms that can generate density-dependent sex ratios. Variation in number of female offspring may depend on the density of hosts, female or male parasitoid or in response to the proportion of females per hosts in a patch (Hassell et al., 1983; Comins and Wellings, 1985; Lozano et al., 1997; Meunier and Bernstein, 2002). According to the mechanism at work in the parasitoid population, the host–parasitoid equilibrium densities and stability conditions can be different.

We have explored the last of these proposed mechanisms of sex ratio density-dependence, in which female parasitoids can access the density of conspecifics, or their traces by encounter rates of parasitized hosts (Amat et al., 2009). In this context, higher encounter rates with parasitized hosts had consequences to variations in parasitoid local demography due to (1) the reduction of parasitoid reproductive success and (2) changes in the sex ratio, altering the rates of parasitism on patches.

Density dependency processes avoid the occurrence of population explosions and decrease risks of extinction (Hassell et al., 1983; Hanski, 1999; Bonsall et al., 2002). Empirical and theoretical studies have shown that higher parasitoid aggregation in patches with high density of hosts has important and strong stabilizing effects on host–parasitoid systems (Sutherland, 1983; Lozano et al., 1997; Hassell, 2000; Briggs and Hoopes, 2004). This is because the risk of a host being parasitized decreases with host density in patches, allowing part of the hosts to escape parasitism.

Spatial heterogeneity combined with density-dependent factors can result in demographic distributions that differ from those in a homogeneous mixed system (Briggs and Hoopes, 2004; Maionchi et al., 2006). In addition, we showed that density-dependent adjustments associated with foraging strategies of the parasitoids can lead to different dynamics and the combined effects of their variation can change the species distribution, resulting in important consequences involving self-regulation in parasitoid populations, preventing the overexploitation of hosts, facilitating or hindering host dispersal through the landscape and allowing the persistence of the communities. In this context, important ecological consequences to host–parasitoid dynamics was observed in nature in relation to the mechanism for sex ratio variation (Hamilton, 1967; Godfray and Werren, 1996) and the development of decision rules to adjust parasitoid foraging according to local conditions (Fretwell and Lucas, 1970; Charnov, 1976; Sutherland, 1983; Fauvergue et al., 2006; Macke et al., 2011).

Interactions between hosts and parasitoids under medium effects of interference competition exhibited high fluctuations in their metapopulation sizes. In contrast, the demographic fluctuations observed in hosts interacting with parasitoids under high interference of foragers exhibited cyclic fluctuations around two metapopulation sizes after stabilization. Therefore, different levels of competition affected differently the spatial pattern and the metapopulation dynamic of hosts and parasitoids.

The spatial patterns of species distribution are influenced by a combination of dispersal rates and demographic fluctuations of subpopulations and can lead to the formation of traveling waves (or other patterns) of host and parasitoid abundances within the metapopulation arena (Hassell, 2000; Hassell et al., 1991). The dispersal rates and synchrony levels generated by different fluctuations of subpopulations are important factors to define the spatial

distribution of species (Levins, 1969; Hanski and Gilpin, 1997). The extinction of subpopulations and the time to their recolonization is strictly linked to the dispersal potential of individuals. The dispersion should be large enough to allow the recolonization (rescue effect) of extinct patches, but not too large to avoid the synchronization of all patches (Hassell et al., 1991; Hanski and Gilpin, 1997; Hassell, 2000). Different spatial patterns may appear depending on the synchrony levels generated.

In this study, the demographic processes of the interference of conspecifics and offspring sex ratio adjustment interfered with the population dynamics, changing the fluctuations in abundance controlled by dispersal rates. Different degrees of competition led to different spatial patterns of species distribution. Fluctuations in parasitoid subpopulations generated by the intermediate effects of conspecific interference led to traveling waves in host and parasitoid population abundances. However, under conditions of significant competitive interference, the intrinsic demographic control in parasitoid populations was higher, allowing hosts to spread to all patches in the metapopulation arena. In this case, the host population tended to be uniformly distributed, although the parasitoids' distribution varied across the arena.

The rate of parasitoid dispersal affected the recolonization of peripheral patches when parasitoid populations experienced intermediate levels of interference competition. Under high levels of competition, qualified sites were recolonized faster. However, once a colony was established in a patch, the parasitoid subpopulation remained in that patch for fewer generations than under intermediate levels of competition. Our simulations suggest that parasitoid dispersal abilities are not crucial for recolonization in instances of high competition, given that the populations remain small due to demographic controls. Therefore, the patches are often of good quality and the fraction of dispersing species is small. In these cases, the time for recolonization shown in Fig. 8b was generally not larger than a single time-step, reflecting the oscillations of the local populations instead of the effect of dispersing species. This fact can also be related to the complete and constant occupancy of the arena by hosts. Finally, under levels of high competition, medium or high adjustments to the sex ratio were relatively unimportant to host–parasitoid dynamics. When the adjustment was low, some parasitoid subpopulations remained extinct for long periods of time as a consequence of low host dispersal. However, when host dispersal rates were higher, the hosts' complete occupancy of the arena led to the same timeframe for recolonization that was previously observed in parasitoid populations with high levels of interference competition.

