

## Hide or fight? The competitive evolution of concealment and encapsulation in parasitoid-host associations

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I employ a mathematical model integrating the population and co-adaptive dynamics of an insect host and its specialist parasitoid wasp to investigate the competitive evolution of two forms of host resistance: concealment from adult parasitoid location and encapsulation of parasitoid eggs. When only one form of resistance is permitted to evolve, concealment always evolves to frequencies equal to or higher than encapsulation. When both forms of resistance evolve, the outcome depends on the capacity of the parasitoid to evolve counter-measures. Evolution of the host in the presence of the most virulent parasitoid clone results in no differences between the equilibrium frequencies of the two forms of resistance, unless host clone densities are somehow unequally perturbed. When the parasitoid is allowed to co-evolve, the frequency of hosts concealing themselves exceeds the frequency of those capable of encapsulating parasitoid eggs. At equilibrium, there is generally a negative correlation between resistance measures in the host population, and a positive one for counter-measures in the parasitoid population. The mechanism driving the asymmetries between the two forms of host defence is the loss of more reproductive effort by parasitoids when the host encapsulates as compared to when an encounter is missed due to concealment. I predict that hosts should pay greater costs to maintain concealment as compared to encapsulation when they are relatively common and/or parasitism rates relatively low; that is, when regulation of the host population tends to be influenced by other density dependent forces.

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A tantalizing possibility is that evolution of host resistance to parasites may occur at different, characteristic points in individual-level interactions. Given diverse forms of energy constraints and fitness trade-offs, the expression of different types of host response could be expected to vie with one another for expression. Analogous in some ways to classical notions of competition, sets of phenotypic characters may be at odds with one another at a given point in the interaction, or at two or more points in time. Such competitive evolution of phenotypic characters has received little attention (Frank 1993, Dieckmann and Law 1996, Abrahamson and Weis 1997).

Insect host-parasitoid associations constitute model systems for investigating adaptive evolution. They combine notions of both predation and parasitism, in that the result of successful parasitism is always the death of the host, but in some cases the host has the recourse to recover from parasitism via its immune response. Host and parasitoid individuals interact in diverse and complex ways (Godfray 1994), which can be broken down into three principal steps: (1) adult parasitoid search/host concealment, (2) parasitoid attack/host defence, and (3) juvenile parasitoid development/host encapsulation.

The reciprocal evolution of the first of these steps has been analysed employing an integrated model of

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population and adaptation dynamics (Hochberg and Holt 1995). The evolution of host concealment from parasitoid search was found most likely to occur when: (1) the explicit cost of host protection is lower than that of the parasitoid's counter-measure, (2) the parasitoid's power of population increase is intermediate in magnitude, (3) there are low, fixed levels of heterogeneity in parasitism, and (4) background host regulation is weak.

Godfray and Hassell (1991) investigated the evolution of the third of these steps (i.e., encapsulation of the parasitoid) under circumstances where only the host could evolve. They distinguished two types of encapsulation: (1) all or none, where the probability of host recovery is constant, regardless of the number of parasitoid eggs, and (2) dosage-dependent, where the probability decreases with the number of eggs harboured per host. They found that when encapsulation is all-or-none in form, the host strain with a combination of a high probability of encapsulation and high power of increase persisted alone. When host density dependence was added to their model, a polymorphism in encapsulation abilities could arise.

I develop and analyse a population-adaptation model for host-parasitoid associations with the aim of determining which form of host resistance to parasitism has the greater propensity to evolve given equal intrinsic costs: concealment or encapsulation? I discuss the generality of the response to this question with regards to other exploiter-victim interactions.

## The ecological model

Before developing the co-evolutionary model, I describe the underlying ecological model which drives the populations of both species. The type of system envisaged is of an insect host with discrete and non-overlapping generations and a monophagous insect parasitoid with generations synchronized to those of its host. This kind of interaction has enjoyed substantial development in the theoretical parasitoid literature (for review of models, including the essentials presented below, see Hochberg and Holt unpubl.).

The difference equations are of a host at juvenile density  $N_t$  at the beginning of generation  $t$ , and its parasitoid at density  $P_t$ , female adults at some fixed attack interval during host development. The model explicitly assumes that self-limitation in the host population acts at an earlier stage in the host's life-cycle than does parasitism.

The model is

$$N_{t+1} = \lambda N_t g\{N_t\} f\{N_t, P_t\}, \quad (1)$$

$$P_{t+1} = c N_t g\{N_t\} (1 - f\{N_t, P_t\}). \quad (2)$$

The parameter  $\lambda$  is the maximum inter-generational change in the host population, and obviously  $\lambda > 1$  if the host is to persist in the presence of the parasitoid. The parameter  $c$  is the average number of adult parasitoids surviving per parasitized host.

Eqs (1) and (2) are characterized by two complex functions, each of which encapsulate realistic biological phenomena in simple mathematical formulae.

First,  $g\{N_t\}$  is the fraction of hosts escaping density-dependent mortality other than that inflicted by the parasitoid. It is assumed that the host is self-regulated at a stable equilibrium in the absence of the parasitoid; this enables a more lucid analysis of how the parasitoid may or may not disrupt the system.

The function employed is

$$g\{N_t\} = [1 + \theta N_t]^{-1}, \quad (3)$$

where the constant  $\theta$  reflects the per capita level of host self-limitation. This model yields compensatory, stabilising density-dependence, such that in the absence of the parasitoid the host population monotonically approaches an equilibrium at  $(\lambda - 1)/\theta$ .

