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Oviposition strategies, host coercion and the stable exploitation of figs by wasps

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A classic example of a mutualism is the one between fig plants (*Ficus*) and their specialized and obligate pollinating wasps. The wasps deposit eggs in fig ovules, which the larvae then consume. Because the wasps derive their fitness only from consumed seeds, this mutualism can persist only if the wasps are prevented from laying eggs in all ovules. The search for mechanisms that can limit oviposition and stabilize the wasp–seed conflict has spanned more than three decades. We use a simple foraging model, parameterized with data from two *Ficus* species, to show how fig morphology reduces oviposition rates and helps to resolve the wasp–seed conflict. We also propose additional mechanisms, based on known aspects of fig biology, which can prevent even large numbers of wasps from ovipositing in all ovules. It has been suggested that in mutualistic symbioses, the partner that controls the physical resources, in this case *Ficus*, ultimately controls the rate at which hosts are converted to visitors, regardless of relative evolutionary rates. Our approach provides a mechanistic implementation of this idea, with potential applications to other mutualisms and to theories of virulence.

Keywords: cooperation; *Ficus*; host coercion; mutualism; pollination; virulence

1. INTRODUCTION

One of the clearest examples of the conflict between mutualism and parasitism is the highly coevolved relationship between *Ficus* plants ('figs', Moraceae) and their obligate pollinating wasps (Hymenoptera, Agaonidae; *sensu* Rasplus *et al.* 1998). Dispersing female wasps loaded with pollen from their natal trees arrive at receptive fig trees and dig their way into urn-shaped inflorescences, colloquially also called figs, but technically known as syconia. In monoecious *Ficus* species, syconia are lined with both male flowers and uniovulate female flowers. After entry, the wasp foundresses insert their ovipositors down the styles of female flowers and deposit a single egg per ovule, while simultaneously distributing pollen over many of the female flowers. Pollination can be 'active,' in that foundresses show distinctive behaviours for collecting and depositing pollen (Ramirez 1970; Frank 1984), or 'passive,' in that pollen simply rubs off foundresses' bodies. The developing pollinator wasp larva may feed on the endosperm of the developing seed (Grover & Chopra 1971) or is also able to 'gall' the ovule if the ovule happens not to receive pollen (Jousselin & Kjellberg 2001; E. Jousselin and E. A. Herre, unpublished data). Only pollinated ovules not receiving an egg develop into seeds, which means oviposition causes seed resources to be reallocated to male function by rearing the wasps that disperse pollen. At maturity, male wasps emerge first from their galls, and search for and mate with female wasps still inside their own galls. The female wasps then emerge into the cavity of the syconium, gather or become covered in pollen, and exit in search of a tree with receptive figs. After a foundress successfully enters a fig, she rarely emerges again (but see Gibernau *et al.* 1996 and below).

The fig–wasp mutualism exhibits a clear and fundamental conflict of interest. Individual wasps would benefit from laying eggs in all ovules, but the evolutionary spread of such a strategy would preclude seed production and eventually drive the host population extinct. In fact, oviposition levels rarely exceed 70–80% of ovules, with levels of 50–60% being typical (Herre 1989; Nefdt & Compton 1996). The search for mechanisms that can limit oviposition and stabilize the pollinator–seed conflict has spanned more than 30 years (e.g. Galil & Eisikowitch 1968*a*, 1971; Janzen 1979*a*,*b*; Murray 1985; Verkerke 1986; Kjellberg *et al.* 1987; Bronstein 1988*a*,*b*; Frank 1989; Herre 1989, 1996, 1999; Addicott *et al.* 1990; West & Herre 1994; Ganeshaiah *et al.* 1995; Nefdt &

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Compton 1996; Anstett *et al.* 1997; Herre & West 1997; Jousselin *et al.* 2001, 2003; Weiblen 2002).

As with most mutualisms, the classic explanations invoked to explain cooperation do not apply: figs and wasps are not kin, there is no chance for reciprocal altruism, seeds and wasps disperse over long distances, and syconia heavily laden with wasp larvae are not selectively aborted. Instead, suggested explanations for why foundresses do not oviposit in all ovules are tied to the observations that style length is highly variable (Janzen 1979*a*,*b*; Ganeshaiah *et al.* 1995, 1999) and that foundresses lay eggs primarily in shorter-styled flowers (Herre 1989; West & Herre 1994; Nefdt & Compton 1996; Jousselin *et al.* 2001). As a result, researchers have suggested three general stabilizing mechanisms (Herre 1999; Jousselin *et al.* 2002).

