The evolution of parasites from their hosts: intra- and interspecific parasitism and Emery's rule

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In some taxa of Hymenoptera, fungi, red algae and mistletoe, parasites and their hosts are either sibling species or at least closely related (Emery's rule). Three evolutionary mechanisms have been proposed for this phenomenon: (i) intraspecific parasitism is followed by sympatric speciation; (ii) allopatric speciation is followed by secondary sympatry and the subsequent parasitism of one sibling species by the other; and (iii) allopatric speciation of a species with intraspecific parasitism is followed by secondary sympatry, in which one species becomes an obligate parasite of the other. Mechanisms (i) and (ii) are problematic, while mechanism (iii) has not, to our knowledge, been analysed quantitatively. In this paper, we develop a model for single- and two-species evolutionary stable strategies (ESSs) to examine the basis for Emery's rule and to determine whether mechanism (iii) is consistent with ESS reasoning. In secondary sympatry after allopatric speciation, the system's evolution depends on the relative abundances of the two sibling species and on the proportional damage wrought by parasites of each species on non-parasitic members of the other. Depending on these interspecific effects, either the rarer or the commoner species may become the parasite and the levels of within-species parasitism need not determine which evolves to obligate parasitism.

Keywords: Hymenoptera; social parasitism; evolutionary stable strategy

1. INTRODUCTION

Social parasitism is widespread in the Hymenoptera (Wilson 1971). In some taxa, the parasites and their hosts are sibling species (the 'strict' version of 'Emery's rule'; Emery 1909; Wilson 1971; Elmes 1978; Bolton 1988; Heinze & Buschinger 1988; Ward 1989; Bourke & Franks 1991). In others, the parasites and their hosts are separately monophyletic, although of course the ancestral hosts and parasites may have been sibling species (the 'loose' version of Emery's rule (e.g. Ronquist 1994; Ward 1996; Lowe & Crozier 1997)). These phenomena are not confined to hymenopterans: Emery's rule also applies to groups of fungi, red algae and perhaps mistletoe (Goff *et al.* (1997) and references therein). Three sequences of events have been suggested to lead to either strict or loose conformity with Emery's rule.

- (i) Obligate parasites may be produced by the sympatric speciation of parasites from their conspecific hosts (Buschinger 1965, 1970, 1986, 1990; Bourke & Franks 1991).
- (ii) A non-parasitic species may split allopatrically into two sibling species. In secondary sympatry, one species may then evolve to parasitize the other (Wilson 1971). This process is essentially no differ-

ent from that resulting in parasitism by distantly related organisms. However, strict conformity with Emery's rule would be more likely because parasites can pass more easily through the defences of a sibling species than through those of less closely related species.

- (iii) Finally, intraspecific parasitism may arise and be maintained at some intermediate frequency in a population that then undergoes allopatric speciation. Slight biological differences cause one daughter species (species 1) to show a higher level of parasitism than the other (species 2). Upon regaining sympatry, each species can parasitize the other. The imbalance in the selection on parasitism on the two species causes species 1 to become wholly parasitic on species 2 (Starr 1979).

As Bourke & Franks (1991) point out, the difficulty with hypothesis (i) is its requirement for full reproductive isolation to emerge without allopatry. Hypothesis (ii) cannot account for the strict version of Emery's rule unless parasites are unable to parasitize non-sibling species. Starr's hypothesis, (iii), has not yet been formulated in sufficiently quantitative terms to allow rigorous examination. In this paper, we use a model for single- and two-species evolutionary stable strategies (ESSs) to examine the hypotheses proposed to account for both strict and loose versions of Emery's rule.

2. INTRASPECIFIC PARASITISM

We model a population of communal breeders in which each individual can either cooperate or act as a social para-

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Figure 1. Fitness of non-parasites (solid line) and parasites (dashed line) in relation to the frequency of parasites, p . The ESS, p^* , is the value for which $w_P = w_N$; in this case, $p^* = 0.219$. Parameter values: $F = 4$; $c = 1.3$.

site—by entering a colony, and killing and replacing brood, or simply by dumping eggs; in either case, the parasitism results in a cost to the hosts. It is common in cases of interspecific parasitism that at most one parasitic female occupies a host nest (e.g. Alford 1975, p. 97; Buschinger & Klump 1988), so the number of host brood lost is independent of the number of parasites arriving at the nest. The same outcome could result if the host brood were vulnerable for only a limited period, e.g. as eggs (Batra *et al.* 1993).