Second,  $f\{N_t, P_t\}$  is the proportion of juvenile hosts escaping parasitoid attack. I assume that concealment acts to lower the effective search area of the parasitoid, and that encapsulation acts to lower the effective population of viable parasitoid eggs.

$f\{N_t, P_t\}$  is

$$f\{N_t, P_t\} = \exp\left(\frac{-a_c a_e P_t}{1 + a_c N_t g\{N_t\}/\eta}\right), \quad (4)$$

where  $a_c$  is the reduction in search area of the parasitoid (assumed otherwise to be equal to unity) due to concealment,  $a_e$  is the reduction in parasitoid eggs surviving to juveniles due to encapsulation, and  $\eta$  is the maximum number of hosts encounterable per female parasitoid when the  $a_c N_t g$  hosts exposed to attack are numerous. Note that host defences via concealment and encapsulation are assumed to act independently of one another, and both are constrained to be in the interval (0, 1).

## Ecological results

Moderate levels of concealment or encapsulation promote host population persistence, but each with different relationships to maximum parasitoid population growth (reflected by  $\eta$ ) (Fig. 1). The main qualitative difference between the two forms of resistance is that, for sufficiently low  $\eta$ , locally stable populations are

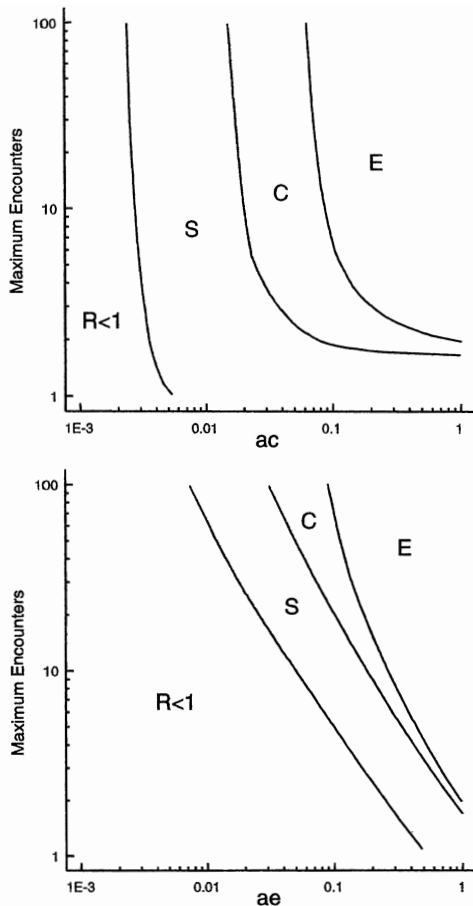


Fig. 1. Outcomes of the ecological model as a function of level of (a) host concealment  $ac$ , and (b) host encapsulation  $ae$ , and the maximum number of encounters with exposed hosts ( $\eta$ ). Numerical simulation studies were carried out by introducing the parasitoid at low densities into a system with the host at its ecological equilibrium. The model was then iterated until either (1) the parasitoid failed to invade the system (area  $R < 1$ ), or (2) the host and/or parasitoid population dropped below an arbitrary density of  $10^{-9}$ , indicating extinction (area  $E$ ), or (3) both host and parasitoid populations did not change by more than  $10^{-7}$  of their values for 100 consecutive generations, indicating equilibrium stability (area  $S$ ), or (4) conditions (2) and (3) were not met for more than 10 000 generations, indicating non-equilibrated populations (area  $C$ ). See Table 1 for parameter values.

more likely for hosts resisting by concealment as compared with those employing encapsulation (Fig. 1). This occurs because parasitoids conserve part of their reproductive capacity by redirecting it away from concealed hosts, whereas they squander it in encounters with encapsulating hosts. Fig. 1 shows that for any given level of host resistance, the parasitoid has a greater impact on host dynamics for concealment as compared to encapsulation.

Table 1. Parameter values kept constant throughout this study.

Parameter	Symbol	Value
Number of clones	$n_e, n_c$	10
Scaling constants	$\hat{a}_c, \hat{a}_e$	1
Host power of increase	$\lambda$	5
Intraspecific competition	$\theta$	0.004
Parasitoid adults emerging per host	$c$	1

### The co-evolutionary model

The behaviour of the ecological model rests on constant parameters for host resistance and parasitoid virulence. The co-evolutionary model developed below considers selection on two phenotypic characters in the host, each promoting resistance at a different point in the host's life-cycle, and two counter-measures in the parasitoid, each opposing the respective measures of host resistance. I assume that hosts are divided into a  $n_c \times n_e$  array of clonal populations, each with a specific potential to be concealed from ( $ic$ ), and to encapsulate ( $ie$ ), parasitoids from each of a corresponding array of  $n_c \times n_e$  parasitoid clones with counter-measures  $jc$  and  $je$ , respectively, against concealment and encapsulation (Fig. 2). Frank (1993, 1994) has developed similar models for host-parasite interactions.

### Hosts surviving parasitism

$a_c$  is determined by the simple difference between the rank of parasitoid clones for anti-concealment ( $jc$ ) and host clones for concealment ( $ic$ ),

$$a_c \{ic, jc\} = \frac{\hat{a}_c}{n_c} (jc - ic + 1), \quad (5)$$

as long as  $jc \geq ic$ ; otherwise,  $a_c = 0$ .  $\hat{a}_c$  is a scaling constant restricted to the range (0, 1).