(i) Short ovipositors. Ovules in outer layers of flowers are unavailable for oviposition because their styles are longer than foundress ovipositors (Galil & Eisikowitch 1968*a*; Janzen 1979*b*; Ganeshaiah *et al.* 1995).

(ii) Unbeatable seeds. Ovules in outer layers of flowers are unavailable for oviposition because they are mechanically or chemically resistant to oviposition or larval development, rendering these seeds 'unbeatable' to foundresses. The latter interpretation is supported by the fact that parasitic galling wasps in the genus *Idarnes*, which oviposit from outside the syconium, also lay in inner-layer ovules, despite the longer distance (West & Herre 1994). The first two hypotheses both rely on an, as yet, unidentified evolutionary constraint.

(iii) Insufficient eggs. Insufficient foundresses arrive to fill all ovules in a syconium, as observed in several *Ficus* species (Nefdt & Compton 1996). This hypothesis relies on wasp abundance being regulated elsewhere in its life history.

As stated, these explanations have some problems. The short-ovipositor hypothesis cannot be general because many wasp species have ovipositors that can reach most, or all, ovules (Bronstein 1988*b*; Herre 1999). Nefdt & Compton (1996) compared style lengths with ovipositor lengths in 10 *Ficus* species. In five species, accessibility of ovules ranged from 90% to 99%, and in three other species, accessibility exceeded 70%. In only two species did the percentage of inaccessible ovules roughly match the percentage of ovules that develop into seeds. The insufficient-eggs hypothesis cannot be a sufficient general explanation because many syconia of many *Ficus* species regularly receive more than enough foundresses to fill all ovules, but seeds are still produced in those syconia (e.g. Herre 1989; Anstett *et al.* 1996). Finally, the unbeatable-seeds hypothesis must assume that *Ficus* has been able to evolve a stable counter-defence against over-exploitation, despite the fact that wasps most probably evolve more quickly than their plant hosts, as wasps have generation times that are orders of magnitude shorter (West & Herre 1994; Weiblen 2002). Furthermore, it is known that some galler species can oviposit in longer-styled flowers (Compton & Nefdt 1990; Cook & Power 1996).

What has been missing in studies of the *Ficus* system is a general theoretical framework within which hypotheses can be generated, tests devised and effect sizes compared. We use a simple foraging theory to argue that the complex 'style landscape' of the syconium, combined with other morphological traits, particularly ovule size, lowers oviposition rates to below that needed to fill all ovules, thereby helping to stabilize the mutualism. We also argue that the three hypotheses above can be incorporated into this more comprehensive model in such a way as to avoid the problems listed above, and we describe additional aspects of *Ficus* biology that could further reduce wasp oviposition rates. Finally, we briefly propose some empirical tests.

2. MODEL

Each wasp must budget her time between searching (probing floral styles for egg-free ovules) and handling (pushing eggs down styles). For simplicity, we assume that multiple foundresses arrive in strict sequence, meaning that later-arriving foundresses suffer especially reduced fecundity (e.g. Kathuria *et al.* 1999). Of course, this is one end of an extreme, the other end being that all foundresses effectively arrive simultaneously. However, with one exception that we will revisit below, n foundresses arriving in sequence and n arriving together are identical (either the nth foundress suffers most, or all foundresses suffer most in the last $1/n$ of their lives). We also assume that it is in the interests of the foundress to avoid 'double-laying', laying an egg in an ovule that already contains an egg, since both larvae will probably either die, or one will cannibalize the other, owing to insufficient food resources.

(a) *Model 1: pseudointerference only*

In the simplest system, we assume that all ovules are qualitatively equivalent, and that styles are selected at random. We further assume that wasps can instantaneously choose the optimal oviposition strategy. In that case, a simple explanation for fig wasps failing to lay eggs on all ovules at high foundress density is pseudointerference (wasting time probing flowers that already contain eggs). As the proportion of ovules with eggs increases, the time spent searching for ovules without eggs increases too, and accordingly, the oviposition rate will decrease with time and foundress number. To create this model we define the following parameters: N, the number of ovules per syconium; t, time-units, each unit defined as the time needed to walk to and probe a single style; T, foundress lifespan inside the syconium, in units of t; k, the time it takes to lay an egg, defined as a multiple of the time it takes to probe a style; P_t, the proportion of ovules with eggs; and R_t, the rate of egg laying at time t.

