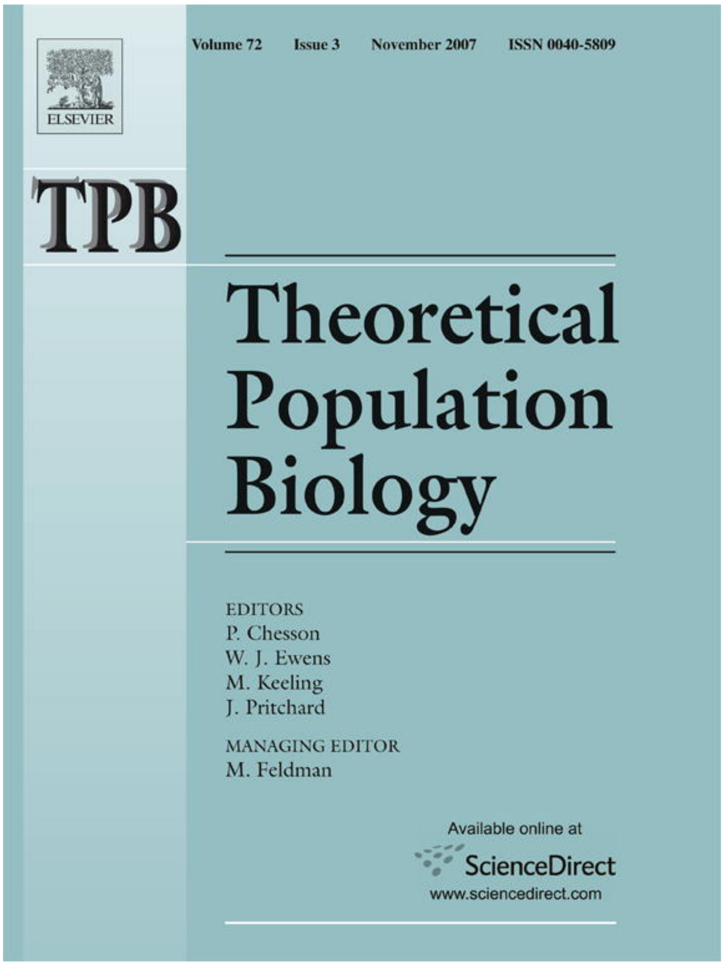

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Superparasitism as a differential game

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Abstract

Superparasitism refers to a female parasitoid laying an egg in a host already parasitized by a conspecific. In solitary species, only one offspring per host is expected to complete development, hence the game. Hosts are often clumped in patches and several females exploiting such an aggregate of resource make its state change over time, hence the dynamical character of the game. Two coupled questions arise: (i) Is it worth accepting a parasitized host? (ii) When to leave the host patch? Through these decisions (i) the competition for healthy hosts and (ii) the trade-off between leaving in quest of a better patch and staying to make the patch less profitable for other parasitoids (this is a way to lower superparasitism likely to occur after having left the patch) are addressed. The aim of this work is to characterize a strategy that would be evolutionarily relevant in such a situation, as it directly concerns females' reproductive success. Investigating a (synchronous) nonzero-sum two-player differential game allows us to characterize candidate dynamic evolutionarily stable policies in terms of both oviposition and patch-leaving decisions. For that matter, the game is (in the most part of the parameter space) completely solved if the probability that superparasitism succeeds is assumed to be close to one-half, a fair value under direct competition. The strategic equilibrium consists, for each females, in (i) superparasitizing consistently upon arrival on the patch, and (ii) leaving when the loss of fitness due to superparasitism likely to occur after its departure is reduced to zero. The competing females are thus expected to leave the patch as they arrived: synchronously. Superparasitism does not necessarily lead to a war of attrition.

Keywords: Differential games; Evolutionarily stable strategies; Behavioural ecology; Foraging theory; Superparasitism

1. Introduction

Many species of insects, known collectively as parasitoids, are free-living as adults but, as juveniles, develop parasitically on other 'host' species, killing the host in the process (Reynolds and Hardy, 2004). As parasitoids' foraging behavior and reproductive success are closely related (Godfray, 1994), these species, beyond being useful auxiliaries for biological control against phytophagous pests (Wajnberg and Hassan, 1994), are considered as a privileged model to test theoretical models of foraging behavior based on a natural selection rationale (Stephens and Krebs, 1986; Wajnberg et al., 2007).

A commonly observed phenomenon in this species is *superparasitism*, which refers to a female parasitoid laying an egg in a host already parasitized by a conspecific. In solitary species, only one offspring per host is expected to complete development. Therefore, superparasitism yields, at the population level, a decrease in parasitoids efficiency at reproducing, hence also at controlling the pest population. Better understanding in which fashion these auxiliaries parasite each other may thus contribute to improve biological control programmes, both at the level of mass rearing and in the field.

Whether superparasitism would result from parasitoids' disability to discriminate between healthy and parasitized hosts has long been an open and controversial question (van Alphen and Visser, 1990). Nowadays, it is well known

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that parasitoids can avoid superparasitism (Speirs et al., 1991) via detecting, for instance, a host-marking pheromone left by a predecessor (Roitberg and Mangel, 1988). Moreover, parasitoids are also often able to discriminate hosts parasitized by themselves from those attacked by their fellows (Hubbard et al., 1987). Furthermore, some species can even map such a chemical signal to a kinship coefficient (Marris et al., 1996; van Baaren and Boivin, 1998; Lizé et al., 2006).

From the actual nature of this discrimination ability, one can easily imagine that the behavioral trait that consists in accepting or not a parasitized host has been subject to strong selective pressures. In this respect, van Alphen and Visser (1990) substantiate the evidence, both empirical and theoretical, that superparasitism as well as its avoidance can be adaptive, in particular when several females are simultaneously present on the same host patch. Another interpretation of the adaptive significance of superparasitism, or the fact that it could be controlled by a virus, is addressed by Varaldi et al. (2003), Reynolds and Hardy (2004), Gandon et al. (2006). In the present paper, however, we shall ignore such a possibility.

Synovogenic species of parasitoids produce eggs throughout their lifetime whereas proovogenic ones emerge with a fixed, finite egg load. Eggs are thus costly, either explicitly in terms of physiological requirements to egg-load renewal, or implicity due to egg-limitation. Therefore, parasitoids' diet selection specificity is that, beyond being costly in time, accepting a low quality resource (an already parasitized host) also implies spending an egg. There is thus a trade-off to find between current and future opportunities, themselves subject to uncertainties. Typically, dynamic state variable models, e.g. (Iwasa et al., 1984; Mangel, 1989; Roitberg et al., 1992; Weisser and Houston, 1993), take into account the physiological state of the parasitoid (e.g. its age and its egg-load) and let it evolve in a stochastic environment, making its life expectancy uncertain, as well as the number and quality of hosts to be encountered in the future. Dynamic programming then allows one to find the optimal state feedback oviposition policy. Who controls Nature (Roitberg et al., 1993), i.e. the hazard, can thus elaborate a scenario which may be falsified through experiments. Without having necessarily a dynamic component, the articles (Charnov and Stephens, 1988; Sirot et al., 1997; Glaizot and Arditi, 1998; Plantegenest et al., 2004) also address superparasitism as a host-selection problem (a one-player game, or a game against Nature), ignoring the fact that this isolated parasitoid is also likely to be superparasitized afterwards. Optimal policies found are thus close to those of the classical diet selection theory. Interestingly, such individual strategies may stabilize hosts-parasitoids population dynamics (Sirot and Křivan, 1997; Bernstein, 2000).

However, as the fitness of an individual may be affected by another one through superparasitism, such a situation is clearly a game; a Stackelberg game, essentially, as parasitized hosts are vulnerable to subsequent attacks in a fashion which depends on the state of the patch left (indirect competition) (Sjerps and Haccou, 1993). Also, it may happen that several females are simultaneously present on a patch and compete for hosts (Wajnberg et al., 2004; Goubault et al., 2005), which situation corresponds to a Nash game (direct competition). Moreover, as the patch state changes over time, the game has a dynamic component. Two coupled questions arise:

- Is it worth accepting a parasitized host? As females are assumed to probe the patch at random, finding a healthy host among those already parasitized is time consuming. On the other hand, healthy hosts, which represent the best quality resource, are limited in quantity; hence the competition. One would thus expect that females reject parasitized hosts first, focusing on healthy hosts as long as they remain quite abundant.
- When to leave the host patch? One has to avoid wasting its time searching for the last healthy host remaining in the patch while there are other opportunities in the environment. On the other hand, the more depleted the patch, the less profitable for other parasitoids, thus the lower the superparasitism likely to occur after having left the patch.