Similarly, parasitoid density in eq. (4) is now scaled by the function  $a_e$ , whence

$$a_e \{ie, je\} = \frac{\hat{a}_e}{n_e} (je - ie + 1), \quad (6)$$

if  $je \geq ie$ , else  $a_e = 0$ . The constant  $\hat{a}_e$  scales the relation, and  $n_e$  is the number of encapsulation/anti-encapsulation classes in both species.

The fraction of hosts of clone ( $ic, ie$ ) escaping parasitism is given by a modification eq. (4),

$$f_{ic,ie} = \exp \left\{ - \left[ \sum_p \left( \frac{a_e a_c P}{1 + \frac{g}{\eta} \sum_h a_c N} \right) \right] \right\}. \quad (7)$$

I use the notation  $\Sigma_h$  for the summation over all host clones and  $\Sigma_p$  for the same over all parasitoid clones.

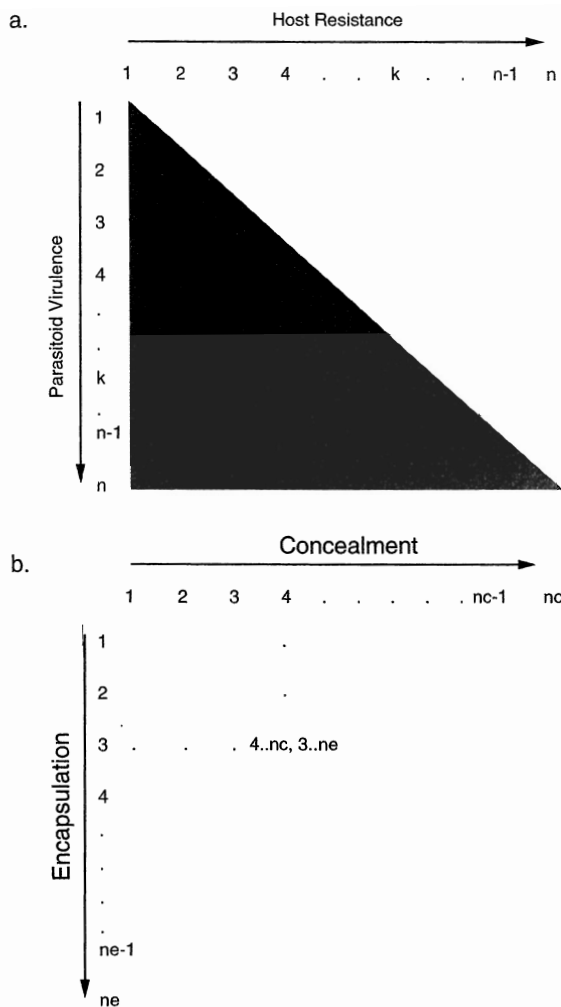


Fig. 2. Schematic diagram of the co-evolutionary model for (a) the case of  $n$  clones of host resistance and  $n$  clones of parasitoid virulence, and (b)  $n_c$  potentials of host concealment and  $n_e$  potentials of host encapsulation. In (a) parasitoids of any given virulence potential  $k$  can parasitize any host of resistance potential  $k$  or less, with increasing efficacy as the difference between parasitoid and host clones increases. (b) shows the example of the parasitoid clones with virulence potentials which can successfully parasitize a host clone of concealment potential 4 and encapsulation potential 3.

### Costs

Concealment, encapsulation and their counter-measures come at constitutive costs to the host and parasitoid clones. By 'costs' I mean reductions in the reproductive values of hosts and parasitoids in the absence of any density dependent interaction. These costs are deducted independently of one another from the host's finite rate of increase as

$$\lambda_{ic,ie} = \lambda - \varepsilon_{ic}ic - \varepsilon_{ie}ie, \quad (8)$$

where  $\lambda$  is the maximum (i.e., cost free) finite rate of

increase, and  $\varepsilon_{ic}$  and  $\varepsilon_{ie}$  are the costs of maintaining potentials  $ic$  for concealment and  $ie$  for encapsulation for clone  $(ic, ie)$ .

Similarly, for the parasitoid

$$c_{jc,je} = c - \varepsilon_{jc}jc - \varepsilon_{je}je, \quad (9)$$

where  $c$  is the maximum (cost free) number of parasitoid progeny produced per parasitized host, and  $\varepsilon_{jc}$  and  $\varepsilon_{je}$  are the costs of maintaining potentials  $jc$  for concealment and  $je$  for encapsulation.

### Population changes

The densities of any host clone  $(ic, ie)$  and any parasitoid clone  $(jc, je)$  in generation  $t + 1$  are

$$\dot{N}_{ic,ie} = \lambda_{ic,ie} N_{ic,ie} g f_{ic,ie} \quad (10)$$

$$\dot{P}_{jc,je} = c_{jc,je} g \sum_h [N(1-f)\Phi_{jc,je}]. \quad (11)$$

where  $\dot{N}$  and  $\dot{P}$  are shorthand for host and parasitoid densities, respectively, in generation  $t + 1$ .