The rate of resource acquisition (rate of egg laying), R_t, is

$$1/(\text{handling time} + \text{search time}). \tag{2.1}$$

Search time, in terms of the number of probes before an egg-free ovule is found, is

$$\sum_{i=0}^{\infty} i\, p_t^i (1 - p_t) = \frac{p_t}{1 - p_t}; \tag{2.2}$$

for example, if $p_t = 0.5$, then $0.5/(1 - 0.5) = 1$. That is, if half the ovules have eggs, then a foundress probes, on average, one ovule with an egg before probing an egg-free ovule.

Handling time is $1 + k$. The 1 represents the time spent probing the style of an egg-free ovule, and k represents the time spent ovipositing, in multiples of probing time-units t.

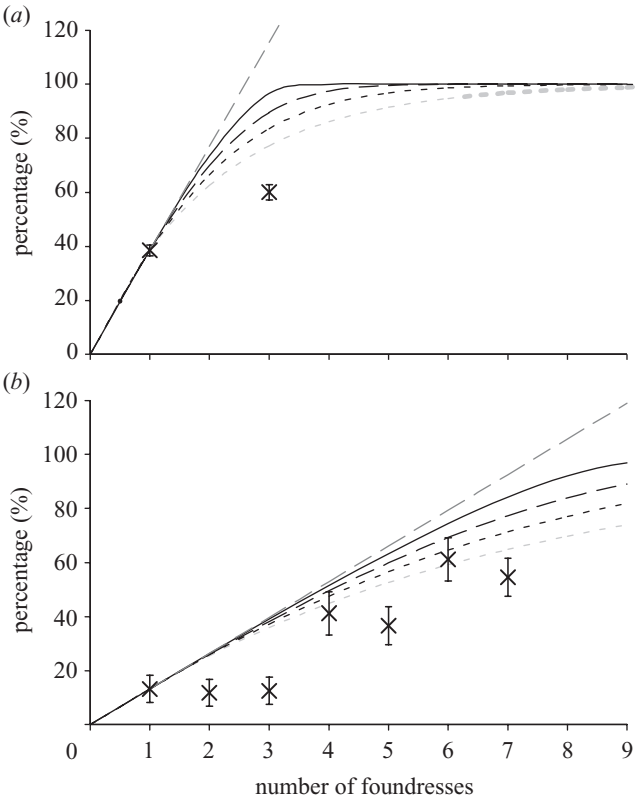

Figure 1. Oviposition profiles for model 1, with pure pseudointerference. (*a*) *Ficus microcarpa*. (*b*) *Ficus maxima*. In both figures, the straight left-hand line (dashed) is a null model without pseudointerference, or equivalently, if there are public markers indicating which styles already result in ovules with eggs. The curved lines, from left to right, are for values of k equal to 10, 3, 1 and 0, respectively. Crosses mark the observed data, and error bars enclose one standard error. Pseudointerference alone can reduce oviposition profiles below the null case.

Thus, the rate of oviposition is

$$R_t = (1 + k + p_t/(1 - p_t))^{-1}, \tag{2.3}$$

making the proportion of ovules with eggs by time t

$$p_t = \sum_{i=0}^{t-1} R_t \Big/ N. \tag{2.4}$$

We parameterize our model using *Ficus microcarpa* data (Jousselin *et al.* 2001; see electronic Appendix A). The proportion of ovules that one foundress lays eggs in, P_T, is 38.5%. However, we do not have k. Nonetheless, we can estimate the lifespan T of a wasp, in terms of units of probing events, for any value of k, by iterating equation (2.4) until $p_t = 38.5\%$. At this point $t = T$. Once we have the lifespan of a foundress, we can predict the proportion of ovules that F foundresses will lay eggs on as $p_{F \times T}$. We can then solve for the value of k that predicts the observed proportion of ovules oviposited in by three foundresses (57.0%). We call the function relating foundress number to oviposition percentage the 'oviposition profile'.

However, this simple model predicts that three foundresses should lay more eggs than is observed (figure 1*a*), the lowest predicted value of P_{3T} being 77.2% (at the biologically unrealistic $k = 0$). Thus, though this model predicts the right form of relationship between foundress density and the proportion of ovules with eggs, it does not predict a level of pseudointerference sufficient to explain observed relationships. By contrast, note that without pseudointerference, the null expectation is that three foundresses should lay in $3 \times 38.5\% = 115.5\%$ of ovules, and thus, even this simple model can produce a reduction in oviposition levels. Moreover, repeating the above procedure for *Ficus maxima*, in which $p_T = 13.2\%$, yields a closer match of predicted to observed values (figure 1*b*), the reason being that such a low value of p_T implies a short foundress lifespan, and thus, less time for later foundresses to overcome the effect of pseudointerference.