In these respects, van der Hoeven and Hemerik (1990) focus on oviposition decisions as a function of the host expected value (its current state and the expected future number of attacks, depending on the number of parasitoids present in the neighborhood and their strategy), eggs being possibly costly, but ignored patch-leaving decisions. Also, Mangel (1992) addresses the question 'at what point in its life should an individual parasitoid begin attacking previously parasitized hosts?'. An environment where hosts are regularly and homogeneously distributed is considered, healthy hosts being depleted by a population of parasitoids during a fixed time horizon. In a similar fashion, Visser et al. (1992) investigate when several females together depleting a patch would be expected to switch to superparasitism. The time horizon depends this time on the females' oviposition policies. Yet, it is given by Charnov's marginal value theorem (Charnov, 1976b), which does not take into account a specificity that belongs to parasitoids: the fact that a host (as opposed to a prey) is, due to the possibility of superparasitism, never definitely acquired, at least as long as conspecifics are present on the patch. Seeing its fellows leaving thus yields an abrupt increase of the fitness expected from the patch. Such a situation is, in this respect, similar to classical interference competition, where random patch-leaving times (a war of attrition) arise (Sjerps and Haccou, 1994a). As Visser et al. (1992) ignore the latter point, the female parasitoids are, in their model, *a priori* assumed to leave the patch at the same, deterministic, time. Conversely, Haccou et al. (2003) focus on patch-leaving strategies, assuming that females adopt a myopic oviposition policy, see Appendix C.3. It yields a switching-rule that only depends on the current state of the patch, whatever happens, and which can thus be fixed *a priori*. Such a (possibly fair, this is one of the questions addressed in this paper) assumption considerably simplifies the game and leads the authors to investigate an asymmetric war of attrition with mistakes in perception of patch state (Haccou and Glaizot, 2002).

In the present paper, our aim is also to investigate what strategy evolution is supposed to have shaped for parasitoids competing for patchily distributed hosts. We shall thus refer to the concept of evolutionarily stable strategy (ESS) (Maynard Smith, 1982), both in terms of oviposition and patch-leaving policies. Contrary to our predecessors, we shall not assume either oviposition or patch-leaving policy as being arbitrarily fixed, as both are surely coupled. However, we shall make some simplifying assumptions that are detailed in Section 2, describing our model. Section 3 states the game and suggests a solution that, if relevant, can be retrieved through a more usual formalism, which appears in Section 4. Section 5 then addresses the existence of an equilibrium in pure strategies.

2. Model

Our model is based on the following assumptions, some of them being further discussed in Appendix B.

2.1. Assumptions

(i) Parasitoids are solitary: a host begets at most one parasitoid.
(ii) Parasitoids are assumed to be egg-unlimited; we ignore any egg cost.
(iii) There is no kinship between the females: our measure of fitness is thus the expected number of offsprings per female (Sjerps and Haccou, 1994b).
(iv) Females probe the patch at random.
(v) There is no *interference*: females' efficiency at finding and attacking a host is not altered by the fact that conspecifics are present on the patch.
(vi) This is a two-player game: at most two females can be simultaneously present on the patch.
(vii) Both females arrive at the same time on a patch initially composed of healthy hosts only.
(viii) We assume that there is no additional superparasitism from another female after the opponent has left.
(ix) A host cannot undergo more than one attack per female; we ignore self-superparasitism in any fashion. We shall refer to *admissible* hosts as those which have not been attacked by the focal female.
(x) The probability that superparasitism succeeds, i.e. that the survivor results from the second egg laid, is assumed to be a constant, denoted π, lower or equal to $\frac{1}{2}$.
(xi) Parasitoids recognize (e.g. via a marking pheromone)
  - healthy hosts,
  - hosts once-parasitized by themselves,
  - hosts once-parasitized by a conspecific,
  - and hosts twice-parasitized, whatever the rank of attacks.

2.2. Modelling patch dynamics

Let us introduce two parameters (see Hamelin et al., 2007a for a detailed description of the model):

- $\alpha > 0$: the time taken to move from one host to another and to probe it,
- $h > 0$: the handling time or the time required to lay an egg in a host.

Let x be a state vector containing the proportions $x_i \in [0,1], \sum_i x_i = 1$ of each type of resource available in the patch, i.e.:

- x_0: proportion of healthy hosts remaining in the patch,
- x_1: proportion of hosts once-parasitized by female 1,
- x_2: proportion of hosts once-parasitized by female 2,
- x_3: proportion of hosts twice-parasitized.

Let $\dot{x} := \mathrm{d}x/\mathrm{d}t$, where t stands for the patch residence time.

Let $u, v \in [0,1]$ be the parasitized–host-acceptance rates associated to each female (healthy hosts are always accepted). In a sense, these controls stand for the females propensities to superparasitism.

Although both females are assumed to arrive at the same time on the patch, they are free to leave at any time (why and how is there an incentive to leave is detailed in Section 3.1).

Let $y = (y_1, y_2)$ be a state vector containing two boolean variables attesting for both females presence on the patch; $y_i = 0$ is said to be an 'absorbing state' as once switched to zero, it cannot switchback to one.

In a similar fashion to Holling (1959), Hamelin et al. (2007a,b), an assumption of random probing on the patch yields the following dynamics: let

$$D_1 := \alpha + h(x_0 + u x_2), \quad \phi_{01} := y_1 x_0 / D_1, \quad \phi_{13} := v y_2 x_1 / D_2,$$

$$D_2 := \alpha + h(x_0 + v x_1), \quad \phi_{02} := y_2 x_0 / D_2, \quad \phi_{23} := u y_1 x_2 / D_1, \tag{1}$$

and our dynamics are given by

$$\begin{cases} q\dot{x}_0 = -\phi_{01} - \phi_{02}, & x_0(0) = 1, \\ q\dot{x}_1 = +\phi_{01} - \phi_{13}, & x_1(0) = 0, \\ q\dot{x}_2 = +\phi_{02} - \phi_{23}, & x_2(0) = 0, \\ q\dot{x}_3 = +\phi_{13} + \phi_{23}, & x_3(0) = 0. \end{cases} \tag{2}$$

In fact, x_3 is not needed as a state variable since it is given by $x_3 = 1 - x_0 - x_1 - x_2$.

3. Stating the game

3.1. Time is fitness

Following Charnov (1976b), McNamara et al. (2001), Hamelin et al. (2007a–c), we shall consider that the time has a cost $\gamma^\star > 0$ per unit, in terms of missed opportunities. It prevents parasitoids from wasting their time on a no longer profitable patch. Indeed, under patch depletion, finding an admissible host is increasingly costly in time, thus leaving in quest of a fresh patch becomes more and more worthwhile, in spite of an uncertain travel-time. Charnov's marginal value theorem states that the optimal giving-up time for a lone forager is when its intake-rate drops precisely to $\gamma^\star$, the best ratio 'fitness acquired' over 'time invested' a forager can expect in its environment; $\gamma^\star$ thus reflects the quality of the environment.

3.2. A two-player nonzero-sum game

We consider the following two-player nonzero-sum differential game (Isaacs, 1965):

$$J_1(\psi_1, \psi_2) = \int_0^{t_1} (\phi_{01} + \pi\phi_{23} - \gamma^\star)\,\mathrm{d}t - \int_0^{t_2} \pi\phi_{13}\,\mathrm{d}t,$$

$$J_2(\psi_1, \psi_2) = \int_0^{t_2} (\phi_{02} + \pi\phi_{13} - \gamma^\star)\,\mathrm{d}t - \int_0^{t_1} \pi\phi_{23}\,\mathrm{d}t,$$

subject to Eqs. (1) and (2) with

$$u(t) = \psi_1(x(t), y(t)) \quad \text{and} \quad v(t) = \psi_2(x(t), y(t)).$$

The J_i's are both females' payoffs (their expected number of offsprings resulting from the considered patch, minus the cost associated to the time invested), as a function of their state-feedback strategies ψ_i's. The t_i's are the females respective residence time. As both females are assumed to be identical and to enter the patch at the same time, the game is said to be symmetric, which means: $J_1(\psi_1, \psi_2) = J_2(\psi_2, \psi_1)$. We shall conventionally let the subscript $-i$ refer to player i's opponent and stress that the ψ_i's are *functions* that map $(x_0, x_i, x_{-i}, y_{-i})$ to the decisions of each player, in terms of both oviposition and patch leaving decisions.

