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Asymmetric larval mobility and the evolutionary transition from siblicide to nonsiblicidal behavior in parasitoid wasps

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The widespread evolution of gregarious development in parasitoid wasps presents a theoretical challenge because the conditions under which larval tolerance can spread in an intolerant population are very stringent (the individual fitness of larvae developing together must increase with clutch size). Recent empirical work has suggested that gregarious development can arise through the loss of larval mobility rather than through the gain of tolerant behavior. Using analytical genetic models, we explored whether decreased mobility presents a less stringent route to gregariousness than the gain of tolerance. Reduced mobility can spread under a wide range of conditions. The critical condition for the spread of immobility is much less stringent than that for larval tolerance. In contrast with previous models of tolerance, the criterion for the spread of a rare immobility allele is independent of any bias in the sex ratio and the likelihood of single sex broods. Superparasitism increases the stringency of the criterion for the spread of immobility, whereas double killing relaxes the criterion. Tolerance can subsequently replace immobility if there is any cost to the retention of fighting ability. Our results suggest that asymmetric larval mobility may explain many instances of the evolution of gregarious development. *Key words:* clutch size, Hymenoptera, larval behavior, parent–offspring conflict, population-genetic models. *[Behav Ecol 14:182–193 (2003)]*

Parasitoid wasps (Hymenoptera) lay eggs in or on the bodies of other arthropods. The developing wasps feed on the host, eventually killing it. Parasitoids can be classified as either solitary or gregarious (Godfray, 1994). Solitary species are characterized by having larvae that attempt to kill brood mates, including siblings, until only one individual remains to consume the host. Many solitary species have larvae with formidable mandibles (Quicke, 1997; Salt, 1961). Rivals are eliminated by physical attack in a series of fights (or potentially by physiological suppression) (Godfray, 1994). The relentless nature of lethal fighting has led to it being dubbed "ultra-siblicide" (Mock and Parker, 1997). In contrast, gregarious species have larvae that successfully develop together and are generally regarded as being nonsiblicidal.

One consequence of the siblicide of solitary larvae is that it may prevent a parent from achieving its optimum clutch size. This is an example of the evolutionary phenomenon of parent–offspring conflict, in which the optima for genes expressed in an adult and its progeny differ (Alexander, 1974; Godfray, 1995; Trivers, 1974). The evolution of parent–offspring conflict (Trivers, 1974) was originally framed in the context of inclusive fitness theory (Hamilton, 1964a,b). Many of the important assumptions of inclusive fitness models are often violated (Grafen, 1984; Michod, 1982). In particular, the assumption of weak selection is not valid within the context of the siblicidal behavior of solitary wasps (Rosenheim, 1993). The evolution of siblicide in parasitoids has previously been examined within the framework of explicitly genetic models (Godfray, 1987; Rosenheim, 1993).

The initial models for the evolution of siblicide in parasitoid wasps demonstrated that the condition for a nonsiblicidal allele to invade a population of siblicidal individuals is very stringent: the fitness of tolerant individuals must initially rise with clutch size (Godfray, 1987). Tolerance could potentially spread in a fighting population only if very large clutches are laid by females (between 10 and 20 eggs depending on the precise details of the model and assuming a decline in individual fitness with increasing clutch size for tolerant larvae) (Godfray, 1987, 1994). Given such a formidable requirement, the solitary state might be irreversible. The behavior of solitary parasitoids has been cited as an example of directionally biased evolution, with siblicidal fighting being a locally absorbing state (Harvey and Partridge, 1987; Williams, 1992). These models also demonstrated that populations with small, gregarious broods are vulnerable to invasion by an intolerant (siblicidal) allele and led to the speculation that species with small gregarious broods (consisting of broods of up to four tolerant larvae) should be extremely rare (Godfray, 1987).

The phylogenetic distribution of solitary and gregarious behavior strongly suggests that the solitary state is ancestral (Mayhew, 1998a) and species with small, gregarious broods are widespread (Mayhew, 1998b; Mayhew et al., 1998). The recent challenge has been to demonstrate mechanisms that may facilitate the transition from solitary to gregarious behavior. Earlier models have focused on sex ratio bias (Godfray, 1987; Ode and Rosenheim, 1998) and single-sex broods (Rosenheim, 1993), phenomena widely associated with many species of parasitoids. These factors can marginally relax the conditions for a tolerant allele to invade an intolerant population. However, the levels of individual fitness required in multiple clutches are still relatively high.

Previous models assumed that tolerant larvae could not fight and would always be found and hence killed by any intolerant larvae if present. Thus, the solitary (intolerant) and the gregarious (tolerant) states constitute a dichotomy without intermediate behavioral phenotypes. This assumption has recently been tested. Empirical evidence from multiparasitism experiments with the solitary *Anaphes victus* Huber and the gregarious *Anaphes listronoti* Huber (two closely related sympatric sister species of Mymaridae endoparasitoids) demonstrated that gregarious larvae can retaliate and

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Table 1
Outcomes of matings and the subsequent fights within broods involving a rare immobility allele (clutch size = 2: *G* = immobility allele)

		Outcome fighting within broods			Fitness of survivors with the rare allele	
	P (Brood)	P (2 *G*/*Gg*)	P (1 *G*/*Gg*)	P (0 *G*/*Gg*)	*f*(2)	*f*(1)
G × *gg* mating						
Gg Gg	1/4	1	0	0	2×1/4	0
g g	1/4	0	0	1	0	0
Gg g	1/2	0	1/2	1/2	0	1/4
Gg × *g* mating						
Gg Gg	1/16	1	0	0	2×1/16	0
gg gg	1/16	0	0	1	0	0
G G	1/16	1	0	0	2×1/16	0
g g	1/16	0	0	1	0	0
Gg gg	1/8	0	1/2	1/2	0	1/16
Gg g	1/8	0	1/2	1/2	0	1/16
Gg G	1/8	1	0	0	2×1/8	0
G gg	1/8	0	1/2	1/2	0	1/16
G g	1/8	0	1/2	1/2	0	1/16
g gg	1/8	0	0	1	0	0

successfully fight. When both a gregarious larva and a solitary larva were placed together in a host, the gregarious larva had an equal probability of being the individual that successfully emerged (Boivin and van Baaren, 2000). *In vitro* observations of the parasitoid larvae showed that the rate of movement differed between the two species, with the larvae of the solitary *A. victus* being significantly more mobile. In larger clutches the probability of a single mobile larva successfully emerging matched the expected a priori probabilities under the assumption that the two types of larvae had equal fighting ability and that immobile larvae did not fight each other (Boivin and van Baaren, 2000).

Immobility (with fighting) may provide a less stringent route from siblicidal behavior to nonsiblicidal behavior in parasitoids (Pexton and Mayhew, 2001). We tested this hypothesis by modeling the invasion of alleles encoding for immobility and mobility under a range of scenarios within the framework of Godfray's original models (Godfray, 1987). Our focus concentrated on those clutch sizes thought to be vulnerable to the spread of siblicidal behavior. We also investigated the conditions required for a rare tolerance allele to spread as mobility varies.

Immobility and mobility in small clutches

The spread of an allele for immobility in clutches of two

We assume that the population is composed of individuals with mobile fighting larvae. If more than one egg is laid per host, the mobile larvae will search the host and engage in fights until only one larva survives (evidence of physiological suppression is exiguous, and in the absence of clear mechanistic details we do not consider it in these models). There are no costs to the production of weapons, to moving or to searching. There is no risk of serious sublethal injury. All larvae are assumed to have equal fighting ability. Immobility and mobility are assumed to be controlled by two alleles (*G* for immobility, *g* for mobility) at the same locus. The allele for immobility is dominant, and, assuming haplodiploidy, immobile individuals have the genotypes *GG, Gg,* or *G* and mobile individuals *gg* or *g*. The simplifying assumption of a clear dominant-recessive relationship between alleles at a single locus is an important feature of all previous models, thus facilitating direct comparisons between our results and those of previous workers.

We assume that immobile larvae do not search the host, but in an encounter with a mobile larva have an equal probability of winning the fight. Fights are assumed to occur only between pairs of individuals, and eggs are placed at random. Mobile larvae search the host quickly but randomly and will always find any other larvae present.