Host density dependence is assumed to be influenced equally, per capita, by all host clones and to affect each equally, where

$$g = \left[ 1 + \theta \sum_h N \right]^{-1}. \quad (12)$$

The function  $\Phi_{jc,je}$  is the fraction of hosts of clone  $(ic, ie)$  expected to produce progeny of parasitoid clone  $(jc, je)$ , once both types of host defence are taken into account. I assume that there are no differences in within-host competition between parasitoid clones and that encounters with the host are independent of one another. This means that the proportion of hosts of a given clone  $(ic, ie)$ , successfully parasitized by parasitoids of clone  $(jc, je)$  is simply the relative frequency of the intensity of parasitism of that clone. This frequency,  $\Phi_{ic,ie,jc,je}$ , is the term in parentheses of eq. (7), divided by the term in square brackets of eq. (7), or

$$\Phi_{ic,ie,jc,je} = \frac{a_c \{ic, jc\} a_e \{ie, je\} P_{jc,je}}{-\ln[f_{ic,ie}] \left( 1 + \frac{g}{\eta} \sum_h a_c N \right)}. \quad (13)$$

### Simulation methods

Preliminary numerical simulations revealed a considerable diversity of model behaviours. To limit the dynamical possibilities, the following procedure was adopted. [Clearly, other procedures will be necessary to more fully explore the range of outcomes produced by this or similar models]. For all simulations, the host was set to

its carrying capacity (assuming costs to resistance, this is  $N_{1,1} = (\lambda - 1)/\theta$ ). In generation 1 of any simulation the remaining host clones (all  $N_{ic,ie \neq 1}$ ) are introduced at very low densities ( $10^{-9}$ ). In this same generation, either one (in simulations where the parasitoid does not co-evolve) or all (parasitoid does co-evolve) parasitoid clones were simultaneously introduced into the system at this same low density. Rather than make explicit assumptions about how mutation and migration act as seeds of clonal diversity, and how clonal extinction erodes this, I assumed that any clone present in the system in generation 1 persisted thereafter at densities of at least  $10^{-9}$ ; that is, any densities falling below this level in an arbitrary generation  $t$ , were re-initialized to this level in generation  $t + 1$ . This permitted the possibility of re-invasion of low frequency clones at any time during the simulation, as could occur if mutation or immigration were in progress. The system was run for 5000 generations, and the relative frequencies of host clones in the final generation recorded.

Because stable polymorphisms often resulted, it was sometimes difficult to visually determine the relative frequencies of the two forms of resistance. Therefore, the measure of evolution used below is the mean per capita investment in a given form of resistance (or countermeasure for the parasitoid). For instance, the per capita investment of the host in concealment is simply

$$\sum_h \varepsilon_{ic} (ic - 1) N_{ic,ie} / \sum_h N.$$

## Evolutionary results

I only present results of numerical simulations resulting in constant host and parasitoid populations after 5000 generations of simulation. Studies of temporal patterns in the population densities of the different clones will be deferred to a subsequent study.

### Evolution of a single form of resistance

The following patterns dominated numerical simulation studies (Fig. 3):

(1) For identical costs, the host invests the same or more in concealment than in encapsulation.

(2) Higher potential encounter rates ( $\eta$ ) are accompanied by greater investment in resistance. For sufficiently high  $\eta$ , levels of both types of resistance converge on the same level of investment (not shown).

(3) Investment in resistance is equal or greater in co-evolutionary systems than in non-co-evolutionary ones (in which only the most effective parasitoid clone is present). In the examples of Fig. 3, co-evolution makes a sizable difference to the outcomes of resistance via concealment (cf. Figs 3a, c), but no difference to those involving encapsulation (cf. Figs 3b, d).

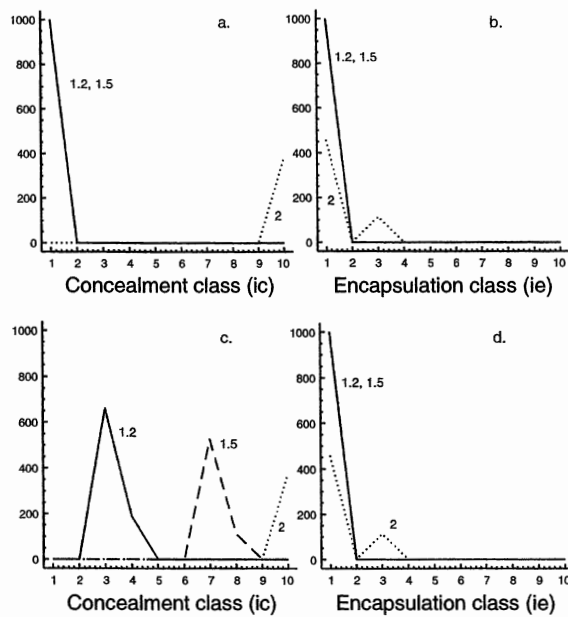


Fig. 3. Equilibrium densities of host clones when only one form of resistance evolves. (a) Host concealment when only host evolves. (b) Host encapsulation when only host evolves. (c) Like a, but parasitoid co-evolves. (d) Like b, but parasitoid co-evolves. Numbers next to curves refer to the potential encounter rate with hosts,  $\eta$ . In cases where the parasitoid does not co-evolve (a and b), only the most virulent clone of the parasitoid is present ( $jc = 10$  or  $je = 10$ ). Parameter values:  $\varepsilon_{ic} = \varepsilon_{ie} = 0.2$ ,  $\varepsilon_{jc} = \varepsilon_{je} = \varepsilon_i/5$ .

### Co-evolution of concealment and encapsulation

Enabling both forms of resistance to evolve simultaneously yields the following results (Fig. 4):

(1) Each form of resistance persists at the same or lower levels of investment than in the respective cases where they evolved independently of one another (cf. curves  $\eta = 2$  in Figs 3a, b with axes  $ic$  and  $ie$ , respectively, in Figs 4c and d). This indicates that the two forms of resistance compete for expression through their costs.