3.2.1. At last alone

For instance, the $\psi_i(x, 0)$'s (0 stands for $y_{-i} = 0$) are known as given by the classical diet selection theory (Charnov, 1976a; McNamara et al., 2001; Hamelin et al., 2007b). Indeed, once its opponent has gone, one faces a patch that contains two types of admissible resources: healthy hosts and those once-parasitized by the opponent, respectively, x_0 and x_{-i}. According to the classical diet selection theory, two scenarios may occur:

- either $\pi < \gamma^\star h$ and the optimal policy is to reject parasitized hosts,
- or $\pi \geqslant \gamma^\star h$ and the optimal policy is to accept them.

In both situations, the optimal patch-leaving time is ruled by Charnov's marginal value theorem, which states that the patch should be depleted until the abundance of acceptable resources drops to a given value: for any x, let

$$r(x_0, \mathsf{x}) = \frac{\gamma^\star \alpha}{(1 - \gamma^\star h)x_0 + (\pi - \gamma^\star h)\mathsf{x}},$$

- if $\pi < \gamma^\star h$ (only healthy hosts are depleted) then Charnov's patch leaving-rule corresponds to leave when $r(x_0, 0) \geqslant 1$,
- otherwise (parasitized hosts are also attacked) leaving when $r(x_0, x_{-i}) \geqslant 1$ is optimal. Under such a scenario, one can show that $r(x_0, x_{-i})x_{-i}$ is the proportion of hosts once-parasitized by female $-i$ that escape superparasitism after its departure.

From now on, we shall assume $\pi > \gamma^\star h$ as it can be shown that otherwise, a parasitized host should never be accepted under competition (the contrary would have been surprising).

3.2.2. Back to the game

It remains to be determined the evolutionarily stable pair of $\psi_i(x, 1)$'s (1 stands for $y_{-i} = 0$). Proceeding as in Hamelin et al. (2007b), we look for the best-response policy for a focal female against a strategy assumed to be adopted by its opponent: this in order to exhibit a strict and symmetric Nash equilibrium, as it corresponds to an ESS. More precisely, a Nash equilibrium $(\psi_1^\star, \psi_2^\star)$ is said to be symmetric here if both $\psi_i^\star$'s are obtained as the same function $\psi_i^\star(x, y) = \psi^\star(x_0, x_i, x_{-i}, y_{-i})$.

Assume that female 2 adopts a policy $\psi_2^\star(x, 1)$ which consists in

- playing $v = 1$ (attacking any admissible host encountered)
- and leaving when $r(x_0, x_2) \geqslant 1$.

In other words, assume that female 2 is prepared to wait for the departure of female 1 unless $r(x_0, x_2) \geqslant 1$: if it leaves, then its opponent also has to leave immediately. There is thus no superparasitism likely to occur after its departure, hence no subsequent loss of fitness to expect.

Throughout our reasoning, we shall refer to Fig. 1. The idea is the following: if the best-response to an opponent playing $\psi_2^\star$ leads to mutual superparasitism (notice that $u = v$ maintains $x_1 = x_2$ all along the trajectory followed) and to leave when reaching the intersection of the manifolds $r(x_0, x_1) = 1$ and $r(x_0, x_2) = 1$ (both females thus leave simultaneously) then this scenario actually corresponds to a confrontation $\psi_1^\star$ versus $\psi_2^\star$ and the pair $(\psi_1^\star, \psi_2^\star)$ is clearly a symmetric Nash equilibrium.

4. Reformulating the game as a control problem

Assuming that female 2 adopts $\psi_2^\star$ as a strategy and focusing on female 1, we are led to investigate a control

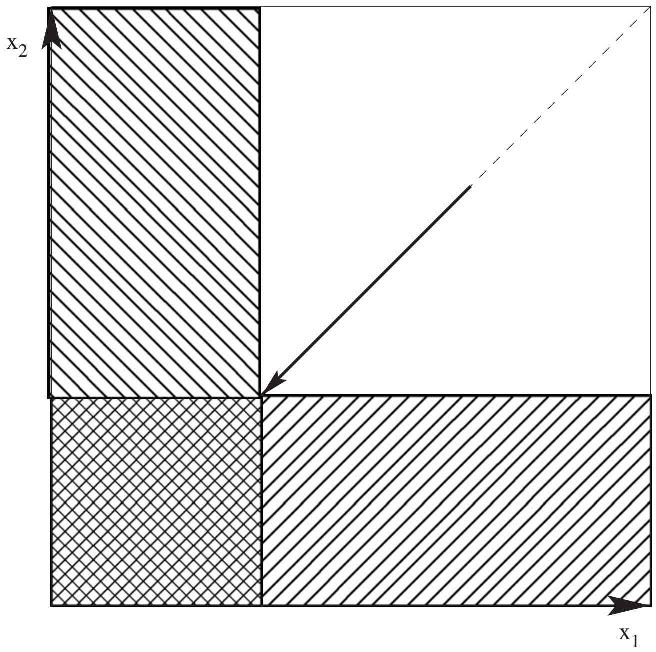

Fig. 1. This figure represents the plane (x_1, x_2). The vertical and horizontal lines respectively describe the manifolds $r(x_0, x_1) = 1$ and $r(x_0, x_2) = 1$. The cross-hatched regions correspond, respectively, to $r(x_0, x_2) \geqslant 1$ and $r(x_0, x_1) \geqslant 1$. The arrow represents the projection of the end of the trajectory mentioned in the body of the paper.

problem where Pontryagin's maximum principle (Pontryagin et al., 1962) can be called upon (with due care to the game context). Our aim is thus to maximize the following criterion, with respect to both $t^\star$ and u:

$$J = \int_0^{t^\star} L(x, u, v)\,\mathrm{d}t + K(x(t^\star)), \quad \text{with}$$
$$L = \phi_{01} + \pi(\phi_{23} - \phi_{13}) - \gamma^\star,$$

where v is actually fixed to 1, $t^\star$ is a free patch-leaving time such that

$$t^\star \leqslant \inf\{t \mid r(x_0(t), x_2(t)) \geqslant 1\}$$

and

$$K(x) \coloneqq \begin{cases} qk(x) & \text{if } r(x_0, x_1) < 1 \text{ and } r(x_0, x_2) < 1, \\ 0 & \text{otherwise}, \end{cases} \tag{3}$$

with $k(x) \coloneqq -\pi x_1[1 - r(x_0, x_1)]$. The terminal cost K represents, for the focal female, the possible loss of fitness due to superparasitism likely to occur after its departure (loss computed using Charnov's departure rule for its opponent according to the results recalled in Section 3.2.1).

By definition of $\psi_2^\star$, female 2 remains present up to female 1's departure. Hence $y_2 = 1$ all along the trajectory followed. The state variable y is thus obsolete; this is the reason why it is omitted.

It turns out that we can reduce the number of parameters via letting $\zeta = \gamma^\star h$ and $\omega = \alpha/h$ (this is equivalent to taking h as the time unit). Also, let $\mathcal{D}_1 = D_1/h = \omega + x_0 + ux_2$ and $\mathcal{D}_2 = D_2/h = \omega + x_0 + vx_1$ and their ratio be $\mathsf{R} \coloneqq \mathcal{D}_1/\mathcal{D}_2$.

Moreover, let $s(t)$ be an increasing function such that $\mathrm{d}t \eqqcolon qh\mathcal{D}_1\,\mathrm{d}s$ and denote $\mathring{x} \coloneqq \mathrm{d}x/\mathrm{d}s$,

$$\varphi_{01} \coloneqq x_0, \quad \varphi_{13} \coloneqq vx_1\mathsf{R},$$

$$\varphi_{02} \coloneqq x_0\mathsf{R}, \quad \varphi_{23} \coloneqq ux_2,$$

and our dynamics $\mathring{x} \eqqcolon f(x, u, v)$ become

$$\begin{cases} \mathring{x}_0 = -\varphi_{01} - \varphi_{02}, & x_0(0) = 1, \\ \mathring{x}_1 = +\varphi_{01} - \varphi_{13}, & x_1(0) = 0, \\ \mathring{x}_2 = +\varphi_{02} - \varphi_{23}, & x_1(0) = 0. \end{cases}$$

Also, let $\delta \coloneqq x_1 - x_2$. We have

$$\mathring{\delta} = \omega(ux_2 - vx_1)/\mathcal{D}_2, \quad \delta(0) = 0. \tag{4}$$

Hence, as $\delta(0) = 0$ and $v = 1$, the bisecting plane is a barrier in this problem; i.e. the trajectory clearly evolves in the part of the state-space where $x_1 \leqslant x_2$ and remains in the bisecting plane iff $u = 1$ all along the path followed. As a consequence, the discontinuity of $K(x)$ (not that of its gradient) could have been ignored in the criterion statement, see Eq. (3). Yet, it might have been misinterpreted, hence the non ambiguous formulation of Eq. (3).