The immobility allele is extremely rare, and so the frequency of *GG* females will be approximately zero. Females mate once, and mating is panmictic. As *G* males are rare, there are two possible matings involving the immobility allele: *gg* × *G* and *Gg* × *g*, which occur with the approximate frequencies *x* and *y*, respectively. The sex ratio is equal, as is the proportion of single and mixed-sex broods. Additionally, parasitoids are never egg limited during life, clutch size has no effect on future clutches produced, and superparasitism never occurs. The effects of relaxing many of these assumptions are examined later. Let the fitness of an individual that develops on its own be 1. The fitness of an individual developing in a group of *c* larvae is $f(c)$. We initially assume that all females lay a clutch of two (Table 1). The frequencies of *G* and *Gg* are: $freq(G) = [f(2)/4 + 1/8]y$; $freq(Gg) = [f(2)/2 + 1/4]x + [f(2)/4 + 1/8]y$. To calculate x' and y', the frequencies of males and females carrying the immobility allele in the next generation, we have to divide by the total number of males and females in the population. As the *G* allele is rare, the total number of males and females in the population can be approximated by the progeny of *g* × *gg* matings (frequency ≈ 1), which are ½*g* and ½*gg*. The spread of the allele can be written as recurrence equations in a matrix form:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \Lambda \\ 2\Lambda & \Lambda \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}, \quad (1)$$

where

$$\Lambda = [f(2)/2 + 1/4]. \quad (2)$$

The immobility allele will spread if the dominant eigenvalue (λ) of the matrix is >1. The characteristic polynomial is $\lambda^2 - \lambda\Lambda - 2\Lambda^2 = 0$. Moreover, the dominant eigenvalue is $\lambda = 2\Lambda$. Therefore, the generic condition for the spread an allele given Equation 1 as the form of the matrix (in this case an immobility allele) is $2\Lambda > 1$. This gives the critical condition for the spread of an immobility allele as $f(2) > \frac{1}{2}f(1)$. This is much less stringent than the criterion for tolerance to spread in a population of mobile fighters, which is $f(2) > f(1)$

Table 2
Outcomes of matings and the subsequent fights within broods involving a rare mobility allele (clutch size = 2: *M* = mobility allele)

		Outcome fighting within broods			Fitness of survivors with the rare allele	
	P (Brood)	P (2 *M*/*Mm*)	P (1 *M*/*Mm*)	P (0 *M*/*Mm*)	*f*(2)	*f*(1)
M × *mm* mating						
Mm Mm	1/4	0	1	0	0	1/4
m m	1/4	0	0	1	0	0
Mm m	1/2	0	1/2	1/2	0	1/4
Mm × *m* mating						
Mm Mm	1/16	0	1	0	0	1/16
mm mm	1/16	0	0	1	0	0
M M	1/16	0	1	0	0	1/16
m m	1/16	0	0	1	0	0
Mm mm	1/8	0	1/2	1/2	0	1/16
Mm m	1/8	0	1/2	1/2	0	1/16
Mm M	1/8	0	1	0	0	1/16
M mm	1/8	0	1/2	1/2	0	1/16
M m	1/8	0	1/2	1/2	0	1/16
m mm	1/8	0	0	1	0	0

(Godfray, 1987). The criterion for the spread of the immobility allele is independent of the frequency of clutches of one that are laid, given that clutches of two have a frequency >0.

The spread of an allele for mobility in clutches of two
We now examine the reverse case and find the criterion for a rare mobility allele to spread in an immobile population. This allows for a comparison of the critical conditions necessary for the spread of rare alleles. The mobility allele (*M* for mobility, *m* for immobility) is dominant, and the genotypes of mobile larvae are *M* and *Mm* (Table 2). The frequencies of *M* and *Mm* are $freq(M) = (1/4)y$; $freq(Mm) = (1/2)x + (1/4)y$. To calculate x' and y', the frequencies of males and females carrying the mobility allele in the next generation, we have to divide by the total number of males and females in the population. As the *M* allele is rare, the total number of males and females in the population can be approximated by the progeny of *m* × *mm* matings, which produce $\frac{1}{2}c[f(c)]$ males and $\frac{1}{2}c[f(c)]$ females [in this case *f*(2)]. Therefore, the recurrence equations can be written as in Equation 1, where $\Lambda = 1/[4f(2)]$.

Immobility and mobility in clutches of three and four
The specific fitness criteria for the spread of rare immobility and mobility alleles in small broods are given in Table 3. The calculations for clutches of three and four are presented in appendix A. The relationship within parasitoids between clutch size and individual fitness that Godfray (1987) assumed is based on a general description of the clutch-size fitness function in parasitoids. The function is $f(c) = j\exp(-hc)$ where *h* is a constant determining the strength of fitness reduction with clutch size and *j* is a normalizing constant that results in *f*(1) = 1. Using this function and solving for the Lack solution (Charnov and Skinner, 1984) gives:

$$f(c) = e^{((1/c)-1)} \quad (3)$$

This equation describes the value of an individual's fitness in clutches of various sizes (Godfray, 1987). It serves a heuristic purpose as a likely upper maximum level of fitness that developing larvae may have in clutches of various sizes (our results in no way depend on Equation 3). For a clutch of two, $f(2) \approx 0.61$. Immobility can invade in clutches of two and be stable against invasion by a mobility allele if $f(2) > 0.50$. Immobility could also invade in clutches of three and be stable against invasion by a mobility allele if $f(2) + f(3) > 0.75$ and $f(3) \geq 0.31$. Mobility can invade if $f(3) < 0.31$. The value of *f*(3) from Equation 3 is $f(3) \approx 0.51$. Hence, immobility can spread in clutches of three under the criteria for *f*(2) and *f*(3). In clutches of four, immobility could invade and be stable against invasion by a mobility allele if $1.45f(2) + 1.5f(3) + f(4) > 1.29$ and $f(4) \geq 0.23$. Mobility can invade if $f(4) < 0.23$. The value of *f*(4) from Equation 3 is $f(4) \approx 0.47$. Therefore, immobility can spread in clutches of four under the criteria for *f*(2), *f*(3) and *f*(4) given by Equation 3.

Extensions of the basic model

A number of biological factors may change the critical condition for the spread of an immobility or mobility allele. We examined the effects of sex ratio bias, single-sex broods, degrees of mobility, the likelihood of a double killing during combat, and the level of superparasitism on the criteria for the spread of alleles in clutches of two. A clutch size of two is likely to be the most important for the initial spread of any allele that facilitates the change from siblicidal to non-siblicidal behavior. Solitary parasitoids can lay multiple-egg clutches under a wide range of circumstances. These will include high levels of intraspecific competition (Rosenheim and Hongkham, 1996; Visser and Rosenheim, 1998), low rates of encounters with hosts (Roitberg et al., 1992) and in response to the precise physiological state of the parasitoid (egg load and energy reserves) (Fletcher et al., 1994; Sirot et al., 1997). We examined immobility and mobility in clutches of two with respect to factors that potentially could change the criteria required for the spread of those alleles.

The effects of sex ratio bias, single-sex broods, degrees of

Table 3
Criteria for the spread of rare alleles in small clutches

Clutch size	Criterion for an immobility allele to spread	Criterion for a mobility allele to spread
2	$f(2) > 1/2$	$1/2 > f(2)$
3	$f(3) + f(2) > 3/4$	$5/16 > f(3)$
4	$f(4) + \frac{3}{2}f(3) + \frac{29}{20}f(2) > \frac{103}{80}$	$29/128 > f(4)$

Table 4
The criteria required for the spread of rare alleles incorporating additional conditions

Variable	Criterion for an immobility allele to spread	Criterion for a mobility allele to spread
Sex ratio bias (θ)	$f(2) > 1/2$	$1/2 > f(2)$
Single sex brood (δ)	$f(2) > 1/2$	$1/2 > f(2)$
Degrees of mobility (v)	$f(2) > 1/2$	$1/2 > f(2)$
Double killings (κ)	$f(2) > (1-\kappa)/2$	$f(2) < (1-\kappa)/2$

mobility, and double killings on the conditions for the spread of rare immobility and mobility alleles are summarized in Table 4 (also see Appendix B, Equations A1 and A2). The $f(2)$ criterion for the spread of immobility is independent of sex ratio bias, the proportion of single-sex broods, and the degree of mobility of immobile larvae so long as they are less mobile than fully mobile larvae. The criterion for immobility to spread is relaxed by the phenomenon of double killing; conversely, double killing increases the stringency of the criterion for mobility to spread (Figure 1).