Our results show that the influence of adjustments to the sex ratio, interference competition and density-dependent dispersal in host–parasitoid systems are complex. For instance, low variation in the sex ratio of parasitoid populations had significant effects on host–parasitoid coexistence when female parasitoids exhibited low or medium levels of interference competition and led to parasitoid extinction. However, when the parasitoid population exhibited higher variations in the sex ratio in response to fluctuations in the size of the host population (medium or high sex ratio degree), its effects were not significant to the population dynamics. The limited influence of the sex ratio has been researched by previous host–parasitoid studies (Comins and Wellings, 1985; Lozano et al., 1997; Meunier and Bernstein, 2002). Theoretical analyses have shown that host–parasitoid systems at equilibrium function independently of the male to female ratio (Comins and Wellings, 1985). Moreover, its effects are usually present in association with other biological factors, such as the host's reproductive rate, the aggregation of parasitoids, parasitoid search efficiency and mutual interference competition (Lozano et al., 1997; Meunier and Bernstein, 2002). In contrast, the level of interference competition was an important factor in constraining

the effectiveness of parasitoids to reduce host populations and determining the species distribution of the landscape.

In general, the restriction of parasitoid attacks resulting from interference competition among conspecifics has been regarded as potentially useful as a biological control for parasites. However, this potential application should be considered with caution, as it depends on the biological factors present in the system. In this study, the increase in interference competition increased the stability of the system. However, under high levels of competition, hosts spread throughout the landscape, making host reduction more difficult.

The tendency for parasitoids to aggregate in high-quality patches has been identified as a stabilizing factor in host–parasitoid dynamics by many studies (Hassell, 2000; Briggs and Hoopes, 2004). This tendency also needs to be considered with caution, given that, in association with changes to the sex ratio and mutual interference, competition tends to reduce the number of females in parasitoid offspring and the rate of parasitoid dispersal, thereby increasing the size and distribution of the host population in the landscape.

Theoretical models for foraging parasitoids have failed to acknowledge the influence of the co-evolutionary aspects of population dynamics acting on interacting species (Bonsall et al., 2002). Many foraging strategies can be used during the exploitation of patches in response to host–parasitoid demographic fluctuations, thereby modifying the amount of time a parasitoid resides in a patch (Hamilton, 1967; Outreman et al., 2005; van Alphen and Bernstein, 2008; Amat et al., 2009). Natural systems are composed of many patches, and these patches have hosts with different levels of profitability and interference competition as a result of host depletion. This scenario hinders the parasitoids' assessment of the profitability of all patches available in the landscape. Female parasitoids should adopt different foraging strategy to maximize the use of hosts before leaving a patch, given that such a decision has high costs, such as exposure to risk of predation or difficulties in finding another suitable patch.

The stability of host–parasitoid systems in which female parasitoid offspring are the determining variable depends on several complex interactions between the intrinsic biological characteristics of the interacting species and cannot be attributed to a single mechanism (Lozano et al., 1997; Meunier and Bernstein, 2002; Macke et al., 2011). In this study, we demonstrated that different behaviors and/or strategies adopted by female arrhenotokous parasitoids, as well as different patch quality requirements and patch uses, can theoretically result in different population distributions. This result indicates that the inclusion of life history traits and co-evolutionary aspects of the host–parasitoid interaction can help researchers to understand the distribution of species in the landscape.

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## References

- Amat, I., Desouhant, E., Bernstein, C., 2009. Differential use of conspecific-derived information by sexual and asexual parasitic wasps exploiting partially depleted host patches. *Behavioral Ecology Sociobiology* 63, 563–572.
- Bernstein, C., Driessen, G., 1996. Patch-marking and optimal search patterns in the parasitoid *Venturia canescens*. *Journal of Animal Ecology* 65, 211–219.
- Bernstein, C., Kacelnik, A., Krebs, J.R., 1988. Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology* 57, 1007–1026.