Our criterion can now be expressed as follows:

$$\mathcal{J} = J/q = \int_0^{s^\star} \mathcal{L}(x, u, v)\,\mathrm{d}s + \mathcal{K}(x(s^\star)),$$
$$s^\star \leqslant \inf\{s \mid r(x_0, x_2) \geqslant 1\},$$

where $\mathcal{L} = \varphi_{01} + \pi(\varphi_{23} - \varphi_{13}) - \zeta\mathcal{D}_1$ and $\mathcal{K}(x) \coloneqq \min\{0, k(x)\}$.

Let λ be an adjoint vector. We have the following Hamiltonian:

$$\begin{aligned} \mathcal{H} &\coloneqq \mathcal{L}(x, u, v) + \langle \lambda, f(x, u, v) \rangle, \\ &= -x_0\lambda_0(1 + \mathsf{R}) + \lambda_1(x_0 - vx_1\mathsf{R}) + \lambda_2(x_0\mathsf{R} - ux_2) \\ &\quad + x_0 + \pi(ux_2 - vx_1\mathsf{R}) - \zeta\mathcal{D}_1. \end{aligned}$$

According to Pontryagin's maximum principle (Pontryagin et al., 1962), if a policy $u^\star(s)$ generating a trajectory $x^\star(s)$ is optimal, then there exists a continuous adjoint trajectory $\lambda(s)$ such that

$$\begin{cases} \mathring{\lambda} = -\nabla_x \mathcal{H}(\lambda, u^\star, x^\star), \\ \lambda(s^\star) = \nabla\mathcal{K}(x(s^\star)), \\ \mathcal{H}(s^\star) = 0, \\ \left| \begin{array}{l} \forall s \in [0, s^\star] \text{ where } u^\star(\cdot) \text{ is continuous}, \\ \mathcal{H}(\lambda(s), u^\star(s), x^\star(s)) = \max_{u \in [0,1]} \mathcal{H}(\lambda(s), u, x^\star(s)). \end{array} \right. \end{cases} \tag{5}$$

The last condition above translates into the switch-function $\sigma \coloneqq \partial\mathcal{H}/\partial u$:

$$\begin{aligned} \sigma = [&-\lambda_0 x_0 - \lambda_1 vx_1 + \lambda_2(x_0 - \mathcal{D}_2) + \pi(\mathcal{D}_2 - vx_1) \\ &- \zeta\mathcal{D}_2]x_2/\mathcal{D}_2 \end{aligned} \tag{6}$$

and the "bang-bang" optimal policy:

$$u^\star = \begin{cases} 1 & \text{if } \sigma > 0, \\ \text{any } u \in [0,1] & \text{if } \sigma = 0, \\ 0 & \text{if } \sigma < 0. \end{cases} \tag{7}$$

The singular case $\sigma = 0$ allows the focal female to either accept a host already parasitized by its conspecific or to reject it, indifferently.

As $\forall i \in \{0,1,2\}$, $\mathring{\lambda}_i = -\partial\mathcal{H}/\partial x_i$, we have the following adjoint equations:

$$\begin{aligned} \mathring{\lambda}_0 = {} & \lambda_0[1 + \mathsf{R} + x_0(1-\mathsf{R})/\mathcal{D}_2] \\ & - \lambda_1[1 - v x_1(1-\mathsf{R})/\mathcal{D}_2] - \lambda_2[\mathsf{R} + x_0(1-\mathsf{R})/\mathcal{D}_2] \\ & + \pi v x_1(1-\mathsf{R})/\mathcal{D}_2 - (1-\zeta), \end{aligned}$$

$$\begin{aligned} \mathring{\lambda}_1 = {} & -\lambda_0 v x_0 \mathsf{R}/\mathcal{D}_2 + \lambda_1 v \mathsf{R}(1 - v x_1/\mathcal{D}_2) + \lambda_2 v x_0 \mathsf{R}/\mathcal{D}_2 \\ & + \pi v \mathsf{R}(1 - v x_1/\mathcal{D}_2), \end{aligned}$$

$$\begin{aligned} \mathring{\lambda}_2 = {} & [\lambda_0 x_0/\mathcal{D}_2 + \lambda_1 v x_1/\mathcal{D}_2 + \lambda_2(1 - x_0/\mathcal{D}_2) \\ & - \pi(1 - v x_1/\mathcal{D}_2) + \zeta]u. \end{aligned}$$

Notice that the scenario $u = v = 1$ maintains $x_1 = x_2$ all along the trajectory followed. Therefore, it also maintains $\mathcal{D}_1 = \mathcal{D}_2$, thus $\mathsf{R} = 1$. Such a symmetry considerably simplifies the dynamics and the adjoint equations.

Indeed, assume that $u = v = 1$ and $x_1 = x_2 =: \xi$. Let then $\mathcal{D} := \omega + x_0 + \xi$, $\Lambda := \lambda_1 + \lambda_2$ and $\varsigma := \sigma/\xi$. It yields the following dynamics, Hamiltonian and switch-function,

$$\begin{cases} \mathring{x}_0 = -2x_0, & x_0(s^\star) =: x_0^\star, \\ \mathring{\xi} = x_0 - \xi, & \xi(s^\star) =: \xi^\star, \end{cases} \tag{8}$$

$$\mathcal{H} = -2x_0\lambda_0 + \Lambda(x_0 - \xi) + x_0 - \zeta\mathcal{D}, \tag{9}$$

$$\varsigma = [-\lambda_0 x_0 - \Lambda\xi - \lambda_2\omega + \pi(\omega + x_0) - \zeta\mathcal{D}]/\mathcal{D}, \tag{10}$$

and, lastly, the following adjoint equations:

$$\begin{cases} \mathring{\lambda}_0 = 2\lambda_0 - \Lambda - (1-\zeta), \\ \mathring{\Lambda} = (\Lambda + \zeta)w, \\ \mathring{\lambda}_2 = -\varsigma w. \end{cases} \tag{11}$$

In a similar fashion to Hamelin et al. (2007b), our aim in the present paper is to exploit this symmetry to integrate backwards the adjoint equations.

5. An equilibrium in pure strategies

In quest of a symmetric Nash equilibrium, we are interested to make clear whether a trajectory given by $u = v = 1$ and ending on the manifold $r(x_0, x_1) = 1$ would satisfy Pontryagin's necessary conditions, i.e. Eq. (5). We shall thus restrict our investigations to the bisecting plane, i.e. the manifold $x_1 = x_2 =: \xi$. Let us refer to the manifold $r(x_0, \xi) = 1$ (a line) as the intersection of the planes $x_1 = x_2$ and $r(x_0, x_1) = 1$, see Fig. 2.

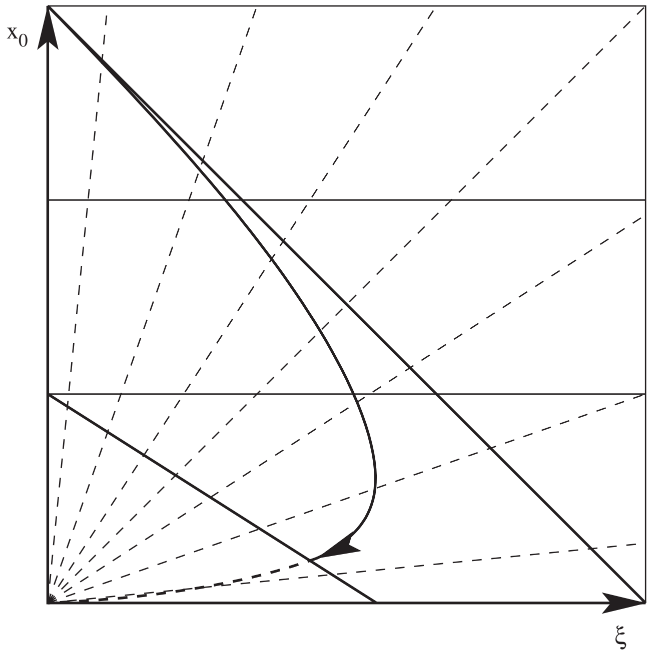

Fig. 2. This figure represents the projection of the bisecting plane $x_1 = x_2$ on the plane (ξ, x_0), ξ denoting either x_1 or x_2. The diagonal line corresponds to the boundary of the state space, i.e. to the line $x_0 + 2\xi = 1$. The other oblique line represents the terminal manifold $r(x_0, \xi) = 1$. The curve typically corresponds to the path followed when the dynamics are governed by the pair $(u = 1, v = 1)$. It starts from the point $(x_0 = 1, \xi = 0)$ and goes toward $(0, 0)$. The lower horizontal line corresponds to $x_0 = \zeta\omega/(1-\zeta)$. The upper horizontal line represents the manifold $x_0 = \omega\pi/(1-\pi)$.