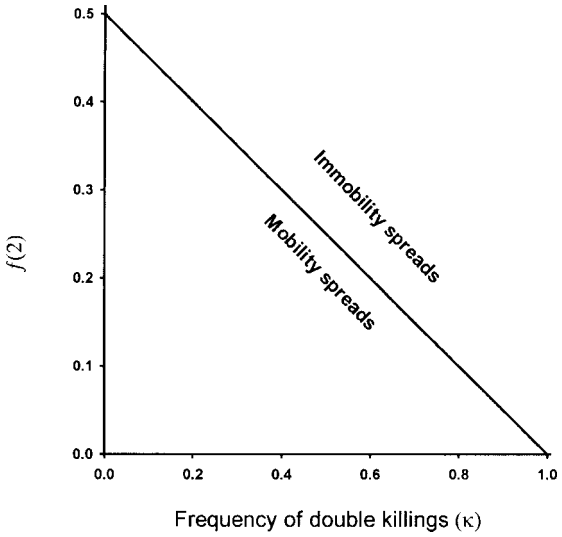

Figure 1
The change in the fitness criterion $f(2)$ (the fitness of an immobile individual developing in a clutch of two) for either immobility or mobility to spread with the likelihood of a double killing occurring during combat.

Superparasitism
Superparasitism is the phenomenon of eggs from more than one female being placed together in the same host. The consequence of such conspecific superparasitism on the invasion of alleles was investigated by calculating the change in $f(2)$ if other females had also attacked hosts. We assume that additional eggs may have also been laid in such hosts so that larvae are in multiple broods of 2 or $2 + n$. The precise order in which eggs are laid does not affect the outcome of fighting within broods. Females never lay additional eggs in hosts that they themselves have previously oviposited eggs into (no self-superparasitism occurs sensu Rosenheim and Hongkham, 1996) or that have been superparasitized (i.e., hosts in the $2 + n$ state). Females with the invading allele are so rare that they never also lay eggs in hosts that also contain larvae with the rare allele. The other assumptions of the simplest models still apply. If additional larvae are present then the outcomes of fighting will change.

We calculate the change in the invasion criteria of rare immobility and mobility alleles under the conditions of superparasitism that results in broods with eggs from two females. Let ξ be the proportion of parasitized hosts in which females with the rare allele have laid n additional eggs (hence $1 - \xi$ is the proportion of ordinary hosts with basic clutches of two, laid by females carrying the rare allele). Let ϕ be the rate at which females of the background population will have laid n additional eggs. As females with the invading allele are so rare, the overall rate of superparasitism in the population, ϕ, is determined by females from the background population. Therefore, ξ and ϕ are independent variables. The criteria for both an immobility and mobility allele to spread are summarized in Table 5 (also see appendix C, Equations A3–A10). The variation in the critical value of $f(2)$ with ξ and ϕ can be seen in Figure 2. The value at which ξ and ϕ are equal and $f(2)$ meets Godfray's value (≈ 0.61) for the spread of immobility is approximately 0.08 (when additional eggs in hosts produce broods of $2 + 1$ larvae) and 0.06 (when additional eggs in hosts produce broods of $2 + 2$ larvae).

Superparasitism can occur at a rate of approximately 6–8% and immobility can still spread in the population. Substituting these values into the expressions for the invasion of mobility demonstrates that an allele for mobility could not spread under such conditions. Thus, unlike the basic model of immobility in which $f(2)$ was independent of the proportion of clutches of 2 or 1 laid, $f(2)$ is not independent if additional larvae are present. Even if equal numbers of eggs are present in hosts (the $2 + 2$ case), the $f(2)$ criterion still rapidly increases with the rate of superparasitism.

Nonrandom searching and fighting order
Our basic model assumes that mobile larvae search hosts quickly but randomly, and hence in the appropriate clutches the order of fights is random. Consequently, in clutches with two or more mobile larvae and a single immobile larva the probability of the immobile larva surviving is simply the reciprocal of clutch size.

We briefly explore the effects of deviations from random searching. In clutches of two with one mobile larva and one immobile larva, it is immaterial if the mobile larva randomly searches or finds the immobile larva more directly. Equally, nonrandom searching does not change the likelihood of survival in clutches with a single mobile larva plus multiple immobile larvae. In such scenarios, the mobile larva will always be involved in the first fight and any subsequent fights. The first clutch combination in which nonrandom searching could change the survival probabilities of larvae is in a clutch of three with two mobile larvae and one immobile larva present. Hence, we focus on deviations from random searching with respect to the spread of mobility and immobility alleles in clutches of three.

In those clutch combinations consisting of two mobile larvae and a single immobile larvae we can modify the likelihood of a mobile larva being the individual that survives and develops. Let ω be the probability of a mobile larva emerging from a two mobile larvae and one immobile larva clutch, hence $1 - \omega$ is the probability that the immobile larva survives and emerges. All of the other assumptions of the basic model hold. The condition required for immobility not to spread in clutches of three is:

$$(1-\omega) = \frac{13}{12} - [f(2) + f(3)]. \quad (4)$$

If $f(2) + f(3) > 1.0834$, then the condition that must be

Table 5
The criteria for the spread of rare alleles under superparasitism

Conditions	Criterion for an immobility allele to spread	Criterion for a mobility allele to spread
Broods of 2 or 2 + 1; $\xi \neq 1$, $\phi \neq 0$	$f(2) > \left(\frac{1-\frac{\xi}{3}}{1-\xi} - \frac{1}{2}\right) + \frac{\phi}{12(1-\xi)}(1+7\xi) + \frac{\phi}{2}$	$\frac{1}{2} - \frac{3}{8}\xi + \phi\left(\frac{19}{72}\xi - \frac{11}{36}\right) > (1-\phi)f(2) + \phi f(3)$
Broods of 2 or 2 + 2; $\xi \neq 1$, $\phi \neq 0$	$f(2) > (1-\phi)\left(\frac{\frac{1}{2}+\frac{11}{80}\xi}{1-\frac{41}{60}\xi}\right) + \frac{153}{76}\phi$	$\frac{1}{2} - \frac{31}{96}\xi + \phi\left(\frac{31}{96}\xi - \frac{79}{192}\right) > (1-\phi)f(2) + \phi f(4)$

satisfied for immobility not to spread is $1 - \omega < 0$, which is impossible. If individual fitness is simply the reciprocal of clutch size [$f(3) = 1/3$, $f(2) = ½$], then the condition for immobility not to spread is $1 - \omega = ¼$. If all larvae have equal fighting ability and there is a nonzero probability of the immobile larva not being involved in the first fight, then $1 - \omega > ¼$, and immobility would still spread. When the immobile larva is always in the first fight but retains an equal fighting ability, then the criterion for the spread of immobility in clutches of three specifically becomes $f(2) + f(3) > 0.83$.

In the reverse case of mobility spreading in an immobile population, for mobility to spread, the condition is:

$$\omega > \frac{48}{12} f(3) - \frac{7}{12}. \quad (5)$$

If we substitute the $f(3)$ value generated from Equation 3, then the condition for mobility to spread would require $\omega > 1.47$, which is impossible because ω can never exceed a value of one. If $f(3) = 1/3$, then a value of $\omega > 3/4$ would allow mobility to spread. However, under equal fighting ability for both mobile and immobile larva, ω can never be greater than 3/4. Again, if the immobile larva was always involved in the first fight but retained equal fighting ability, the specific criterion for the spread of mobility marginally would change to $f(3) < 0.33$. Therefore deviations from random searching by mobile larvae (resulting in a nonrandom order of fights) do not significantly change the qualitative results with respect to the spread of a rare mobility allele and can only prevent the spread of a rare immobility allele under specific circumstances in initial clutches of three.