It might seem counterintuitive that the oviposition profile rises with increasing handling time, k, but this is a consequence of our parameterization procedure. Since we do not have clock time estimates of foundress lifespans (T), we estimate the lifespan of the first foundress in terms of how many probing time-units (t) are needed to fill the observed percentage of ovules. For instance, $141t = T$ is needed for a foundress to fill 38.5% of ovules in *F. microcarpa*, at $k = 1$. If we increase k to, say, 10, the new estimated lifespan of the first foundress must now increase to 695 units to accommodate the increased workload. Since we then assume, conservatively, that succeeding foundresses all enjoy the same lifespan, total oviposition percentages therefore rise accordingly. We will relax this assumption of equal lifespans across foundresses in model 3.

(b) *Model 2: variation in style length and ovule quality*

A more realistic model of oviposition strategies accounts for the fact that wasps preferentially lay in ovules with short styles, presumably to maximize their laying rate by reducing handling time, even if this leads to some time wasted rejecting ovules with long styles. In support, Nefdt & Compton (1996) have reported that observed foundresses 'often probed down a number of styles before ovipositing in one of them (distinguished by a pumping action of the gaster) and … they seemed more likely to oviposit when the style was short'. As short-styled ovules free of eggs become rare, it eventually pays to accept ovules with longer styles. Again, in support, Nefdt & Compton (1996) have found that the mean style length of occupied flowers in three *Ficus* species increases with the proportion of ovaries occupied by wasp progeny (see Galil & Eisikowitch 1968*b*). An important consequence of style-length variation is that the first foundress is greatly advantaged because she gets to concentrate on the shortest styles.

To extend our first model, such that wasps can choose to ignore some ovules, we divide ovules into three categories: inner, middle and outer, as defined by their style lengths: L_1, L_2 and L_3. This allows us to compare our results directly with the data of Jousselin *et al.* (2001), and it greatly simplifies the modelling, while having little effect on the predictions. We then define the three possible search strategies wasps may employ: lay on L_1 only, lay on L_1 and L_2 only, or lay on L_1, L_2 and L_3, yielding oviposition rates of $R_{t,1}$, $R_{t,2}$ and $R_{t,3}$. The wasp chooses at each moment the strategy yielding the highest rate of egg laying.

To calculate $R_{t,1}$, $R_{t,2}$ and $R_{t,3}$ we need search time (finding and probing styles that are either too long or that end in ovules already containing an egg), and handling time (probing and laying an egg in an acceptable ovule).

The time spent searching unacceptable styles is the number searched ($\bar{p}/(1-\bar{p})$ from equation (2.2), where $\bar{p}$ is the proportion of unacceptable ovules) multiplied by the average time spent searching. For $R_{t,1}$, because any style longer than L_1 is rejected, this yields a simple extension of equation (2.3); if we define time-units as the time to probe a style of average length ($\bar{L}$), then a foundress uses only a fraction of the standard time-unit, $L_1/\bar{L}$, to oviposit in an inner style.

$$R_{t,1} = [(L_1/\bar{L})(1 + k + p_t/(1 - p_t))]^{-1}. \quad (2.5)$$

We are assuming that foundresses can differentiate long from short styles only by probing them, consistent with reports from the literature (Galil & Eisikowitch 1968*b*; Nefdt & Compton 1996). For example, short and long styles are closely packed, and the development of styles is often such that a uniform stigmatic surface is presented to foundresses (Verkerke 1986; Ganeshaiah *et al.* 1999). These observations suggest that style lengths are concealed from foundresses.

For $R_{t,2}$, the basic approach is as follows. Styles are placed in four categories:

(i) inner and full, these are rejected and take $L_1/\bar{L}$ to search;
(ii) inner and empty, these are accepted and take $L_1/\bar{L}$ to search;
(iii) middle and full, or outer and either full or empty, these are rejected and take $L_2/\bar{L}$ to search; and
(iv) middle and empty, these are accepted and take $L_2/\bar{L}$ to search.