A required preliminary to integrate backwards the adjoint equations is to characterize their boundary conditions, i.e. the optimal end-time.

5.1. At the end-time

As $\mathcal{K}(x)$ is not differentiable on the manifold $r(x_0, x_1) = 1$, the only information we have on the candidate final adjoint λ is that it belongs to the corresponding sub-differential, see Eq. (5). Thus no explicit expression of the Hamiltonian on the candidate terminal manifold $r(x_0, \xi) = 1$ allows us to directly address whether it can be zero, as required by Eq. (5). Nevertheless, Appendix A.1 shows that it cannot be zero elsewhere in the bisecting plane $x_1 = x_2$. In other words, a trajectory governed by the controls $u = v = 1$ has to end on the manifold $r(x_0, \xi) = 1$ to be optimal.

Moreover, Appendix A.1 shows that the plane $r(x_0, x_1) = 1$ is, at least locally, the relevant terminal manifold in the underlying control problem. Hence we can substitute the terminal cost $\mathcal{K}$ by a constraint which requires that the final state belong to the manifold $r(x_0, x_1) = 1$.

Let $\mathcal{M} = 0$, $\mathcal{M} := x_0(1-\zeta) + x_1(\pi - \zeta) - \zeta\omega$, be our terminal manifold. This translates into $\lambda(s^\star) = \nabla\mathcal{K}(x(s^\star)) + \kappa\nabla\mathcal{M}(x(s^\star))$, with $s^\star$ redefined as $s^\star := \inf\{s \mid$

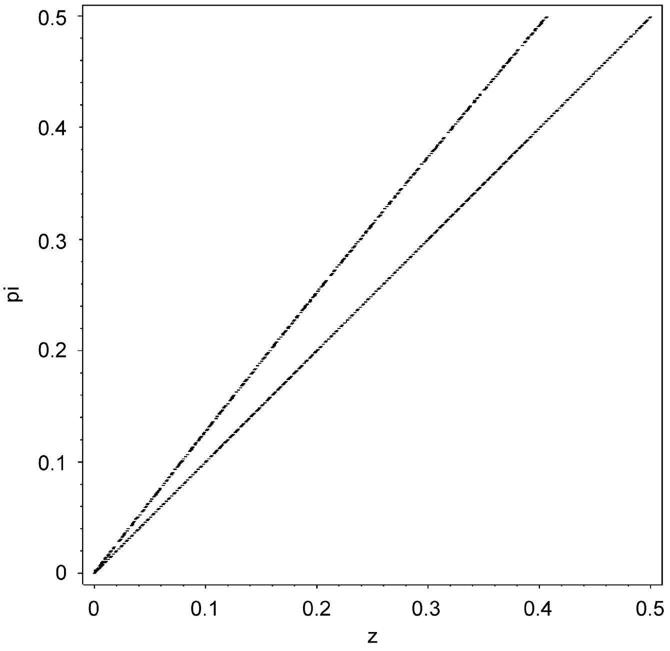

Fig. 3. This figure shows the manifolds $\pi = \bar{\pi}$ and $\pi = \zeta$ in the plane (ζ, π). As we assume $\pi - \zeta \geqslant 0$, the parameter space corresponds to the upper triangle. The region of uncertainty is the middle one.

$\mathcal{M}(x(s)) = 0\}$ and κ a normal to $\mathcal{M}$ given by $\mathcal{H}(x(s^\star)) = 0$, see Appendix A.2.

Last but not least, Appendix A.2 confirms that playing $u = 1$ against $v = 1$ just before leaving on the manifold $r(x_0, \xi) = 1$ indeed maximizes the Hamiltonian in the most part of the parameter space (ω, ζ, π). The region of uncertainty is plotted in Fig. 3 (the uncertainty is due to the absence of knowledge on the final x_0).

5.2. *Backwards from the end-time*

Our aim is now to integrate backwards the adjoint equations from any point of the terminal manifold $r(x_0, \xi) = 1$, this in order to see whether playing $u = 1$ against $v = 1$ satisfies Pontryagin's necessary conditions of optimality.

We saw in Section 5.1 that $\sigma(s^\star)$ is positive in the most part of the parameter space. Yet, there remains an uncertain region. First, we shall assume that $\sigma(s^\star) \geqslant 0$. Investigating the solution trajectory under such an assumption may allow us to more accurately delimit the "terra incognita" in the parameter space (as it may yield information on the final x_0, see Appendix A.2).

We shall thus let fixed the pair of controls $(u = 1, v = 1)$ while integrating backwards the adjoint equations, at least as long as σ remains positive. Indeed, a sign change of σ represents a technical obstacle, see Appendix D.1. Nevertheless, it does not mean that this approach is necessarily fruitless in terms of information on the game solution, as we shall see.

As long as σ remains positive, we have, according to Eq. (8), the following dynamics

$$\begin{cases} x_0(s) = x_0^\star \mathrm{e}^{2(s^\star - s)}, \\ \xi(s) = (x_0^\star + \xi^\star)\mathrm{e}^{(s^\star - s)} - x_0(s). \end{cases}$$

One sees that, under such dynamics, the ratio $\rho := \sqrt{x_0}/(x_0 + \xi)$ is invariant.

Eqs. (8), (9) and (10) yield

$$\mathring{\varsigma} = \varsigma + (1 - 2\pi)x_0/\mathcal{D}, \quad \varsigma(s^\star) =: \varsigma^\star. \tag{12}$$

One sees that, if $\pi = \frac{1}{2}$, ς keeps the sign of $\varsigma^\star$, assumed positive in this section. Hence there is no switch point for $\pi = \frac{1}{2}$. Moreover, we stress that as σ is strictly positive, this result is robust; i.e. it remains true at least for some π in a left neighborhood of $\frac{1}{2}$. Appendix D.2 gives an idea of what is likely to happen for values of π significantly lower than one-half.

As, for $\pi = \frac{1}{2}$, the trajectory is smooth and known to leave ρ invariant, one can easily determine the final x_0 as a function of the parameters of the model. Therefore, we are able to accurately characterize the region of validity of this scenario, as compared to Fig. 3. From Fig. 4, we see that, indeed, our result surely holds if $\zeta \leqslant 0.4$ (as previously observed in Fig. 3) but also in approximately one-half of the formerly uncertain region plotted in Fig. 3.

However, what happens to the right of the dividing line in Fig. 4 remains to be known. Notice that this line describes the manifold $\varsigma(s^\star) = 0$ in the parameter space. Interestingly, one sees from Eq. (12) that in such a case the switch function is zero all along the trajectory. This is not insignificant, as it corresponds to a bi-singular trajectory, *sensu* Hamelin and Bernhard (2007). In other words, it might happen that beyond this line equilibria involving mixed oviposition strategies arise.

6. Discussion

We addressed superparasitism as a differential game and showed that lies, in the most part of the parameter space, a strict and symmetric Nash Equilibrium (thus an ESS) in pure strategies. This provided that the probability π that superparasitism succeeds is close or equal to one-half (the upper bound). Nevertheless, this particular case is likely to be the most relevant one. As argued in Appendix B, a superparasitism success rate of one-half is a fair value under direct competition.