Tolerance, fighting, and variable mobility

Given that immobility (with fighting) can spread in a population with fighting larvae that are highly mobile, can tolerance subsequently invade an immobile population? We investigated the possible conditions in a clutch size of two for fighting behavior to be replaced by tolerance and tolerance to be replaced by fighting as mobility varies. We characterize tolerance as not being able to fight; hence if encountering a fighting larva, tolerant individuals are always killed. The same assumptions as in the basic model still apply.

The spread of tolerance

Let T be a dominant allele for nonfighting tolerance, t an allele for fighting ability, $1 - v$ is the probability that larvae do not encounter each other, and v is the probability that they do. Thus both tolerant larvae and immobile larvae have the same rate of movement but only differ in their ability to fight. The likelihood of a fighting larva and tolerant larva encountering each other is the same as the likelihood of two fighting larvae encountering each other. Tolerant larvae will also encounter each other with the same probability. When two tolerant larvae encounter each other, they cannot harm the other larva. Immobile larvae will always kill a tolerant larvae if they encounter them, and if two immobile larvae encounter each other, then, again, a lethal fight will occur. Let the fitness of tolerant individuals be $\Psi(c)$. The individual fitness of a larva with fighting ability is $f(c)$. The frequencies of T and Tt are $freq(T) = (1/2)\Psi(2)(1 - v/2)y$; $freq(Tt) = (1/2)\Psi(2)(1 - v/2)y + \Psi(2)(1 - v/2)x$. To generate x' and y' (the frequencies of males and females carrying the tolerance allele in the next generation), we divide by the total number of males (t) and females (tt), but in this case, because the background immobile progeny will fight if they encounter each other, the frequencies are $(1 - v)f(2) + v/2$. This results in a matrix as in Equation 1, where $\Lambda = \Psi(2)(1 - v/2)/[2f(2)(1 - v) + v]$. Solving the characteristic polynomial gives:

$$\Psi(2) > \frac{f(2)(1-v) + \frac{1}{2}v}{1 - \frac{1}{2}v}. \quad (6)$$

When $v = 0$, $\Psi(2) > f(2)$, indicating that the tolerant larvae have to experience a less sharp decline in fitness compared with immobile fighters for tolerance to spread. As v increases, the conditions for tolerance to spread become increasingly stringent (Figure 3a). When $v = 1$, all larvae are fully mobile, so fighting larvae always encounter tolerant larvae, and therefore the individual fitness of developing tolerant larvae must rise with clutch size as in Godfray (1987).

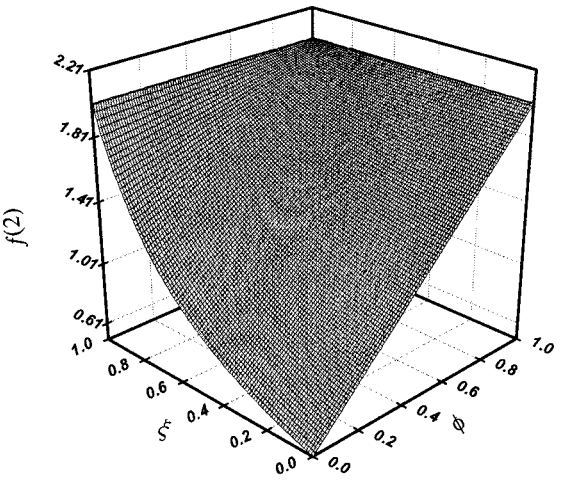

Figure 2
The increase in the fitness criterion $f(2)$ for immobility to spread when the laying of additional eggs by different females into hosts results in broods of 2 + 2 eggs. ξ the proportion of eggs laid by females carrying the immobility allele (or fertilized by a male with the immobility allele) into previously parasitized hosts; ϕ the proportion of eggs laid by ordinary females with mobility allele into previously parasitized hosts.

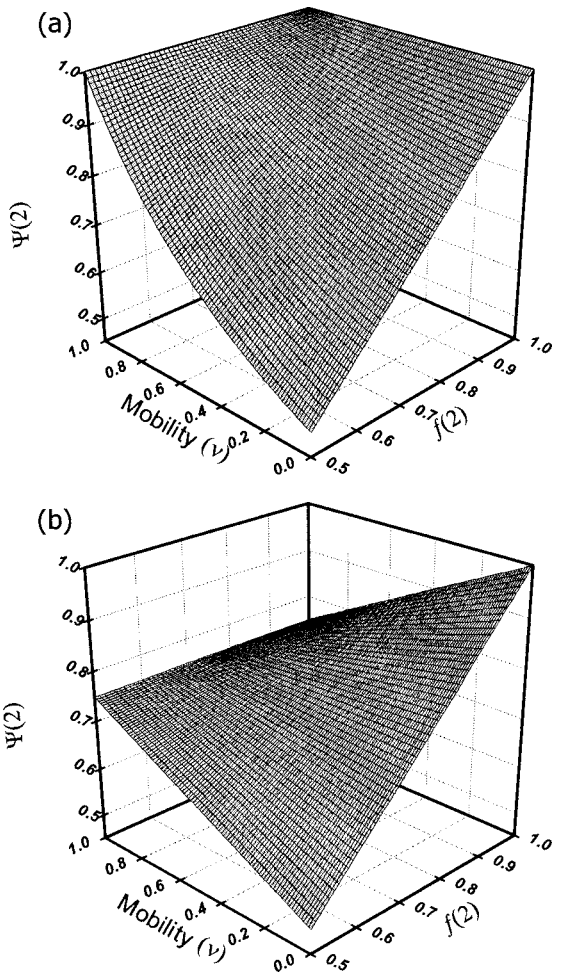

Figure 3
(a) The change in the fitness criterion $\Psi(2)$ (the fitness of a tolerant individual developing in a clutch of two) required for tolerance to spread in an population of fighters with differing degrees of mobility (v). (b) The change in the fitness criterion $\Psi(2)$ for fighting to spread in a tolerant population with differing degrees of mobility (v).

The spread of fighting

Let J be a dominant allele for fighting ability, j an allele for tolerance, 1– v the probability that larvae do not encounter each other, and v the probability that they do. Fighting larvae will always kill tolerant larvae if they encounter them (as before when tolerant larvae encounter each other, they cannot damage each other in any way). If immobile fighters find each other, there is a lethal fight. Let the fitness of tolerant individual be $\Psi(c)$. The individual fitness of a fighting larva is f(c). The frequencies of J and Jj are $freq(J) = (1/2)f(2)(1-v)y + (3/8)vy$; $freq(Jj) = (1/2)f(2)(1-v)y + (3/8)vy + f(2)(1-v)x + (3/4)vx$. To generate x' and y', we divide by the background frequencies of males (j) and females (jj), which are $\Psi(2)$. This results in a matrix of the form of Equation 1 where $\Lambda = (1-v)f(2)/[2\Psi(2)] + 3v/[8\Psi(2)]$. Solving the characteristic polynomial gives:

$$f(2) > \frac{\Psi(2) - \frac{3v}{4}}{1-v}. \qquad (7)$$

When $v = 0$, the condition for immobility with fighting ability to spread is $\Psi(2) < f(2)$. The tolerant larvae have to experience a sharper decline in fitness compared with those with fighting ability in order for immobility with fighting to spread. As v increases, the condition for immobility to spread becomes less stringent (Figure 3b). Extending the models of fighting and tolerance as mobility varies demonstrates that biological factors such as sex ratio bias, single-sex broods, and double killings can alter, in this context, the conditions for the spread of rare alleles if $v \neq 0$ (see Table 6 for generalized conditions and also Appendix D, Equations A11–A16, and Figure 4). However, the effects are relatively small with respect to sex ratio bias or single-sex broods and are only seen at extremely high levels of mobility.