We define the frequency of parasites as p ; non-parasites (frequency $1 - p$) found colonies each of which contains F non-parasites. The mean number of parasites per nest is $pF/(1 - p)$, so if parasites are randomly distributed, the probability that a nest is parasitized is $1 - \exp[-pF/(1 - p)]$. In each parasitized nest, the offspring of c of the foundresses are killed and replaced. (This may occur if only one parasite can survive in a nest. Alternatively, parasitism may be limited if only a fraction of the foundresses' offspring are vulnerable or if the young are at risk only during a particular developmental stage.) The fitness of a parasite (w_P) is then $c[\text{fraction of nests parasitized}]/[\text{mean parasites per nest}]$:

$$w_P = \frac{c(1 - p)[1 - e^{-pF/(1 - p)}]}{pF}, \quad (2.1)$$

and that of a non-parasite (w_N) is the number of surviving offspring, averaged over parasitized and unparasitized nests:

$$w_N = e^{-pF/(1 - p)} + (1 - c/F)[1 - e^{-pF/(1 - p)}]. \quad (2.2)$$

As

$$\lim_{p \rightarrow 0} \frac{w_P}{w_N} = c, \quad (2.3)$$

parasitism spreads in a non-parasitic population provided $c > 1$; and parasitism clearly cannot become fixed, as

$$\lim_{p \rightarrow 1} \frac{w_P}{w_N} = 0. \quad (2.4)$$

There is thus an internal equilibrium, at which $w_P = w_N$; the ESS value of p can be found by iteration. Figure 1 shows how the fitnesses of parasites and non-parasites vary

with p , and the predicted equilibrium level of parasitism, p^* . Table 1 shows how p^* varies with F and c . Provided $c > 1$, p^* increases with F and c/F towards an asymptote at c/F , the fraction of a colony's brood that a parasite kills and replaces.

If the population is split by a geographical barrier, the above reasoning will hold for each sub-population and parasitism will reach an equilibrium level in both. If they undergo allopatric speciation and subsequently return to sympatry, parasitic members of each species may be able to parasitize nests of either.

3. TWO SPECIES

The two sibling species now coexist, at densities N_1 and N_2 ; their colony sizes are F_1 and F_2 and their levels of parasitism p_1 and p_2 . A parasite of species i in a colony of species j kills and replaces the offspring of c_{ij} of its hosts. The mean number of parasites (of both species) per nest (of either) is $[\text{total parasites}]/[\text{total nests}]$, i.e.

$$\mu = \frac{N_1 p_1 + N_2 p_2}{N_1(1 - p_1)/F_1 + N_2(1 - p_2)/F_2}. \quad (3.1)$$

By extension from equation (2.1), the fitness of a parasitic member of species i is

$$w_{P_i} = \frac{1 - e^{-\mu}}{N_1 p_1 + N_2 p_2} \left[N_1(1 - p_1) \frac{c_{i1}}{F_1} + N_2(1 - p_2) \frac{c_{i2}}{F_2} \right], \quad (3.2)$$

and, by extension from equation (2.2), that of a non-parasite

$$w_{N_i} = e^{-\mu} + \frac{1 - e^{-\mu}}{N_1 p_1 + N_2 p_2} \left[N_1 p_1 \left(1 - \frac{c_{1i}}{F_1} \right) + N_2 p_2 \left(1 - \frac{c_{2i}}{F_2} \right) \right]. \quad (3.3)$$

The evolution of parasitism in the two species depends now on the functions relating each species' ESS to the current level of parasitism in the other: on $p_1^*(p_2)$ and $p_2^*(p_1)$. Figure 2 illustrates how the system approaches the two-species ESS from any initial position in p_1 – p_2 space.

If the species differ only in colony size, F , or only in the number of brood replaced by a parasite, c (with $c_{11} = c_{12}$ and $c_{21} = c_{22}$), then whichever species has the higher single-species ESS level of parasitism will also be the predominant parasite in the two-species system, as predicted by Starr (1979). The extent to which this species monopolizes parasitism depends on its relative density, as shown in figures 3 and 4. The total parasite load lies between those at the two single-species equilibria, p_1^* and p_2^* . If the predominant parasite (species 1 in figures 3 and 4) is scarce, it is fully parasitic ($p_1^* = 1$) and the shortfall in total parasite load is made up by partial parasitism by species 2. There is a narrow range over which species 1 is fully parasitic and species 2 not at all; and finally, as species 1 becomes numerically dominant, it is polymorphic for parasitism and species 2 is non-parasitic. Thus, the two-species ESS is, for low, medium and high densities of species 1, (sp. 1 obligate; sp. 2 facultative), (obligate; non-parasitic) and (facultative; non-parasitic), respectively.

If the two species differ in both F and c , other outcomes are possible. They can be predicted from the ESS levels of parasitism in the two-species system when one species is extremely rare. If species 1 is rare, species 2's level of parasitism is at its single-species ESS, p_2^* , and

Table 1. The ESS level of parasitism, p^* , for various values of F , the number of females in a colony, and c/F , the proportion of the brood that are killed and replaced by the parasite.

		c/F				
		0.1	0.25	0.5	0.75	0.9
F	2	0	0	0	0.748	0.9
	4	0	0	0.489	0.75	0.9
	8	0	0.226	0.5	0.75	0.9
	16	0.07	0.249	0.5	0.75	0.9
	32	0.097	0.25	0.5	0.75	0.9

Figure 2. Phase diagram showing the functions $p_1^*(p_2)$ (solid line) and $p_2^*(p_1)$ (dashed line). Arrows show the directions in which the system will evolve: horizontal arrows show the changes in p_1 , vertical arrows show the changes in p_2 . From any initial state, the system will evolve towards the region between the two lines and will subsequently move towards the two-species ESS shown by the solid circle. Parameter values: $N_1 = 700$; $N_2 = 1000$; $F_1 = 10$; $F_2 = 7$; $c_{11} = c_{12} = 4.5$; $c_{21} = c_{22} = 2$. The single-species equilibria for species 1 and 2 are $p^* = 0.450$ and 0.262 , respectively; at the two-species ESS, species 1 is completely parasitic and $p_2 = 0.0332$.