However, if for some biological reason this probability had to be considered significantly lower than one-half, it is likely (as it makes sense) that the strategies mentioned in Appendix D.2 are solution of the game. It consists in rejecting parasitized hosts until healthy hosts be depleted down to a given level under which any admissible host has to be accepted. However, it does not correspond to a myopic oviposition policy: this is the result of a trade-off between short-term stakes (competition for healthy hosts) and longer-term anticipation as (i) time is costly (in terms

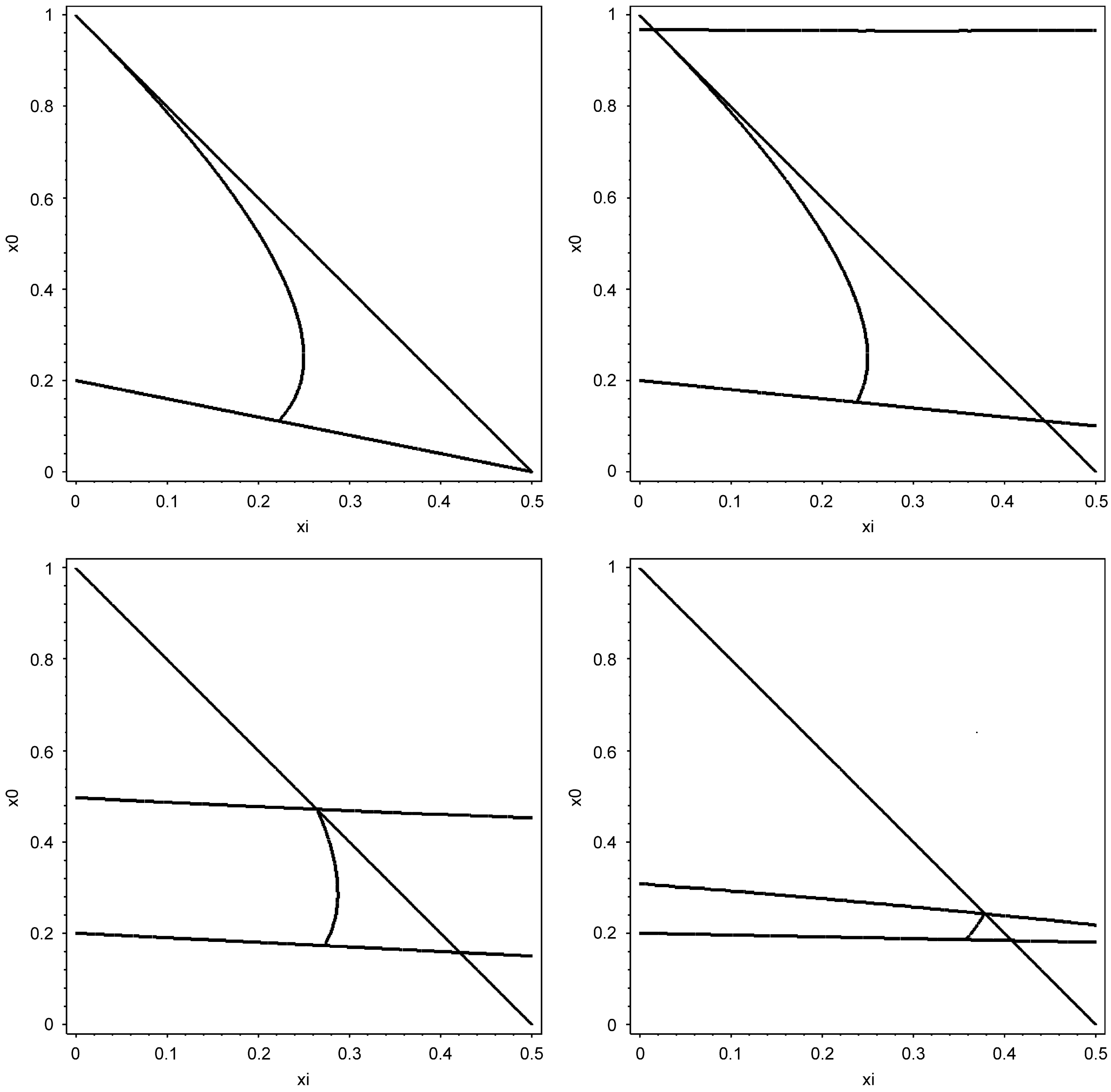

Fig. 4. This graph represents, in the parameter space (ζ, ω), the boundary where the switch-function, at the end-time, taken with $u = v = 1$, changes sign. In the larger region, the switch-function is positive.

of missed opportunities), (ii) one can loose fitness due to superparasitism that may occur after its departure.

For instance, let us come back to the case where superparasitism success rate is close to one-half. The strategic equilibrium consists, for each female, in attacking any admissible host encountered, upon arrival on the patch. Typically, a short-sighted strategy would consist in rejecting parasitized hosts first, as there are plenty of healthy hosts around. Let us attempt to formulate an explanation: as time is costly and parasitized hosts, after all, acceptable, they will be good to take when the patch will be further depleted. So why reject a host to accept it later? To focus on healthy hosts and thus take an advantage over the opponent? Is it really worthy? This was precisely the question addressed by this differential game. Such a non-myopic strategy already occurred in the classical diet selection game (Hamelin et al., 2007b), thus the outcome is not so surprising at first sight.

However, the novelty in the superparasitism game is that such a result holds whatever the parameters' values (even if short-term stakes *a priori* seem to prevail over longer-term ones). Our interpretation lies upon a component of the game that was not present in diet selection: the expected value of the best quality resource (healthy hosts) actually depends on the game outcome itself.

Therefore, if the game solution scenario leads healthy hosts to be attacked for the most part (as it arises if $\gamma^\star$ or α are close to zero), their resulting expected value is not much greater than that of an once-parasitized host: being selective then makes little sense. On the other hand, if the superparasitism success rate is really lower than one-half, the expected value of a healthy host remains as much greater; in this case rejecting parasitized hosts first makes sense.

To summarize, when π is close to one-half, whatever the parameters values, the difference between the expected value of a healthy host (which depends on the ESS itself) and that of a once-parasitized host, is, at equilibrium, never significant enough to make a selective oviposition policy worthy. Modelling such a situation as a dynamic game allowed us to capture such a fixed point.

Moreover, our model shows that assuming a myopic oviposition policy (as Haccou et al., 2003 do) is not necessarily the best, neither the simplest, possible approximation. However, for π significantly lower than one-half, the ESS oviposition policy is qualitatively close to the myopic one, as it also consists in switching from rejecting to accepting parasitized hosts.

Also, our model shows that superparasitism does not necessarily imply a war of attrition, or mixed (randomized) patch-leaving strategies, as predicted by Haccou et al. (2003). As argued in Appendix C, it seems that the main difference between Haccou et al. (2003)'s model and most relevant lies in the fact that we find convenient (and quite realistic, see below) to set a limit to one attack per host per female. In Haccou et al. (2003)'s model there is no such a limit. Therefore, as any host lost by superparasitism can be recovered, the incentive to stay on the patch is greater. Hence the occurrence of a war of attrition. Nevertheless, assume that $\pi = \frac{1}{2}$; parasitizing a host already parasitized by both contestants would yield an offspring to the focal female with a probability $\frac{2}{3}$, hence a gain of $\frac{1}{6}$. Therefore, if $\frac{1}{6} < \zeta < \frac{1}{2}$ (quite good environment), our model prevails as a third attack would be unworthy.

Let us come back to the real life. Visser (1992) and coworkers performed laboratory experiments with *Leptopilina heterotoma* and *Asora tabida*, after having predicted a switch in the oviposition policy and a common, deterministic, patch-leaving time. Although having continuously observed several females depleting a patch, the question of a possible switching oviposition strategy was not addressed; the hosts were afterwards dissected to count the number of parasitoid eggs. Making statistics on the oviposition dynamics when several females deplete the patch indeed seems herculean. Concerning patch-leaving times, however, Wajnberg et al. (2004) and Goubault et al. (2005) observed a polymorphism in the population; in other words, it seems to corroborate Haccou et al. (2003)'s model, which predicts a war of attrition, or mixed strategies. However, in both experiments, parasitoid species (*Trissolcus basalis* and *Pachycrepoideus vindemmiae*) were precisely selected from their quarrelsome character and it is well known that foraging under such interference (as defined in Section 2) leads to a war of attrition (Sjerps and Haccou, 1994a; Hamelin et al., 2007c). It would be interesting to perform experiments with peaceful species to make clear whether observed mixed patch-leaving strategies result from interference or superparasitism *per se*, which may also result in a war of attrition (Haccou et al., 2003).

Finally, future planned work includes:

- Further investigating the region where mixed oviposition strategies possibly arise, i.e. to the right of the dividing line in Fig. 4. We plan to use an approach similar to that developed in Hamelin and Bernhard (2007).
- Solving the asynchronous, or asymmetric, game, at least locally. In other words, is our result robust to a slight initial asymmetry ($x_1(0) \neq x_2(0)$)?