DISCUSSION

Our primary finding is that a rare immobility allele can spread in small clutches without the requirement that the individual fitness of developing larvae increase with clutch size. Immobile larvae with fighting ability display ipso facto a form of conditional tolerance: if engaged they will kill but cannot (or do not actively) seek out other individuals. Effectively, immobility is a trait that de facto results in an assortative interaction between individuals that share the trait compared to individuals that do not (Wilson and Dugatkin, 1997). Immobile fighting larvae do not attack each other, but all immobile larvae can potentially attack mobile fighting larvae. In contrast, mobile fighting larvae are equally prone to attack other mobile larvae or immobile larvae. Previous models postulated that gregarious development required larvae that could not fight. Tolerant (nonfighting) larvae are entirely vulnerable to aggression. If larvae are highly mobile, tolerant larvae can only survive if all other members of the brood are also tolerant. Immobile fighting larvae can potentially survive in any type of brood. The fitness requirements for the spread of an immobility allele are substantially lower than for any of the previous models based on complete (nonfighting) tolerance and complete mobility [in clutches of two immobility will spread if $f(2) > \frac{1}{2} f(1)$, compared to $f(2) > f(1)$ for tolerance to spread in a population of mobile fighters; Godfray, 1987].

The criteria for immobility to spread in clutches of three and four require values of $f(3)$ and $f(4)$ that are less stringent than the criteria required for a rare mobility allele to spread in clutches of three or four. Only a few broods will contain three or four immobile larvae; hence fighting with the mobile larvae present produces complex brood-size combinations. When mobility is the rare allele, mobile larvae will be involved in a long series of fights until one mobile larva remains or all mobile larvae are killed. This suggests that for certain fitness functions immobility could spread but would not be stable. However, for many fitness functions (including Godfray's), immobility would be stable. Immobility can spread and be stable in those small broods that previously had been thought vulnerable to a siblicidal fighting allele (Godfray, 1987). The results of our basic population-genetic models for immobility–mobility are qualitatively similar to the trends found by Smith and Lessells (1985) in their game theoretic models of larval competition strategies (based on contest and scramble processes) developed for unrelated granivorous insects that develop within single seeds (also see Colegrave, 1994).

Variations of the basic immobility–mobility model

We extended our basic model to assess the influence of a series of factors on the criteria for rare immobility and mobility alleles to spread. A minimum requirement for gregariousness is that two individuals successfully share a host; hence our focus was mainly on initial clutches of two. The criteria for

Table 6
The criteria for the spread of rare alleles with variable mobility incorporating additional conditions

Variable	Criterion
For tolerance allele to spread	
Sex ratio bias (θ)	$\Psi(2) > \dfrac{4f(2)(1-v)+2v}{\left(1-\frac{v}{2}\right)+\left(1-\frac{v}{2}\right)^{1/2}\left(9-v\left(\frac{1}{2}+\theta 8\right)\right)^{1/2}}$
Single-sex broods (δ)	$\Psi(2) > \dfrac{4\left((1-v)f(2)+\frac{v}{2}\right)}{\left(1-\frac{1}{2}v\right)+\left(1-\frac{1}{2}v\right)^{1/2}\left(9-\frac{17}{2}v+8\delta v\right)^{1/2}}$
Double killings (κ)	$\Psi(2) > \dfrac{(1-v)f(2)+\frac{v}{2}(1-\kappa)}{\left(1-\frac{v}{2}\right)}$
For an immobility or reduced mobility allele to spread	
Sex ratio bias (θ)	$\frac{1}{4}(1-v)f(2)+\frac{3v}{16}+\frac{1}{4}\left((1-v)f(2)+\frac{3v}{4}\right)^{1/2}\left(9(1-v)f(2)+v\left(\frac{3}{4}+4\left(\frac{1-\theta^2}{1-\theta}\right)\right)\right)^{1/2} > \Psi(2)$
Single-sex broods (δ)	$\frac{1}{4}(1-v)f(2)+\frac{3v}{16}+\frac{1}{4}\left((1-v)f(2)+\frac{3v}{4}\right)^{1/2}\left(9(1-v)f(2)+\left(\frac{35}{4}-4\delta\right)v\right)^{1/2} > \Psi(2)$
Double killings (κ)	$f(2) > \dfrac{\Psi(2)+\frac{v}{4}(\kappa-3)}{(1-v)}$

both immobility and mobility to spread are independent of the degree of mobility of immobile larvae if any asymmetry in movement rates exists between mobile and immobile larvae. As the probability of a double killing involving both individuals in a fight increases, the criterion for a mobility allele to invade becomes more stringent; hence, the criterion for immobility to spread is relaxed. Unlike previous models of tolerance and intolerance, we find that sex ratio bias (Godfray, 1987; Ode and Rosenheim, 1998) and the incidence of single-sex broods (Rosenheim, 1993) do not change the criteria for either immobility or mobility to spread.

Sex ratio biases and single-sex broods have been previously demonstrated to marginally relax the conditions for the spread of nonfighting tolerance, yet they do not change the criterion for immobility to spread in a population of mobile fighters (at least in clutches of two). An invading tolerant allele requires that a brood completely consist of tolerant individuals for the allele to be present in the next generation. These kinds of broods are rare (see Godfray, 1987; Rosenheim, 1993), but if more all-female broods are laid, then one type of these rare tolerant broods will increase in frequency (females are more likely to be carrying the tolerant allele due to the haplodiploid genetic system). As previously mentioned, an immobility allele is not dependent on such rare broods to be present in the next generation.

Superparasitism always increases the stringency of the criteria for the spread of both rare immobility and mobility alleles. However, for a range of overall rates of superparasitism in the population, immobility can spread, but mobility cannot (a potential example of hysteresis). For a mobile larva, every additional immobile larva represents yet another opponent that will be engaged in combat. This makes the probability of a mobile larva being eventually killed much higher, thus dramatically reducing the probability that it will eventually be left to develop on its own. Estimating the rate of superparasitism in the field is difficult, and we know of no rigorous examples in the literature. It is therefore difficult to know if the rates of superparasitism that in our models will allow immobility to spread are low, high, or moderate in natural populations.

The spread of a rare immobility allele is robust to nonrandom searching by mobile larvae in the case we examined. For a realistic fitness function, a mobility allele cannot spread even if in those clutch combinations consisting of a single immobile larva and multiple mobile larvae, mobile larvae never fight each other first and immobiles are always involved in the first fight. Even if individual fitness is only the reciprocal of clutch size, so long as there is a nonzero probability of a single immobile larva not being involved in the first fight (in clutches consisting of multiple mobile larvae and single immobile larva), then immobility can still spread in our example. For more generous fitness functions, an immobility allele could still spread even if, in multiple mobile and single immobile clutches, the immobile larva was always involved in the first fight.

Tolerance and variable mobility

In examining the spread of a rare tolerance allele in a population of immobile fighters (or such a population with reduced mobility), we found that, as the degree of mobility increases, so the criterion for invasion becomes more stringent. If mobility (or searching activity) is effectively zero (little or no movement), then the condition for tolerance to spread is simply that the fitness of tolerant individuals in clutches of two must be greater than that of individuals with the ability to fight. This would imply that a less sharp decline in fitness with clutch size occurs in tolerant individuals or that tolerant and fighting wasps have the same form of fitness function but that immobile fighters have an intrinsically and marginally lower level of fitness. A reduction in fitness in fighting individuals could be due to the costs of developing and maintaining weapons that are unlikely to be borne by nonfighting, tolerant larvae. If we consider reduced mobility (with fighting) and tolerance, a number of significant biological factors (sex ratio bias, single-sex broods, and double killings) can modify the criteria for the spread of such rare alleles, but only when levels of mobility are highly elevated. When complete mobility is considered, our results correspond to the outcomes of previous models (Godfray, 1987; Rosenheim, 1993), which implicitly assume all larvae (fighting and nonfighting types) are completely mobile and hence invariably encounter each other.