$$w_{p_2} = w_{N_2} = 1 - p_2^*. \quad (3.4)$$

The fitnesses of parasitic and non-parasitic members of species 1 approach

$$\lim_{N_1 \rightarrow 0} w_{p_1} = \frac{c_{12}}{c_{22}} w_{p_2} = \frac{c_{12}}{c_{22}} (1 - p_2^*), \quad (3.5)$$

and

$$\lim_{N_1 \rightarrow 0} w_{N_1} = 1 - \frac{c_{21}/F_1}{c_{22}/F_2} (1 - w_{N_2}) = 1 - \frac{c_{21}/F_1}{c_{22}/F_2} p_2^*. \quad (3.6)$$

To simplify the notation, we now define $k_{ij} = c_{ij}/F_j$. Species 1 will be parasitic when rare if

$$\frac{k_{12}}{k_{21}} > \frac{k_{22}/k_{21} - p_2^*}{1 - p_2^*}. \quad (3.7)$$

It will be the predominant parasite at all relative den-

Figure 3. The relationship between the relative abundance of species 1 (as a proportion of the sum of the two populations) and the ESS levels of parasitism in species 1 (dotted line), species 2 (dashed line) and the system as a whole (solid line). Parameter values: $F_1 = 10$; $F_2 = 12$; $c_{11} = c_{12} = c_{21} = c_{22} = 4$.

Figure 4. The relationship between the relative abundance of species 1 (as a proportion of the sum of the two populations) and the ESS levels of parasitism in species 1 (dotted line), species 2 (dashed line) and the system as a whole (solid line). Parameter values: $F_1 = 10$; $F_2 = 10$; $c_{11} = c_{12} = 5$; $c_{21} = c_{22} = 4$.

sities (as in figures 3 and 4) if, when species 2 is rare, its ESS is non-parasitism: $p_2^* = 0$. This is the case if

$$\frac{k_{12}}{k_{21}} > \frac{1 - p_1^*}{k_{11}/k_{12} - p_1^*}. \quad (3.8)$$

Species 1 is thus the predominant parasite if inequalities (3.7) and (3.8) are both true; if both are false, species 2 is the parasite. If, however,

Figure 5. The relationship between the relative abundance of species 1 (as a proportion of the sum of the two populations) and the ESS levels of parasitism in species 1 (dotted line), species 2 (dashed line) and the system as a whole (solid line). Parameter values: $F_1 = 12$; $F_2 = 10$; $c_{11} = c_{12} = 4.5$; $c_{21} = c_{22} = 4$.

Figure 6. The relationship between the relative abundance of species 1 (as a proportion of the sum of the two populations) and the ESS levels of parasitism in species 1 (dotted line), species 2 (dashed line) and the system as a whole (solid line). Parameter values: $F_1 = 12$; $F_2 = 10$; $c_{11} = 3$; $c_{12} = 4$; $c_{21} = 1.2$; $c_{22} = 4$.

$$\frac{k_{22}/k_{21} - p_2^*}{1 - p_2^*} < \frac{k_{12}}{k_{21}} < \frac{1 - p_1^*}{k_{11}/k_{12} - p_1^*}, \quad (3.9)$$

then whichever species is the rarer parasitises its commoner sibling (figure 5); and if

$$\frac{1 - p_1^*}{k_{11}/k_{12} - p_1^*} < \frac{k_{12}}{k_{21}} < \frac{k_{22}/k_{21} - p_2^*}{1 - p_2^*}, \quad (3.10)$$

it is the commoner species that is the parasite (figure 6).

4. DISCUSSION AND CONCLUSIONS

The evolution of this system depends on the destruction wrought by the parasitic members of each species on the non-parasitic members of the other; i.e. on the ratio k_{21}/k_{12} . For obligate parasitism to arise rapidly, the predominant parasite must generally be rare, either under 'normal' circumstances (figures 3 and 4) or by the rarity effect (figure 5). Even with partial parasitism, however, one species is more parasitic than the other. Traits that enhance the ability to resist parasitism are likely to be

more strongly selected in the less parasitic of the two species. The consequences of the spread of such traits would be both a lowering of the fitness of conspecific parasites and selection for improved parasitic ability in heterospecific parasites. An arms race may thus drive the system towards a final state in which one species is an obligate parasite on the other, provided that the host is sufficiently abundant.

Starr's (1979) proposed sequence of events is compatible with ESS reasoning, but the species with the higher level of within-species parasitism need not become the predominant parasite in the two-species system. This depends partly on the two species' relative densities, but more importantly on their relative rates of interspecific parasitism.

Under this model, the immediate outcome fits the strict version of Emery's rule. The loose form would then arise either through subsequent speciation in both host and parasite clades or through the parasite transferring to novel but related hosts.

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