Addressing these issues requires to look beyond the bisecting plane $x_1 = x_2$. This was not in the scope of the present paper whose ambition was restricted to exploiting the simplifications offered by the symmetry $x_1 = x_2$. An advanced analysis is thus needed to go further in understanding the superparasitism game.

Acknowledgments

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Appendix A. On the boundary conditions

A.1. Characterizing the terminal manifold

Let H be a final hamiltonian candidate in any point of state space restricted to $x_1 \leqslant x_2$ and $r(x_0, x_1) < 1$; i.e. define

$$\mathsf{H}(x, u, v) := \mathcal{L}(x, u, v) + \langle \nabla k(x), f(x, u, v) \rangle.$$

Let also $\mu := \nabla k$. We have

$$\begin{cases} \mu_0 = \partial k(x)/\partial x_0 = -\pi x_1 (1-\zeta) r^2/(\zeta\omega) < 0, \\ \mu_1 = \partial k(x)/\partial x_1 = -\pi x_1 (\pi - \zeta) r^2/(\zeta\omega) - (1-r)\pi < 0, \\ \mu_2 = \partial k(x)/\partial x_2 = 0. \end{cases}$$

Assume that the dynamics are governed by the pair $(u = 1, v = 1)$. The trajectory thus remains in the bisecting plane $x_1 = x_2 =: \xi$. All along the following reasoning, we shall refer to Fig. 2.

Let ξ be the switch-function associated with H. Substituting the λ_i's by the μ_i's in Eqs. (8) and (9) yields

$$\mathsf{H}(x,1,1) = -2\mu_0 x_0 + \mu_1(x_0 - \xi) + \mathcal{L}(x,1,1)$$

and $\tilde{\xi} = \pi - \zeta > 0$. Hence if a trajectory governed by $u = v = 1$ had to end, in the bisecting plane, before reaching the manifold $r(x_0, \xi) = 1$ (as one cannot go further), then, in the vicinity of the final state, playing $u = 1$ against $v = 1$ would indeed satisfies Pontryagin's necessary conditions, i.e. Eq. (7).

Let us first focus on the limit of H on the manifold $r(x_0, \xi) = 1$, say $\tilde{\mathsf{H}}$. We get

$$\tilde{\mathsf{H}}(x,1,1) = \left(\frac{(1-\pi)\pi x_0}{\pi - \zeta}\left[1 - \frac{1-\zeta}{\zeta\omega}x_0\right]\right) > 0,$$

as having both $x_0 = \zeta\omega/(1-\zeta)$ and $r(x_0, \xi) = 1$ is impossible under the assumed dynamics.

We then calculate

$$\left\langle \begin{pmatrix} x_0 \\ \xi \end{pmatrix}, \begin{pmatrix} \partial \mathsf{H}(x,1,1)/\partial x_0 \\ \partial \mathsf{H}(x,1,1)/\partial \xi \end{pmatrix} \right\rangle$$

$$= x_0[1 - (\pi - \zeta)] + \xi(\pi - \zeta) > 0.$$

Thus, by continuity (along the radial field in Fig. 2), for all x in the region of the bisecting plane where $r(x_0, \xi) < 1$, $\mathsf{H}(x,1,1) > 0$.

Hence leaving in the part of the bisecting plane where $r(x_0, \xi) < 1$ cannot be optimal. Moreover, as H is nothing else than $\partial\mathcal{J}/\partial s$, it is clear that one has to go up to reaching $r(x_0, \xi) = 1$ for leaving (one cannot go further), provided that the optimal trajectory remains in the bisecting plane. Nevertheless, as $\tilde{\mathsf{H}}(x,1,1)$ is strictly positive (as well as the associated switch-function $\tilde{\xi}$), by continuity, it remains so in the neighborhood of $r(x_0, \xi) = 1$. This assertion is, with respect to the underlying problem, relevant in the restriction of the state space given by $x_1 \leqslant x_2$ and $r(x_0, x_1) \leqslant 1$.

Furthermore, in the region of the bisecting plane where $\mathcal{K} = 0$, we clearly have $\partial\mathcal{J}/\partial s = \mathcal{L}(x,1,1) < 0$. Indeed, as mutual superparasitism, along a symmetric trajectory, results in a pure waste of time (as compared to no superparasitism from anyone), $\mathcal{L}(x,1,1)$ is clearly lower than $\mathcal{L}(x,0,0)$ which is negative below the line $x_0 = \zeta\omega/(1-\zeta)$. Thus, by continuity, $\mathcal{L}(x,1,1) < 0$ at least in the neighborhood of $r(x_0, \xi) = 1$. This assertion is, with respect to the underlying problem, relevant in the restriction of the state space given by $r(x_0, x_1) > 1$ and $r(x_0, x_2) \leqslant 1$.

To summarize, the two latter assertions imply that from any point in the neighborhood of the line $r(x_0, \xi) = 1$, the plane $r(x_0, x_1) = 1$ is a terminal manifold for the underlying problem.

A.2. *Characterizing the final adjoint-vector and controls*

The new formulation introduced in Section 5.1 yields

$$\begin{pmatrix} \lambda_0 \\ \lambda_1 \\ \lambda_2 \end{pmatrix} = \kappa \begin{pmatrix} \partial\mathcal{M}/\partial x_0 = 1 - \zeta \\ \partial\mathcal{M}/\partial x_1 = \pi - \zeta \\ \partial\mathcal{M}/\partial x_2 = 0 \end{pmatrix},$$

where κ is a scalar.

We choose κ such that $\mathcal{H} = 0$, as required by Eq. (5) ($\mathcal{H}$ being given by Eq. (9)). It yields $\kappa = \mathcal{L}(x,1,1)/[2(1-\zeta)x_0 - (\pi - \zeta)(x_0 - \xi)]$. Can we assert that σ is, as required by Eq. (7), positive?

Using the fact that $r(x_0, \xi) = 1$ allows us to express σ as a function of x_0 alone, with respect to ξ. Let $\Sigma = \varsigma[\zeta\omega + (1-\pi)x_0](\pi - \zeta)\mathcal{D}$ be a function characterizing the sign of σ on the terminal manifold. We have $\Sigma = ax_0^2 + bx_0 + c$ with $a = (1-\pi)[(\pi-\zeta)^2 + \zeta(1-\zeta)]$, $b = \omega(1-\pi)(\pi^2 - 3\zeta\pi + \zeta^2)$ and $c = \zeta\omega^2\pi(\pi - \zeta)$. As the final x_0 is not known yet as $r(x_0, \xi) = 1$, we at least know that $x_0 \in [0, \zeta\omega/(1-\zeta)]$, our aim is to provide a *lower bound* $\bar{\pi}$ such that $\forall \pi \in [\bar{\pi}, 1/2]$, $\forall x_0 \in [0, \zeta\omega/(1-\zeta)]$, $\sigma \geqslant 0$. It thus consists in solving $\Delta(\pi) := b^2 - 4ac = 0$. However, $\Delta(\pi) = 0$ is a quintic equation thus no closed form expression of $\bar{\pi}$ can be expected. Nevertheless, one can easily notice that $\bar{\pi}$ does not depend on ω and thus only depends on ζ. We see from Fig. 3 that σ is surely positive in a wide part of the parameter space, being potentially negative for small $(\pi - \zeta)/\zeta$.

Appendix B. Further discussion of some assumptions

(ii) We are interested in time-limited rather than egg-limited parasitoids (see the article of van Baalen (2000) for more than a review on the topic) although egg-limitation, when it occurs, certainly plays a role in terms of oviposition policy. A fixed egg cost (such as the physiological cost of egg load renewal per unit) could easily be included in the model. However, it consists in adding another (after $\gamma^\star$, see Section 3.1) difficulty quantifiable parameter in the model. Such an extension is thus envisaged after time-limitation alone will have, hopefully, been fully understood.

(vii) Synchronous arrival of the competing females allows us to investigate a game where the contestants face symmetric situations; i.e. the state of the patch is initially the same for both females. We shall address the dissymmetric scenario in a later paper.

(ix) The limitation to one attack per host per female is a modelling shortcut which allows us to consider the game in perfect information (as opposed to Haccou et al. (2003)'s approach, see Appendix C). Also, although selfsuperparasitism might be relevant under competition, such an efficiency would be biased in our model as we arbitrarily limit the number of attacks that can undergo a host and, for that matter, we ignore any egg cost; i.e. it would suffice to lay two eggs per host to prevent further superparasitism. Making these (strong) assumptions seems to be the simplest way to capture the main component of superparasitism, as compared to predation: the fact that a resource is never definitely acquired.