(2) When the host evolves on its own, the frequency distributions of concealment equal those of encapsulation (Figs 4a, c, e; but, see discussion of Fig. 5 below). This indicates that there is no intrinsic difference between the two forms of resistance when invading the system simultaneously. Note for comparison that when the host evolves alone with a single form of resistance at its disposal, investment is equal or greater in systems with concealment than in those with encapsulation (Fig. 3).

(3) For sufficiently (but not too) pronounced costs, host clones express one or the other (but not both) forms of resistance (Figs 4a, c). As costs decrease, there is an increasing propensity to find host clones simultaneously expressing both forms of resistance (Fig. 4e). At sufficiently high costs, the most susceptible host clone persists alone.

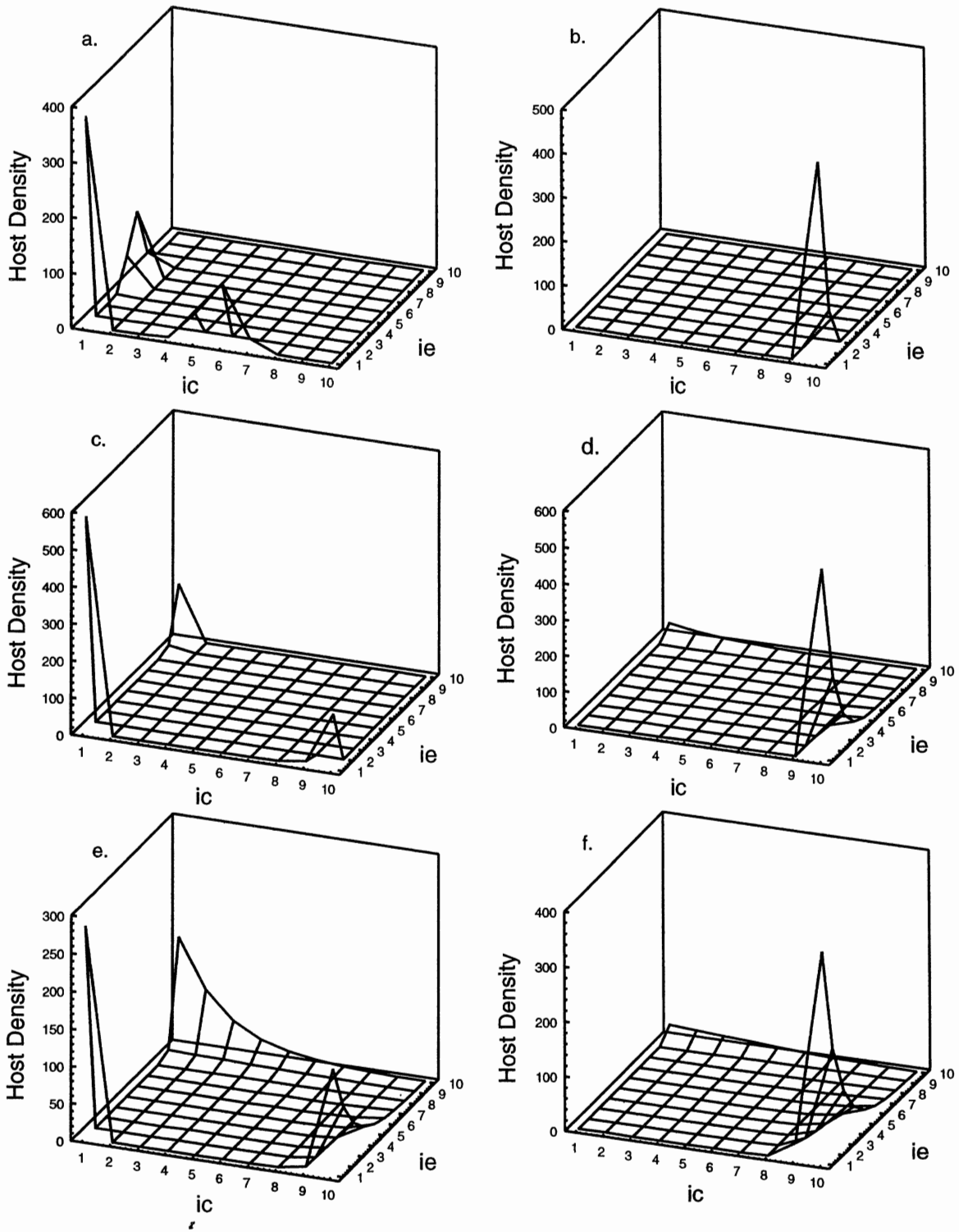


Fig. 4. Equilibrium densities of hosts according to their concealment (*ic*) and encapsulation (*ie*) potentials when the parasitoid (a, c, e) does not co-evolve and (b, d, f) co-evolves. a and b,  $\varepsilon_{ic} = \varepsilon_{ie} = 0.1$ , c and d,  $\varepsilon_{ic} = \varepsilon_{ie} = 0.02$ , and e and f  $\varepsilon_{ic} = \varepsilon_{ie} = 0.001$ . Other parameters:  $\eta = 2$  and  $\varepsilon_{jc} = \varepsilon_{je} = \varepsilon_i/5$ .