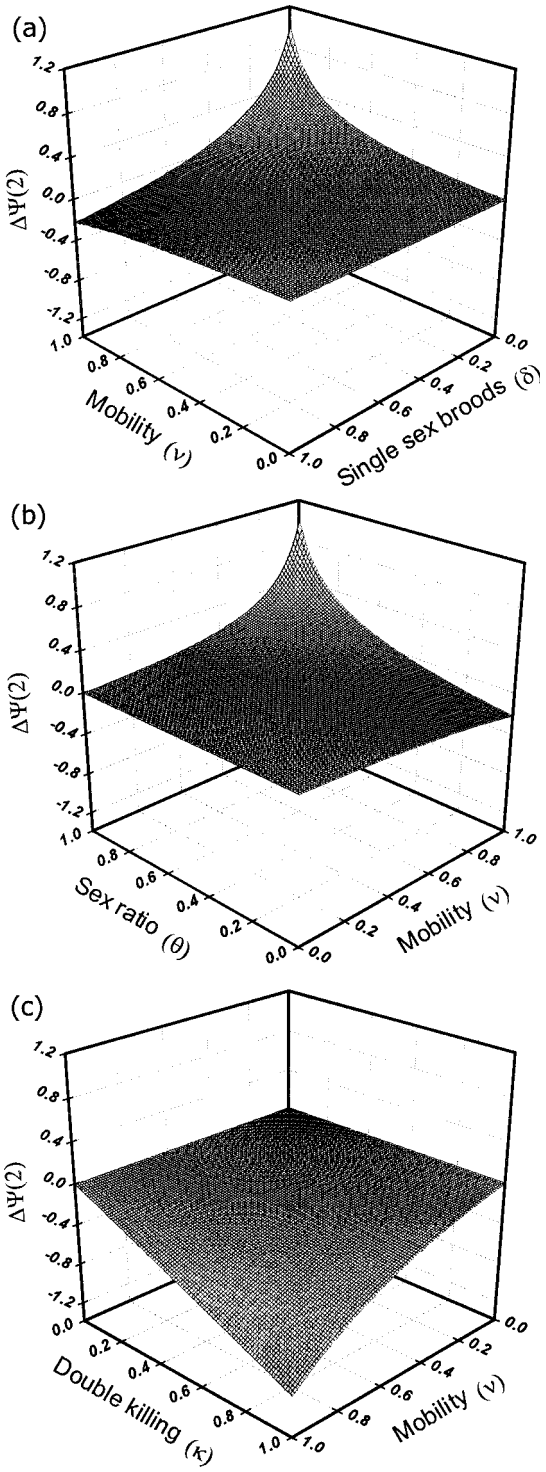

Figure 4
The change in the criterion for tolerance to spread [$\Delta\Psi(2)$] in a fighting population made by incorporating the effects of (a) single-sex broods (δ), (b) sex ratio bias (θ), plus (c) double killings (κ), as the degree of mobility (v) varies [assuming that $f(2)$ is fixed at a given value]. Note that single-sex broods (δ) and sex ratio bias (θ) are mathematically equivalent with respect to changing the conditions for tolerance to spread. When $v = 1$, we recreate for all the additional variables (δ, θ, and κ) the previous results of Rosenheim (1993) and Godfray (1987), respectively. If every clutch of two laid consists of one sex (equally likely to be all male or all female) or only females eggs are laid then given, $v = 1$, the criterion of tolerance to spread is (in our notation) $\Psi(2) > 0.78$.

Conclusions

It is possible that either conditional or complete tolerance are stable evolutionary endpoints. If complete tolerance is the endpoint, this might mean that conditional tolerance due to immobility is a transitory state. This gives credence to the suggestion that, in some parasitoids, morphology and behavior might be separable (Mayhew and van Alphen, 1999). Gregarious species may still have larvae with vestigial mandibles that are completely redundant as weapons. In contrast, if an immobile species was sympatric with a mobile species and they both frequently attacked the same species of hosts, then the interspecific competition resulting from such multiparasitism may strongly favor the retention of fighting ability (as may be the case in the species examined by Boivin and van Baaren, 2000). The force of selective pressure would be against any form of nonfighting tolerance. It is not unreasonable to speculate that such selective pressures (the risk of multiparasitism, the costs of developing functional weapons) may have been important given the diversity seen in the functional forms of parasitoid larvae (Quicke, 1997).

Once the primary proximate mechanism for parent–offspring conflict (mobile fighting larvae) is no longer in place, parents can potentially optimize their clutch size decisions. The conditional tolerance resulting from immobility could serve as a transitional stage toward gregariousness with large clutch sizes and the complete tolerance observed in many species of parasitoid wasps.

Our models suggest that reduced mobility (or potentially a lack of searching behavior) should be a mechanism that frequently results in the evolutionary outcome of gregarious development. Completely tolerant species should generally be less mobile. In ectoparasitoids the family Chrysididae generally have highly mobile larvae, and of 3000 documented species, only one is gregarious (Rosenheim, 1993). This contrasts with their sister family the Bethylidae, in which gregarious development and nonfighting is common, along with reduced mobility (Mayhew and Hardy, 1998). Yet many species of parasitoids retain highly mobile larvae, including some gregarious species. It is possible that high rates of movement are required for reasons not considered in these models. The ability to move, especially in koinobiont endoparasitoids, may help in the manipulation and regulation of hosts or in the avoidance of host defenses. Further study of larval behavior (particularly with respect to endoparasitoids) will enhance our understanding of the costs and benefits of larval mobility. We hope this work will stimulate more empirical investigation of mobility and fighting in parasitoids and contribute to a more complete understanding of the evolution of nonsiblicidal behavior in parasitoid wasps.

APPENDIX A

The spread of immobility and mobility

Because the outcomes of fighting will change with clutch size and the combination of individuals in clutches of a given size, we must calculate each clutch size individually. In turn, for each clutch size, we need to know the number of independent brood types, which is given by $(z + N - 1)!/(z - 1)!N!$, where z is the number of genotypes produced by a cross and N is clutch size. The frequency of any particular brood type is given by $\Omega(1/z)^N$, where Ω is the statistical weight of a particular brood type and $\Omega = N!/n_1!n_2!\ldots n_z!$, where n_i is the number of individuals of genotype i present in a given brood.

The spread of an allele for immobility or mobility in larger clutches
We make the same assumptions as in the previous case of immobility or mobility but increased clutches of either three or four are laid by females. In the case of the spread of immobility in clutches of three, the frequencies of G and Gg are: $freq(G) = [3f(3)/16 + 3f(2)/16 + 7/64]y$; $freq(Gg) = [3f(3)/16 + 3f(2)/16 + 7/64]y + [3f(3)/8 + 3f(2)/8 + 7/32]x$. The recurrence equations can be written as in Equation 1, where $\Lambda = [3f(3)/8 + 3f(2)/8 + 7/32]$.

In the case of the spread of immobility if clutches of four are laid by females, we include the assumption that in broods of two immobile larvae and two mobile larvae simultaneous fighting (two sets of fights at the same time) is equally likely to be the first fighting event as a single fight. The frequencies of G and Gg are $freq(G) = [f(4)/8 + 3f(3)/16 + 29f(2)/160 + 57/640]y$; $freq(Gg) = [f(4)/8 + 3f(3)/16 + 29f(2)/160 + 57/640]y + [f(4)/4 + 3f(3)/8 + 29f(2)/80 + 57/320]x$. The recurrence equations can be written as in Equation 1, where $\Lambda = [f(4)/4 + 3f(3)/8 + 29f(2)/80 + 57/320]$.

In the case of the spread of mobility when females lay clutches of three, the frequencies of M and Mm are $freq(M) = (15/64)y$; $freq(Mm) = (15/64)y + (15/32)x$. The recurrence equations can be written as in Equation 1, where $\Lambda = 5/[32f(3)]$.

In the case of the spread of mobility when females lay clutches of four, the frequencies of M and Mm are $freq(M) = (29/128)y$; $freq(Mm) = (29/128)y + (29/64)x$. The recurrence equations can be written as in Equation 1, where $\Lambda = 29/[256f(4)]$.