- Bonsall, M.B., French, D.R., Hassell, M.P., 2002. Metapopulation structures affect persistence of predator–prey interactions. *Journal of Animal Ecology* 71, 1075–1084.
- Briggs, C.J., Hoopes, M.F., 2004. Stabilizing effects in spatial parasitoid–host and predator models: a review. *Theoretical Population Biology* 65, 299–315.
- Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9, 126–136.
- Charnov, E.L., 1982. *The Theory of Sex Allocation*. Princeton University Press, Princeton, NJ.
- Comins, H.N., Wellings, P.W., 1985. Density-related parasitoid sex-ratio: influence on host–parasitoid dynamics. *Journal of Animal Ecology* 54 (2), 583–594.
- Fauvergue, X., Boll, R., Rochat, J., Wajnberg, E., Bernstein, C., Lapchin, L., 2006. Habitat assessment by parasitoids: consequences for population distribution. *Behavioral Ecology* 17, 522–531.
- Forde, S.E., Thompson, J.N., Bohannan, B.J.M., 2004. Adaptation varies through space and time in a coevolving host–parasitoid interaction. *Nature* 431 (14), 841–844.
- Fretwell, S.D., Lucas, H.L., 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19, 16–36.
- Godfray, H.C.J., 1994. *Parasitoids*. Behavioral and Evolutionary Ecology. Princeton, NJ, Princeton University Press.
- Godfray, H.C.J., Werren, J.H., 1996. Recent developments in sex ratio studies. *Trends in Ecology and Evolution* 11, 59–63.
- Grillenberger, B.K., Zande, L.V.Z., Bijlsma, R., Gadau, J., Beukeboom, L.W., 2009. Reproductive strategies under multiparasitism in natural populations of the parasitoid wasp *Nasonia* (Hymenoptera). *Journal of Evolutionary Biology* 22, 460–470.
- Hamilton, W.D., 1967. Extraordinary sex ratios. *Science* 156, 477–488.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I., Gilpin, M.E., 1997. *Metapopulation Biology Ecology, Genetics and Evolution*. Academic Press, London.
- Hassell, M.P., 1978. *The Dynamics of Arthropod Predator–Prey Systems*. Princeton Univ. Press, Princeton, NJ.
- Hassell, M.P., 2000. Host–parasitoid population dynamics. *Journal of Animal Ecology* 69, 543–566.
- Hassell, M.P., Comins, H.N., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353, 255–258.
- Hassell, M.P., Waage, J.K., May, R.M., 1983. Variable parasitoid sex ratios and their effect on host–parasitoid dynamics. *Journal of Animal Ecology* 52 (3), 889–904.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.
- Lozano, C., Kidd, N.A.C., Jervis, M.A., Campos, M., 1997. Effects of parasitoid spatial heterogeneity, sex ratio and mutual interference on the interaction between the olive bark beetle *Phloeotribus scarabaeoides* (Col., Scolytidae) and the pteromalid parasitoid *Cheiropachus quadrum* (Hym., Pteromalidae). *Journal of Applied Entomology* 121 (1–5), 521–528.
- Macke, E., Magalhães, S., Bach, F., Olivien, I., 2011. Experimental evolution of reduced sex ratio adjustment under Local Mate Competition. *Science* 334, 1127–1129.
- Maionchi, D.O., Reis, S.F., Aguiar, M.A.M., 2006. Chaos and pattern formation in a spatial tritrophic food chain. *Ecological Modelling* 191, 291–303.
- Meunier, J., Bernstein, C., 2002. The influence of local mate competition on host–parasitoid dynamics. *Ecological Modelling* 152 (1), 77–88.
- Murray, J.D., 2000. Pattern formation in integrative biology – a marriage of theory and experiment. *Comptes Rendus de l'Académie des Sciences* 323, 5–14.
- Nicholson, A.J., Bailey, V.A., 1935. The balance of animal populations. Part I. *Proceedings of the Zoological Society of London* 3, 551–598.
- Outreman, Y., Ralec, A.L., Wajnberg, E., Pierre, J.S., 2005. Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behavioral Ecology Sociobiology* 58, 208–217.
- Perry, G., Pianka, E.R., 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* 12, 360–364.
- Reigada, C., de Aguiar, M.A.M., 2012. Host-parasitoid persistence over variable spatio-temporally susceptible habitats: bottom-up effects of ephemeral resources. *OIKOS*. doi:10.1111/j.1600-0706.2011.20259.x.
- Santolamazza-Carbone, S., Rivera, A.C., 2003. Superparasitism and sex ratio adjustment in a wasp parasitoid: results at variance with Local Mate Competition? *Oecologia* 136, 366–373.
- Schreiber, S.J., Fox, L.R., Getz, W.M., 2000. Coevolution of contrary choices in host–parasitoid systems. *American Naturalist* 155, 637–648.
- Shuker, D.M., Sykes, E.M., Browning, L.E., Beukeboom, L.W., West, S.A., 2006. Male influence on sex allocation in the parasitoid wasp *Nasonia vitripennis*. *Behavioral Ecology Sociobiology* 59, 829–835.
- Sutherland, W.J., 1983. Aggregation and the ideal free distribution. *Journal of Animal Ecology* 52, 821–828.
- Tscharntke, T., Klein, A.M., Krues, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8, 857–874.
- van Alphen, J.J.M., Bernstein, C., Driessen, G., 2003. Information acquisition and time allocation in insect parasitoids. *Trends in Ecology and Evolution* 18, 81–87.
- van Alphen, J.J.M., Bernstein, C., 2008. Information acquisition, information processing, and patch time allocations. In: Wajnberg, E., Bernstein, C., van Alphen, J.J.M. (Eds.), *Behavioral Ecology of Insects Parasitoids: From Theoretical Approaches to Field Applications*. Blackwell Publishing, pp. 172–192.
- Wajnberg, E., 2006. Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. *Behavioral Ecology Sociobiology* 60, 589–611.