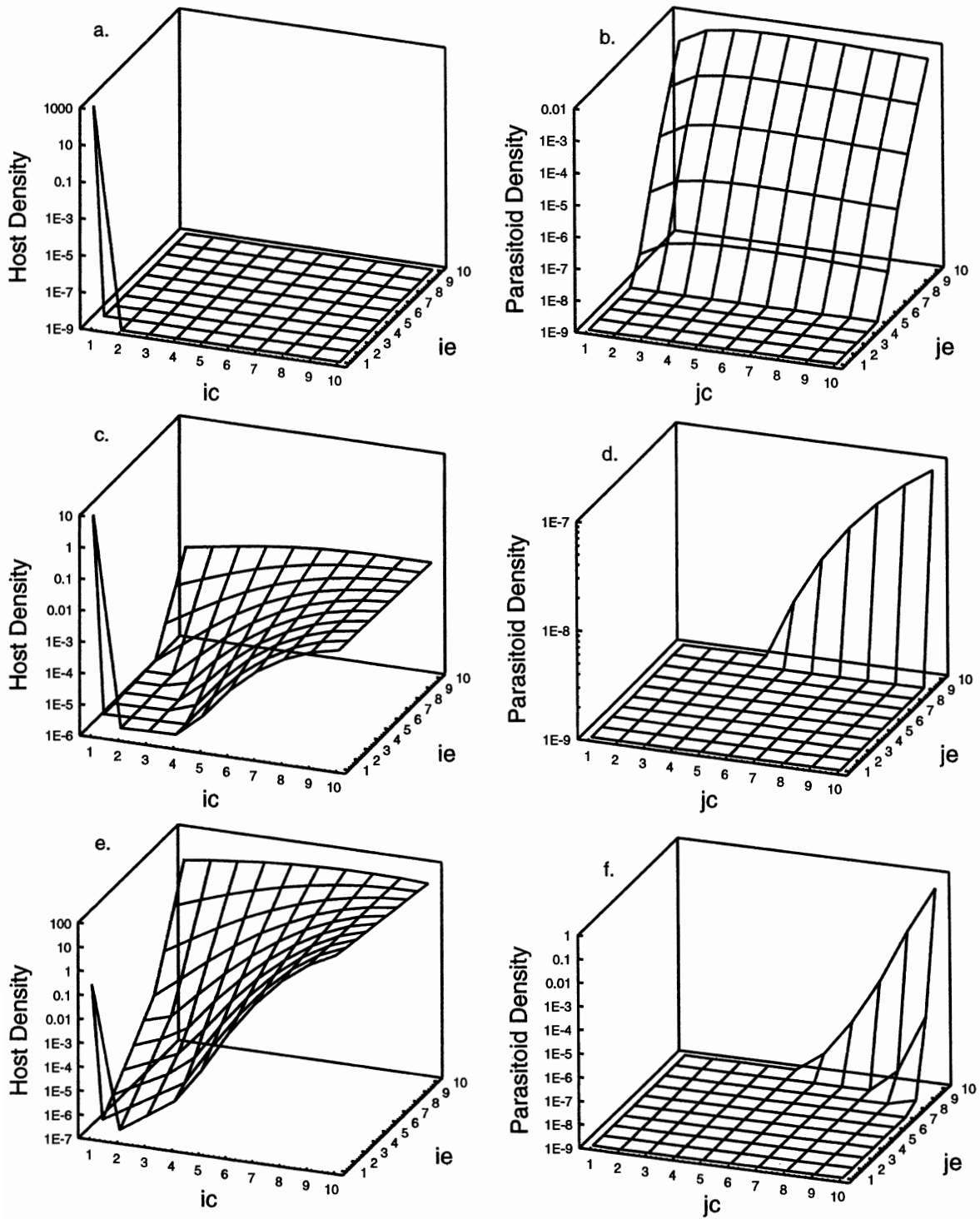


Fig. 5. Temporal replacement of host and parasitoid clones over the first 100 generations of the simulation. Only the most susceptible host clone is present in significant densities in generation 25 (a). At this time, a wave of parasitoid invasion of the most virulent anti-encapsulation clones (b; generation 25) is beginning to sweep from the least virulent anti-concealment clone to the most virulent anti-concealment clone (d; generation 50). As this wave sweeps, a surface of the most resistant host clones invade, with concealing clones slightly more abundant than encapsulating ones (c; generation 50). These gradually give way to the most resistant clones for either concealment or encapsulation (e; generation 100). Eventually the most virulent parasitoid clone for both counter-measures excludes all other clones; this is nearly achieved in f at generation 100. In subsequent generations, the host evolves to the outcome shown in Fig. 4d. Parameters:  $\eta = 2$ ,  $\varepsilon_i = 0.02$ , and  $\varepsilon_j = 0.004$ .

(4) When the species co-evolve, the host invests more in concealment than in encapsulation (Figs 4b, d, f). The investments in the two forms of resistance become increasingly similar as  $\eta$  increases (not shown).

(5) As long as costs for the measures and counter-measures are approximately equal (i.e.,  $\varepsilon_{ic} \approx \varepsilon_{ie}$  and  $\varepsilon_{jc} \approx \varepsilon_{je}$ ) and costs of counter-measures to the parasitoid are not too high, the parasitoid persists monomorphically at the highest virulence levels for both counter-measures (i.e.,  $jc = je = 10$ ). Numerical studies suggest that as costs to both parasitoid counter-measures are increased, the parasitoid invests more in anti-encapsulation than in anti-concealment and the asymmetry in investment between concealment and encapsulation is amplified (not shown).