(x) We consider the probability that superparasitism succeeds as a constant. However, the time elapsed since the first oviposition is likely to have an influence on the outcome, the first offspring developing in the host having progressively a higher probability to survive (the contrary can also happen, depending on the instar of the resident larvae). Nevertheless, the developmental time-scale and that of patch-time-allocation can be uncoupled, as development requires much more time. Thus, neglecting development, one-half seems to be a really fair approximation under direct competition. Let us nevertheless allow for $\pi \leqslant \frac{1}{2}$ (we allow for a possible advantage for the first egg laid) in order to be able to make a sensitivity analysis to this parameter afterwards. In our model, assuming $\pi \geqslant \frac{1}{2}$ (if ever it was biologically relevant) would yield an artefact due to our limitation in the number of attacks that can undergo a host; it may happen in this case that the value of a parasitized host be (irrelevantly) better than the expected one of a healthy host.

Appendix C. The relation with Haccou et al. (2003)'s model

Our model deviates in several ways from Haccou et al. (2003)'s one. This section reviews and argues each of these deviations in order to justify their plurality.

C.1. On the number of attacks that can undergo a host

Haccou et al. (2003) allow the hosts to be attacked an infinite number of times, thus address the game in imperfect information. As argued in Section B, we introduce a limitation to one attack per host per female, as it allows the game to be addressed in perfect information. We stress that this is probably the most relevant difference between both models, as our dynamics are qualitatively similar up to a dilution effect (see Section C.2) and the oviposition policy (myopic or not) has, in our model, no influence in terms of patch leaving strategies (deterministic vs. stochastic, see Section C.3).

C.2. On a dilution effect in the dynamics

Notice that our dynamics, Eqs. (1) and (2), cannot be formally related to those of Haccou et al. (2003), who do not consider the handling time explicitly. Our dynamics are very similar to theirs if we set $h = 0$ in our model. But, if we do so, then, in our model, the vulnerability of a healthy host is no longer lowered by the fact that females may also attack healthy hosts. Such a dilution effect appears, in our model, for $h > 0$. Haccou et al. (2003) capture this component of the dynamics without introducing a handling time by lowering the probability per unit time that a healthy host be attacked when females also accept parasitized hosts. However, this probability is assumed constant thus independent of the ratio ‘heathy hosts to parasitized hosts’, although it will unavoidably be progressively inverted; i.e. the dilution effect, starting from zero, surely increases as healthy hosts are being depleted. This is the reason why we keep the dynamics described by Eqs. (1) and (2), despite the fact that it will be impossible to rigorously compare our results afterwards.

C.3. On a myopic oviposition policy

Haccou et al. (2003) assume that female parasitoids adopt a myopic oviposition policy; it means that they assume host-acceptance decisions as maximizing an instantaneous gain, not the total fitness expected *in fine* from the current patch. Moreover, this instantaneous gain is calculated according to the current values of the resources, ignoring the fact that a host is more or less likely to be superparasitized afterwards, according to the (*a priori* unknown) ESS itself.

In order to compare our results, arises the question of the implications that such an assumption would have in our model, in terms of patch-leaving times. Interestingly, it turns out that the result of Appendix A.1 also implies is that if females were, as in Haccou et al. (2003)'s model, assumed to maximize their instantaneous gain rate L, they would switch from rejecting to accepting parasitized hosts when x_0 drops below $\omega\pi/(1-\pi)$, see Fig. 2. As $\pi > \zeta$, the trajectory would go through the manifold $x_0 = \omega\pi/(1-\pi)$ before reaching $r(x_0, \xi) = 1$. Hence, in our model, which limits the number of attacks per host, females maximizing this instantaneous gain rate would be expected to leave simultaneously, at a deterministic time.

Appendix D. On a possible switch in the oviposition policy

D.1. No bilateral maximum principle

As a complement to Section 5.2, let us mention a technical point. It may happen that σ becomes negative while integrating backwards the adjoint equations. This implies that the focal female has to switch from rejecting parasitized hosts to accepting any admissible host against a non-switching female accepting any admissible host anyway. But if such a switch in the oviposition policy prevails for the focal female, by symmetry, it also prevails for its opponent. In such a situation, one needs to assume a state-feedback switching policy for the opponent. This induces an endogenous discontinuity in the dynamics, thus in the adjoint variables (as this is a game, see e.g. Bernhard, 1977) that compels one to characterize the switch manifold around the bisecting plane to continue backwards through this fence. Contrary to Hamelin et al. (2007b), the simplifying symmetry that makes it conceivable to integrate analytically the adjoint equations is dual and does not only lie on the

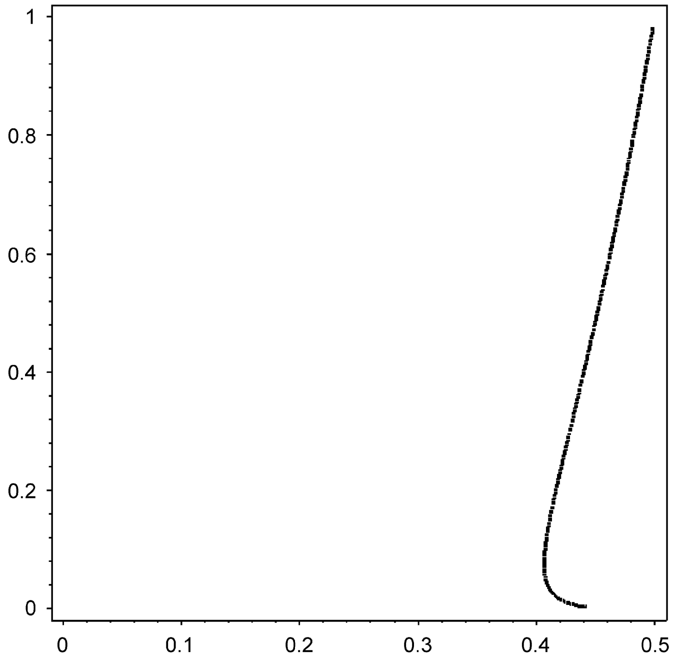

Fig. A1. This figure shows the switch-manifolds in the bisecting plane of the state space (ξ, x_0) for different values of π; respectively, $\pi = \{\frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \frac{1}{5}\}$. We took $\omega = 1$ and $\zeta = \frac{1}{6}$. Are also represented, the boundary of the state space, i.e. the line given by $x_0 + 2\xi = 1$, the terminal manifolds given by $r(x_0^*, \xi^*) = 1$, and the corresponding conjectured trajectories.

controls but also the state variables x_1 and x_2. Therefore, we are cloistered in the bisecting plane. This restriction prevents us from using the synthesis technique out of the bisecting plane, as is necessary to characterize the possible jump discontinuity on the adjoint variables. This is the reason why if such a switch-point appears, we shall be constrained to stop our backwards integration there.

D.2. *A conjecture*

Let $z := x_0 + \xi$. Using both the fact that $\dot{z} = -z$ and that $x_0/z^2 = x_0^\star/z^{\star 2} = \rho^2$, one can easily check that the following expression of σ is indeed solution of the differential equation (12), Section 5:

$$\varsigma = \varsigma^\star \frac{z^\star}{z} - (1 - 2\pi)\frac{x_0^\star}{z z^\star} \times \left[\frac{z^2 - z^{\star 2}}{2} - \omega(z - z^\star) + \omega^2 \ln\left(\frac{\omega + z}{\omega + z^\star}\right)\right],$$

where $\varsigma^\star$ is given by Section 5.1. Moreover, using both the fact that the dynamics let ρ invariant and the relation $r(x_0^\star, \xi^\star) = 1$ allows us to express ς as a function of the current patch state x only.

We are thus able to characterize a switch-manifold in the state space as done in Fig. A1. We conjecture that the evolutionarily stable scenario, starting from $(\xi = 0, x_0 = 1)$, consists (i) in following, with $u = v = 0$, the boundary of the state space (given by $x_0 + 2\xi = 1$) down to a possible intersection with the switch-manifold and (ii) in taking $u = v = 1$ down to the terminal manifold $r(x_0, \xi) = 1$, where both females are invited to leave. However, for π close to $1/2$, no switch-manifold occur in the state space thus, as proved earlier, the game trajectory is given by taking $u = v = 1$ from the initial point down to the terminal manifold.

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