If the number of styles in each of these categories is $n_{\text{i–iv}}$, then the time spent searching for an acceptable egg is

$$\bar{p}/(1-\bar{p}) \times (n_{\text{i}}L_1/\bar{L} + n_{\text{iii}}L_2/\bar{L})/(n_{\text{i}} + n_{\text{iii}}) \quad (2.6)$$

and the time spent ovipositing is

$$(1 + k) \times (n_{\text{ii}}L_1/\bar{L} + n_{\text{iv}}L_2/\bar{L})/(n_{\text{ii}} + n_{\text{iv}}); \quad (2.7)$$

thus

$$R_{t,2} = 1/\left[\frac{\bar{p}}{1-\bar{p}} \times (n_{\text{i}}L_1/\bar{L} + n_{\text{iii}}L_2/\bar{L})/(n_{\text{i}} + n_{\text{iii}})\right] + \left[(1 + k) \times \frac{n_{\text{ii}}L_1/\bar{L} + n_{\text{iv}}L_2/\bar{L}}{n_{\text{ii}} + n_{\text{iv}}}\right]. \quad (2.8)$$

Deriving $R_{t,3}$ follows the same method, but the search times are weighted by the relative frequencies at which styles must be probed to lengths $L_{1,2,3}$ before being accepted or rejected.

To find the proportions of inner, middle and outer ovules a single foundress will lay eggs in, for given values of k, we simulate a wasp searching in a syconium with ovules in the three categories (see electronic Appendix B). $R_{t,1–3}$ are assessed, a laying strategy selected, then a style selected at random. The style is either rejected, or an egg is laid, and time is moved forward accordingly. This process is iterated until the overall proportion of seeds with eggs matches the observed data for a single foundress, yielding an estimate of T (a foundress's lifespan inside a syconium). This process is repeated 1000 times, and the average is taken to be T.

We now run our model for both *F. microcarpa* and *F. maxima* data. For *F. microcarpa*, the parameterized

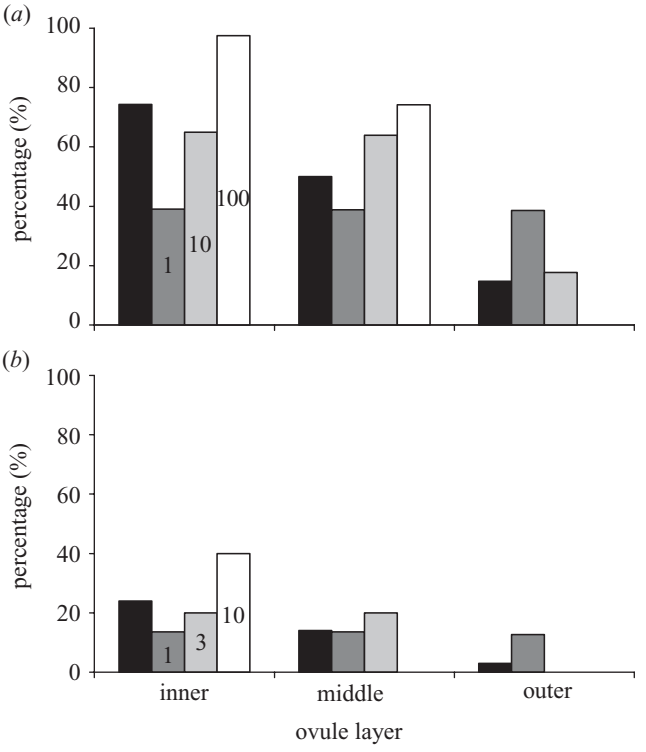

Figure 2. Style-length usage by the first foundress. (*a*) *Ficus microcarpa*. (*b*) *Ficus maxima*. In both figures, for low values of k, foundresses forage indiscriminately, ovipositing down styles of all lengths. However, as k increases, longer styles become proportionally more time-consuming to oviposit in, and thus, earlier foundresses refuse longer styles. Observed data are shown in black, other bars are model predictions and are annotated with values of k.

model predicts that when $k > 1$, short-styled flowers will be used more often than long-styled flowers (figure 2*a*). Further, as a consequence of concentrating on short-styled ovules, a minimum of four foundresses (carrying enough eggs to fill $4 \times 38.5\% = 154\%$ of ovules) is needed to fill 100% of ovules (figure 3*a*). Since three foundresses fill 92.8% of ovules, and since *F. microcarpa* syconia typically receive three or fewer foundresses (Gibernau *et al.* 1996), even the minimal assumptions and approximate parameter estimates used in this second model can partly explain the stability of this mutualism. However, the predicted oviposition profile is much steeper than the observed data and only slightly flatter than the model 1 pseudointerference case (figure 3*a*). Moreover, to produce even these results, it is necessary to assume very long handling times ($k = 100$). Thus, in this species, it is clear that model 2 is not sufficient to explain the observed oviposition profile.