## Discussion

The central prediction of this study is that the investment a host puts into concealment from adult parasitoids should generally exceed that reserved for encapsulating parasitoid eggs. This bias can be understood as follows. From the host's perspective, any encounter with the parasitoid will end in death if the host does not somehow resist at some point in the interaction. As long as there are no pathogenic effects of the parasitoid on the host between the points of attack and encapsulation (see below), a concealed host has exactly the same fitness as an encapsulating one. The situation is very different from the parasitoid's perspective, however. The parasitoid experiences smaller fitness losses in missing an opportunity to parasitize a concealed host than when it loses an offspring in an encapsulating host. When hosts are abundant and/or parasitism rates low, missed encounters due to host concealment can be easily redirected to unparasitized, susceptible hosts. The evolutionary consequence of this for the parasitoid is to put a premium on evading host encapsulation (an intriguing twist to the 'life-dinner principle'; Dawkins and Krebs 1979), with the host investing more in concealment than encapsulation at equilibrium.

However, when the costs to parasitoid counter-measures are sufficiently low, this evolutionary tendency of the parasitoid proves to be ephemeral. In the example shown in Fig. 5, clones virulent against encapsulating hosts eventually give way to those virulent to both forms of resistance. In contrast, host individuals exhibit *either* concealment or encapsulation, but rarely both. These contrasting patterns arise simply because successful defence requires that only one form of resistance operates efficiently; whereas when counter-measure costs are low, it behoves parasitoid individuals to be virulent against all prevalent forms of host resistance, given that they are usually expressed by different individual hosts.

Below, I discuss the results in the light of co-evolution between host and parasitoid.

## Host discrimination

The findings presented here can be interpreted in terms of two contrasting evolutionary options to the parasitoid: discriminating and avoiding protected hosts versus evolving counter-measures to overcome host protection.

First take concealed hosts. The parasitoid individual has two main evolutionary alternatives to increase its fitness: either it passively discriminates (i.e., never comes into contact with concealed hosts) or it evolves counter-measures to locate them. The cost of the former depends on host density, the prevalence of parasitism in the host population, and the frequency of concealing hosts. At high densities/low parasitism/low frequencies of concealment, passive discrimination is not costly because the queued parasitoid egg can be redirected into an exposed host. At low host densities/high parasitism/high frequencies of concealment, it is more probable that the redirected egg will encounter a competing juvenile within an exposed host and perish as a consequence of within-host competition. In this latter case, the parasitoid should put equal weight on evolution of counter-measures to concealment and encapsulation.

Now imagine a situation where the host defends directly against adult parasitoid attack via behavioural or morphological adaptations (not considered in the model presented here). Discrimination of such protected hosts may be possible, but will generally mean that the parasitoid actually expends time and/or energy in so doing. Somewhat similar to the passive discrimination of concealed hosts considered in the present study, such active discrimination will be (transiently) favoured over counter-measures to foil host defence if the cost of active discrimination is slight and there is a good chance that the queued parasitoid egg can safely develop in another host individual.

Finally, take encapsulating hosts. Because they cannot be discriminated in any straightforward way, the parasitoid's evolutionary response is limited to evading encapsulation itself (a manifestation of the 'false target effect'; Weis and Kepelinski 1994).

Given that discrimination of encapsulating hosts is either impossible or extremely costly, and that the cost of actively discriminating defensible hosts should obviously exceed the virtual absence of costs of passively discriminating concealed hosts, I would predict the following: the investment the host puts into concealment should exceed those of defence against adult parasitoid attack and that these two, in turn, should exceed frequencies of encapsulation.



### Other factors and what we (do not) know at present

There are three other factors which may contribute to concealment being more prevalent than encapsulation in host-parasitoid associations. First, as alluded to above, any pathogenic effect of parasitism on the host prior to encapsulation will tend to select for defence via concealment (Hochberg and van Baalen unpubl.). Sources of pathogenicity that select for early defence could include secondary infections due to injury following parasitoid oviposition or host feeding by adult parasitoids. Second, if concealment is an evolutionary product of insect host-plant interactions themselves, then it will be maintained and possibly reinforced by the parasitoid at a smaller cost than would be the case if concealment was a response to the parasitoid alone. Third, even when exposed and unparasitized hosts are rare, the prevalence of concealment should exceed encapsulation if the parasitoid has alternative host species at its disposal. These alternative hosts provide targets for the parasitoid to redirect its offspring when missing encounters with concealed hosts. It is tempting to predict greater concealment as the host range of a parasitoid increases, but the complexity of other ecological and evolutionary factors associated with the exploitation of multiple host populations precludes any generalisations until such models are explored in detail.

There is one notable factor which could bias frequencies of successful resistance towards encapsulation (opposite to the result observed here). If the probability of a parasitoid egg being encapsulated is a function of the number of eggs laid per host (i.e., 'dosage-dependent' encapsulation), then parasitoids which would otherwise be encapsulated can escape when occurring within super-parasitized hosts (Y. Carton, L. Kraaijeveld pers. comm.). This will tend to put a break on the evolution of parasitoid counter-measures to host encapsulation, inflating its population frequency. Again, one should be cautious with this interpretation until models are developed.