APPENDIX B

The spread of immobility and mobility in clutches of two with extra conditions

Sex ratio bias and the spread of immobility or mobility
The same assumptions as in the simplest model apply except that θ is the proportion of males produced by a female, where $0 \leq \theta \leq 1$. In the case of immobility spreading the frequencies of G and Gg are: $freq(G) = [\theta f(2)/2 + \theta/4]y$; $freq(Gg) = (1-\theta) \times [(2(1-\theta)f(2) + \theta)x + (f(2)/2 + 1/4)y]$. We divide by θ and $(1-\theta)$ the number of males (g) and females (gg) in the population. Solving the characteristic polynomial gives:

$$\lambda = \frac{1}{4}f(2) + \frac{1}{8} + \frac{1}{2}\left(\left(\frac{1}{2}f(2) + \frac{1}{4}\right)^2 + 4\left(\frac{1}{2}f(2) + \frac{1}{4}\right)(2(1-\theta)f(2) + \theta)\right)^{1/2}. \quad \text{(A1)}$$

The equation can be solved numerically to show that $f(2) > \frac{1}{2}$ is the condition for immobility to spread, independently of the value of θ.

In the case of mobility spreading the frequencies of M and Mm are $freq(M) = (\theta/2)y$; $freq(Mm) = (1-\theta)x + (1/2)y$. We divide by $2f(2)\theta$ and $2f(2)(1-\theta)$ the number of males (m) and females (mm) in the population. Hence, the condition for mobility to spread is $f(2) < \frac{1}{2}$, independently of the value of θ.

Single-sex broods and the spread of immobility or mobility
The same assumptions as in the simplest model apply except that δ is the proportion of single sex broods produced by a female, where $0 \leq \delta \leq 1$. Single-sex broods are assumed to be equally likely to be all male or all female. In the case of immobility spreading the frequencies of G and Gg are $freq(G) = [f(2)/4 + 1/8]y$; $freq(Gg) = [\delta f(2) + (1-\delta)/2)]x + [f(2)/4 + 1/8]y$.We divide by the frequency of background g ($\frac{1}{2}$) males and gg ($\frac{1}{2}$) females. The matrix of the recurrence equations now becomes:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \frac{f(2)}{2} + \frac{1}{4} \\ 2\delta f(2) + 1 - \delta & \frac{f(2)}{2} + \frac{1}{4} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}. \quad \text{(A2)}$$

Solving the eigenvalue equation demonstrates that the condition for immobility to spread is: $f(2) > \frac{1}{2}$, independently of the value of δ. For the spread of mobility, the frequencies of M and Mm are as the basic model in the main text hence the criterion for mobility to spread is $f(2) < \frac{1}{2}$, independently of the value of δ.

Degrees of mobility and the spread of immobility/reduced mobility or complete mobility
The same assumptions as in the simplest model apply except that v is the degree of mobility where $v = 0$ is the simplest case (complete immobility). In the case of immobility/reduced mobility spreading the frequencies of G and Gg are $freq(G) = [(1-v)f(2)/4 + v/8 + 1/8]y$; $freq(Gg) = [(1-v)f(2)/2 + v/4 + 1/4]x + [(1-v)f(2)/4 + v/8 + 1/8]y$. The eigenmatrix is of the same form as Equation 1, where $\Lambda = (1-v)f(2)/2 + v/4 + 1/4$. Solving the characteristic polynomial gives the criterion for immobility/reduced mobility to spread as: $f(2) > \frac{1}{2}$, independently of the value of v (given $v \neq 1$).

In the case of the spread of complete mobility ($v = 1$) in an immobile/reduced mobility population, the frequencies of M and Mm are as the basic model in the main text. We divide these frequencies by the number of males (m) and females (mm) which is $(1-v)f(2) + v/2$. The eigenmatrix is of the same form as Equation 1, where $\Lambda = 1/[4(1-v)f(2) + 2v]$. Solving the characteristic polynomial gives the criterion for the spread of mobility as: $f(2) < \frac{1}{2}$, independently of the value of v (given $v \neq 1$).

Double killings and the spread of immobility or mobility
The same assumptions as in the simplest model apply except that κ is the probability of a double killing occurring during combat, where $\kappa = 0$ is the simplest case (no double killings). In the case of the spread of immobility the frequencies of G and Gg are: $freq(G) = [f(2)/4 + (1-\kappa)/8]y$; $freq(Gg) = [f(2)/2 + (1-\kappa)/4]x + [f(2)/4 + (1-\kappa)/8]y$. The number of males ($g$) and females ($gg$) is $(1-\kappa)/2$. This results in an eigenmatrix of the form seen in Equation 1, where $\Lambda = f(2)/[2(1-\kappa)] + 1/4$. Solving the characteristic equation gives the condition for the spread of immobility as: $f(2) > (1-\kappa)/2$.

In the case of the spread of mobility the frequencies of M and Mm are $freq(M) = [(1-\kappa)/4]y$; $freq(Mm) = [(1-\kappa)/2]x + [(1-\kappa)/4]y$. To calculate the frequency of these genotypes in the next generation we divide by $f(2)$. Solving the characteristic equation gives the criterion for the spread of mobility as $f(2) < (1-\kappa)/2$.

APPENDIX C

Superparasitism and the spread of immobility or mobility

Immobility and one additional larva
When an immobile female lays an additional egg into previously parasitized host, the immobile larva has a one-third probability of being the one larva to survive and complete their development because they will be in a host with two mobile larvae. For $\phi = 1$, the eigenmatrix is of the same form as Equation 1, where $\Lambda = \xi/6 + [(f(2)/4 + 11/48)(1-\xi)]$. From the characteristic equation:

$$f(2) > \frac{1}{4}\left(\frac{\frac{13}{3}+\xi}{1-\xi}\right). \quad \text{(A3)}$$

However, this expression does not apply if $\xi = 1$ because immobile females no longer lay clutches of two. For $\phi = 0$, the eigenmatrix is of the same form as Equation 1, where $\Lambda = \xi/6 + [(f(2)/2 + 1/4)(1-\xi)]$. From the characteristic equation:

$$f(2) > \frac{1-\frac{\xi}{3}}{1-\xi} - \frac{1}{2}. \quad \text{(A4)}$$

The critical value of $f(2)$ would vary with the overall level of superparasitism as:

$$f(2) > \phi f\langle 2|s\rangle + (1-\phi) f\langle 2|s^*\rangle, \quad \text{(A5)}$$

where s = superparasitism, and s^* = no superparasitism. This results in the generalized expression in Table 5.

Immobility and two additional larvae

The same assumptions as in the previous case apply, except that two additional larvae may be laid into a host from a given type of female. In this case the eigenmatrix is of the same form as Equation 1, where $\Lambda = [19f(2)/120 + 29/160]$. From the characteristic equation, $f(2) > 153/76$. For $\phi = 0$, the eigenmatrix is of the same form as Equation 1, where $\Lambda = \xi[19f(2)/120 + 29/160] + (1-\xi)[f(2)/2 + 1/4]$. From the characteristic equation:

$$f(2) > \frac{\frac{1}{2}+\frac{11}{80}\xi}{1-\frac{41}{60}\xi}. \quad \text{(A6)}$$

As before, Equation A5 applies. This results in the generalized expression in Table 5.

Mobility and one additional larva

The same assumptions apply as in the case of immobility. When a mobile female lays an additional egg into a previously parasitized host, the mobile larva has a one-quarter probability of surviving and completing its development. For $\phi = 1$, the frequencies of M and Mm are: $freq(M) = [7(1-\xi)/48 + \xi/16]y$; $freq(Mm) = [7(1-\xi)/48 + \xi/16]y + [7(1-\xi)/24 + \xi/8]x$. To generate x' and y', we divide by the background frequencies of males (m) and females (mm), but in this case because the background progeny are immobile, they develop in clutches of three if superparasitism occurs. In this case, the eigenmatrix is of the same form as Equation 1, where:

$$\Lambda = \left[\frac{7}{72}(1-\xi) + \frac{1}{24}\xi\right]\frac{1}{f(3)}. \quad \text{(A7)}$$

From the characteristic equation, $7/36(1-\xi) + \xi/12 > f(3)$. For $\phi = 0$, the frequencies of M and Mm are $freq(M) = [(1-\xi)/4 + \xi/16]y$; $freq(Mm) = [(1-\xi)/4 + \xi/16]y + [(1-\xi)/2 + \xi/8]x$. To generate x' and y', we divide by the background frequencies of males (m) and females (mm), but in this case because the background progeny are immobile, they develop in clutches of two. In this case, the eigenmatrix is of the same form as Equation 1, where:

$$\Lambda = \frac{1-\xi}{4f(2)} + \frac{\xi}{16f(2)}. \quad \text{(A8)}$$

From the characteristic equation, $f(2) < (1-\xi)/2 + \xi/8$. As before, Equation A5 applies. This results in the generalized expression in Table 5.