However, for *F. maxima*, there is also preferential use of short-styled ovules (figure 2*b*), and the overall fit of the oviposition profile to data is much closer than in the *F. microcarpa* case (figure 3*b*), with as many as 10 foundresses unable to fill all ovules. Given that the maximum observed number of foundresses per fig is 10 (median = 3; E. A. Herre, unpublished data), style length variation combined with pseudointerference (model 2) is sufficient to explain the stability of mutualism in this species.

Finally, beyond variation in style length, any variation in ovule quality will also alter search strategy. For example,

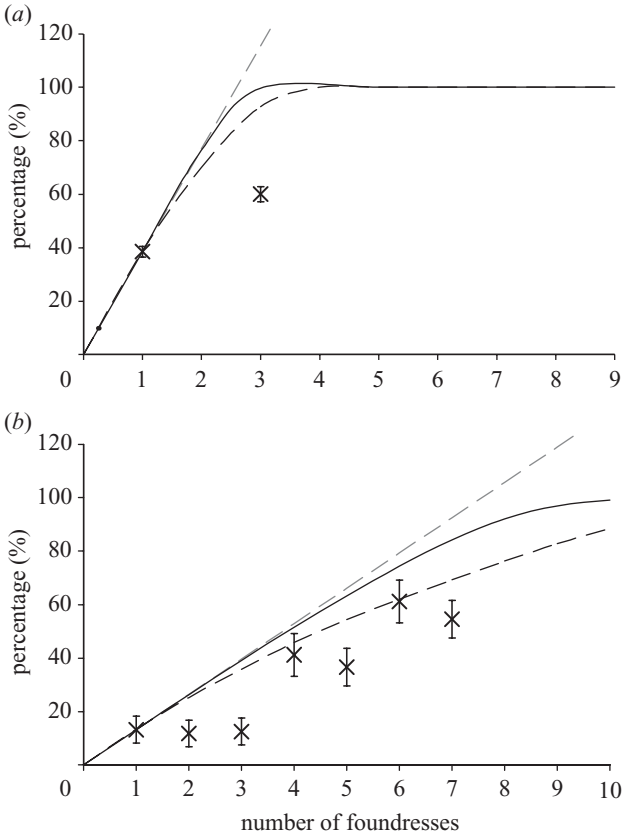

Figure 3. Oviposition profiles for model 2, with pseudointerference and style length variation. (*a*) *Ficus microcarpa*. (*b*) *Ficus maxima*. For higher values of k, earlier foundresses refuse longer styles (figure 2), with the result that, on average, they oviposit in shorter styles than do later foundresses. As a consequence, for higher values of k (100 in (*a*), 10 in (*b*); dashed curves), the oviposition profile rises less steeply with number of foundresses than in the equivalent model 1 cases with the same k values (solid curves). The fit of prediction to observed is closer in *F. maxima*, especially since using microscopes to score egg presence slightly underestimates true oviposition percentages. The leftmost dashed line represents the straight-line null model, as in figure 1. Error bars are standard errors.