Unfortunately, data are very scarce concerning within- and between-population variabilities of insect defences (Hawkins et al. 1987, Weis et al 1992 and papers cited therein, Kraaijeveld 1994), and so tests of the theory presented here are not yet possible. Host protection from parasitism via concealment within plant tissues is a widespread phenomenon (Hawkins 1994), whereas encapsulation ability appears to be rarer (M. Bouletreau and J. van Alphen pers. comm.). Moreover, parasitoids are known to employ a wide range of counter-measures to encapsulation (Godfray 1994: 235–244, Whitfield 1994), and certain specialisations to locate concealed hosts (recently e.g., Hedlund et al. 1996; see Godfray 1994: Chapter 2). It is important to insist that until manipulative experiments and comparative analyses are conducted on these two forms of

resistance, the jury is out as to which dominates in insect herbivore populations and why.

### Extension to predators, pathogens and parasites

The present study proposes that there is an evolutionary premium for the parasitoid to reduce host resistance at that point in the interaction where the former's fitness is most engaged. Although it remains to be verified, this basic result should apply to a range of other enemy-victim interactions. However, the qualitative type of defence may differ in response to qualitatively different types of natural enemies. For instance, herbivorous hosts could protect themselves by either structural concealment within plant tissues against the tactile search that many parasitoids employ, or via chimeric chemicals against olfactory-guided search by parasitoids. One may expect the relevant form of first defence to be camouflage or hiding against visually searching predators, and a second line of defence to be fleeing. Finally, morphological or physiological forms of first defence may be relevant in cases of passive forms of transmission, employed by many parasites and pathogens.

Predator-prey systems differ importantly from parasitoid-host associations in that reproduction is not tightly associated with actual victim encounter. This could mean that the relevant fitness measure in a missed predation attempt for the predator is survival rather than actual reproduction (as assumed in the parasitoid model). Ostensibly, predators risk their survival more when attacking than when stocking prey, even if the relative hazard will often be slight. Somewhat analogous to the parasitoid scenario, I would expect selection pressure on predators to be biased towards reducing a prey's physical defence (assuming prey are abundant). Unlike hosts, however, prey risk injury when attacked even if they successfully defend their lives. This should act to inflate camouflage, hiding or fleeing as compared to physical defence. The net result of reciprocal selection in predator-prey systems should therefore be biases towards successful camouflage, hiding and/or fleeing, as opposed to physical defence.

The competitive evolution of host resistance to parasites and pathogens (such as helminths, microsporidia, viruses, bacteria, fungi and protozoa) is likely to be too complex for the theory developed here to apply in the simple ways outlined above. Here are four reasons. First, many pathogens and parasites multiply within their hosts and therefore both their fitnesses and those of their hosts are co-evolutionarily labile after infection has occurred (e.g., Antia et al. 1994). The parasitoids modelled in this study *always* kill their host as a consequence of successful development. Second, any within-host genetic heterogeneity of parasites (in cases

of multiple infections) potentially modulates the evolution of virulence (e.g., van Baalen and Sabelis 1995). Within-host competition between clones in the present model was assumed proportional to overall parasitism pressure (once both forms of host resistance had acted) by each competing clone (eq. 13); no account was made for the evolution of within-host competition and exploitation (Godfray 1994). Third, costs for barriers to infection and subsequent parasite proliferation may be sub-additive (due to positive genetic correlations). This could mean greater equivalence in the evolution of the two forms of resistance. Fourth, many parasites and pathogens are either vectored by an intermediate organism, or their transmission is promoted by an intermediate host. It is unclear how adding other organisms to a two-species co-evolutionary model would change the course of evolution.

### Future directions

The present study demonstrates one type of intrinsic difference between two different forms of host defence against parasitoids. Three notable points deserve further analysis.

First, it must be stressed that the results presented here are based on dynamically stable systems and on equal initial densities of all active clones (excepting the most susceptible host clone). In unstable systems, numerical simulations suggest that the host may invest more, transiently, in encapsulation as compared to concealment. In stable ones, simulations show that when initial densities of encapsulation clones sufficiently exceed those of concealment clones, the host may invest more in the former at equilibrium (especially if the costs to parasitoid counter-measures are low). This indicates that multiple, locally stable equilibria potentially exist under certain model conditions. It should be interesting to see how additional population and adaptive dynamic factors such as environmental stochasticity, mutation, and migration may influence the host's relative investment.

Second, concealment and encapsulation were both modelled as constitutive forms of defence. A more realistic model would take into consideration a likely induced component to encapsulation; that is, that most or all of the energetic cost associated with encapsulation is paid only when the host is parasitised. Moreover, simulations were limited to only a few cases of cost symmetry, and of cost functions. Frank (1993, 1994) has presented arguments for why the behaviour of co-evolutionary models should depend importantly on the shape of resistance/virulence functions based on quantitative phenotypic characters.

Third, no account was made for within-generation dynamics of parasitoid foraging. One relevant problem here involves parasitoid phenology. If the parasitoid population attacks hosts over an extended period in

time, then parasitoids emerging and effecting their attacks early will be under selection pressure to avoid encapsulation, whereas those emerging and attacking subsequently should be under more equivalent pressures to counter either encapsulation or concealment. Thus, if the time of parasitoid emergence is sufficiently variable and heritable, one may expect the maintenance of high levels of individual to individual variation for counter-measures to host defences. Another issue concerns parasitoid species assemblages, where the theory developed here would predict that superior within-host competitors (Mackauer 1990) should tend to evolve more sophisticated counter-measures to host encapsulation than inferior competitors. This is because the superior competitor can successfully redirect its offspring into more hosts than can inferior ones, simply because its offspring will tend to win regardless of whether the juvenile of another species is present or not.

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