Mobility and two additional larvae

The same assumptions as in the previous case apply, except that two additional larvae may be laid into a previously parasitized host. Thus the frequencies of M and Mm if $\phi = 1$ are: $freq(M) = 17y/192$; $freq(Mm) = 17y/192 + 17x/96$. To generate x' and y', we divide by the background frequencies of males (m) and females (mm), but in this case because the background progeny are immobile, they develop in clutches of four if superparasitism occurs. In this case the eigenmatrix is of the same form as Equation 1, where $\Lambda = 17/[384f(4)]$. From the characteristic equation, $17/192 > f(4)$. For $\phi = 0$, the frequencies of M and Mm are:

$$freq(M) = \xi\frac{17}{192}y + (1-\xi)\frac{y}{4}$$

$$freq(Mm) = \xi\frac{17}{192}y + (1-\xi)\frac{y}{4} + \xi\frac{17}{96}x + (1-\xi)\frac{x}{2}. \quad \text{(A9)}$$

To generate x' and y', we divide by the background frequencies of males (m) and females (mm), but in this case because the background progeny are immobile, they develop in clutches of two. In this case, the eigenmatrix is of the same form as Equation 1, where:

$$\Lambda = \xi\frac{17}{192f(2)} + \frac{1-\xi}{4f(2)}. \quad \text{(A10)}$$

From the characteristic equation, $1/2 - (31/96)\xi > f(2)$. As before, Equation A5 applies. This results in the generalized expression in Table 5.

APPENDIX D

The spread of tolerance (nonfighting) and fighting as mobility varies incorporating extra conditions

Sex ratio bias and the spread of tolerance or fighting

The same assumptions as in the simplest model apply, except that θ is the proportion of males produced by a female, where $0 \le \theta \le 1$. In the case of the spread of tolerance, the frequencies of T and Tt are $freq(T) = \theta\Psi(2)(1-v/2)y$; $freq(Tt) = 2\Psi(2)(1-\theta)(1-v\theta)x + \Psi(2)(1-\theta)(1-v/2)y$. We divide by $2f(2)\theta(1-v) + v\theta$, ($t$ males) and $2f(2)(1-\theta)\times(1-v) + v(1-\theta)$, ($tt$ females) in the population. The matrix of the recurrence equations now becomes:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \frac{\Psi(2)(1-\frac{v}{2})}{2f(2)(1-v)+v} \\ \frac{2\Psi(2)(1-v\theta)}{2f(2)(1-v)+v} & \frac{\Psi(2)(1-\frac{v}{2})}{2f(2)(1-v)+v} \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix}. \quad \text{(A11)}$$

Therefore, solving for λ and with $\lambda > 1$ gives the generalized expression (see Table 6).

In the case of variable mobility and fighting, the frequencies of J and Jj are: $freq(J) = [f(2)(1-v) + 3v/4]\theta y$; $freq(Jj) = [2(1-v)f(2)(1-\theta) + v(1-\theta^2)]x + [(f(2)(1-v) + 3v/4)\times(1-\theta)]y$. We divide by $2\Psi(2)\theta$ (j males) and $2\Psi(2)(1-\theta)$ (jj females) in the population. The matrix of the recurrence equations now becomes:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \frac{f(2)(1-v)+\frac{3}{4}v}{2\Psi(2)} \\ \frac{(1-v)f(2)}{\Psi(2)} + \frac{v}{2\Psi(2)}\left(\frac{1-\theta^2}{1-\theta}\right) & \frac{f(2)(1-v)+\frac{3}{4}v}{2\Psi(2)} \end{pmatrix} \times \begin{pmatrix} x \\ y \end{pmatrix}. \quad \text{(A12)}$$

Therefore, solving for λ and with $\lambda > 1$ gives the generalized expression (see Table 6).

Single-sex broods and the spread of tolerance or fighting

The same assumptions as in the simplest model apply, except that δ is the proportion of single-sex broods produced by a female, where $0 \leq \delta \leq 1$. Single-sex broods are assumed to be equally likely to be all male or all female. In the case of the spread of tolerance, the frequencies of *T* and *Tt* are $freq(T) = [\Psi(2)(1 - v/2)/2]y$; $freq(Tt) = [\Psi(2)(1 - v) + v\delta\Psi(2)]x + [\Psi(2)(1 - v/2)/2]y$. We divide by the frequency of background (*t*) males and (*tt*) females $(1 - v)f(2) + v/2$. The matrix of the recurrence equations now becomes:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \frac{\frac{1}{2}\Psi(2)(1-\frac{v}{2})}{(1-v)f(2)+\frac{v}{2}} \\ \frac{\Psi(2)((1-v)+v\delta)}{(1-v)f(2)+\frac{v}{2}} & \frac{\frac{1}{2}\Psi(2)(1-\frac{v}{2})}{(1-v)f(2)+\frac{v}{2}} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}. \quad \text{(A13)}$$

Therefore, solving for λ and with $\lambda > 1$ gives the generalized expression (see Table 6).

In the case of the spread of fighting behavior, the frequencies of *J* and *Jj* are $freq(J) = [(1 - v)f(2)/2 + 3v/8]y$; $freq(Jj) = [(1 - v)f(2) + (1 - \delta/2)v]x + [(1 - v)f(2)/2 + 3v/8]y$. We divide by the frequency of background (*j*) males and (*jj*) females Ψ(2). The matrix of the recurrence equations now becomes:

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 0 & \frac{1}{2\Psi(2)}\left((1-v)f(2)+\frac{3v}{4}\right) \\ \frac{(1-v)f(2)+\left(1-\frac{\delta}{2}\right)v}{\Psi(2)} & \frac{1}{2\Psi(2)}\left((1-v)f(2)+\frac{3v}{4}\right) \end{pmatrix} \times \begin{pmatrix} x \\ y \end{pmatrix}. \quad \text{(A14)}$$

Therefore, solving for λ and with $\lambda > 1$ gives the generalized expression (see Table 6).

Double killings and the spread of tolerance or fighting

The same assumptions as in the simplest model apply, except that κ is the probability of double killings occuring during combat, where $\kappa = 0$ is the simplest case (no double killings). The frequencies of *T* and *Tt* are $freq(T) = [\Psi(2)(1 - v/2)/2]y$; $freq(Tt) = [(1 - v/2)\Psi(2)]x + [\Psi(2)(1 - v/2)/2]y$. The number of males (*t*) and females (*tt*) is $(1 - v)f(2) + v(1 - \kappa)/2$. This results in an eigenmatrix of the form seen in Equation 1, where:

$$\Lambda = \frac{\frac{\Psi(2)}{2}\left(1-\frac{v}{2}\right)}{(1-v)f(2)+\frac{v}{2}(1-\kappa)}. \quad \text{(A15)}$$

Solving the characteristic equation gives the generalized expression for the spread of tolerance (see Table 6).

In the case of the spread of fighting ability, the frequencies of *J* and *Jj* are $freq(J) = [f(2)(1 - v)/2 + v((1 - \kappa)/8 + 1/4)]y$; $freq(Jj) = [f(2)(1 - v) + v((1 - \kappa)/4 + 1/2)]x + [f(2)(1 - v)/2 + v((1 - \kappa)/8 + 1/4)]y$. The number of males (*j*) and females (*jj*) is Ψ(2). This results in an eigenmatrix of the form seen in Equation 1, where:

$$\Lambda = \frac{f(2)(1-v)+v\left[\frac{1}{4}(1-\kappa)+\frac{1}{2}\right]}{2\Psi(2)}. \quad \text{(A16)}$$

Solving the characteristic equation gives the generalized expression for the spread of fighting as mobility varies (see Table 6).

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