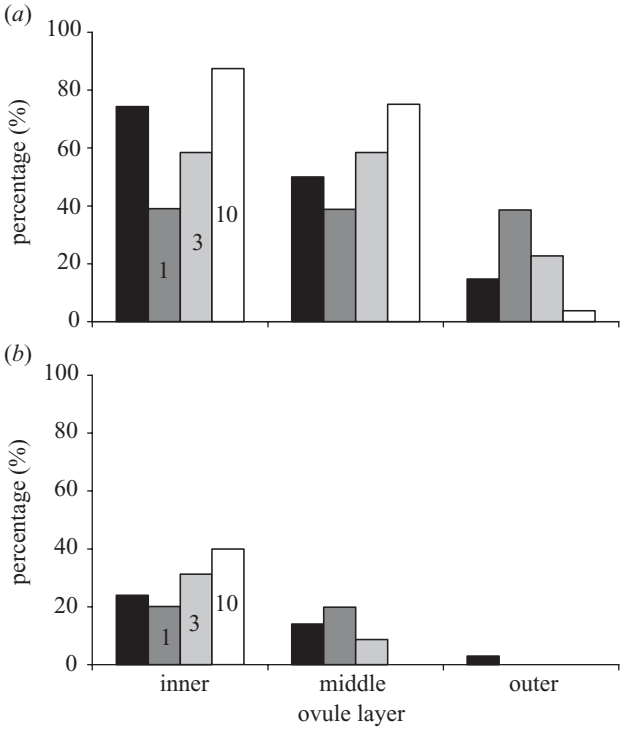

Figure 4. Style-length usage by a single foundress. (*a*) *Ficus microcarpa*. (*b*) *Ficus maxima*. Same as in figure 2, but here, ovule quality is arbitrarily reduced for outer ovules: $M_1 = 1$, $M_2 = 0.8$ and $M_3 = 0.6$. Compared with equal-quality ovules, the use of outer ovules is further depressed for a given value of k. Compare style length usage for $k = 10$ with its equivalent in figure 2. Observed data are shown in black; other bars are model predictions and are annotated with values of k.

Anstett (2001) reports that females in short-styled ovules of *F. microcarpa* are more likely to be mated, and appear to grow larger and emerge earlier. We can incorporate differences in ovule quality by adding the parameters $M_{1,2,3}$:

$$R_{t,1} = M_1[(L_1/\bar{L})(1 + k + p_t/(1 - p_t))]^{-1}, \qquad (2.9)$$

where M_i depends on the probability of an egg producing a wasp from an egg laid in layer i, and also on the quality (strength, health, etc.) of the wasp produced. The effect of allowing inner ovules to be of higher quality ($M_1 > M_2 > M_3$) is that the use of outer-layer ovules is further depressed (figure 4), but the oviposition profiles remain similar in both *Ficus* species (not shown).

Note that in model 2 we have continued to assume that foundresses can detect eggs only by probing ovules, which allows pseudointerference to contribute to a reduction in oviposition rates. In electronic Appendix C, we eliminate pseudointerference from model 2 and find it makes little difference. We explain the reason for this in § 3.

(c) *Model 3: adding more biology*

It is clear that style-length variation and pseudointerference do not explain the entire observed decline in *per capita* oviposition levels as foundress number rises, especially for *F. microcarpa* (figure 3*a*), nor does this simple model explain seed production in syconia that receive enough wasps to fill ovules several times over (e.g. Herre 1989). In part, the mismatch of predicted and observed can be attributed to error in our parameter estimates, again especially for *F. microcarpa* (see electronic Appendix A). We have also so far ignored several aspects of fig biology that potentially can further lower the oviposition profile. We now describe these other aspects (roughly, in decreasing order of plausibility and generality), and we gauge their probable effects.

(i) Increasing handling time. So far, we have assumed that handling time k is a constant function of style length. For example, if two styles differ in length by a factor of two, it takes twice as long to push an egg down the longer style. However, it is known that in monoecious figs, longer styles are narrower and more flexible, which is thought to increase the difficulty of oviposition (Verkerke 1986). The effect of increasing the per-unit-length handling time for longer styles is to increase k with style length, and therefore to further reduce oviposition rates in longer styles. Later foundresses in particular would therefore suffer a shorter effective lifespan and thus, lower oviposition.

(ii) Fixed time of receptivity. In our models, we have assumed that all foundresses enjoy the same lifespan. However, in some species it is known that figs stop being receptive to foundress entry and/or oviposition a fixed time after the first foundress enters. For instance, the semiochemicals that attract dispersing foundresses cease to be produced (Khadari *et al.* 1995), styles wilt and ostiolar bracts stiffen (Nefdt & Compton 1996). It is also possible, though not known, that internal oxygen levels might drop. The result is that later foundresses suffer reduced lifetimes.

(iii) Inefficient search strategies. We have assumed that foundresses always choose the most efficient oviposition strategy available to them throughout their lives (see electronic Appendix B). However, real foundresses will necessarily have to spend time building up a picture of what ovules, at what style lengths, are available before being able to choose an oviposition strategy. In particular, later-arriving foundresses will lose efficiency if they act as if they were the first foundress, thereby wasting time rejecting long styles while looking for now-rare short styles. Thus, we expect multiple foundresses to forage less efficiently than a lone foundress, and predicted oviposition profiles (figure 3) should therefore be taken as upper bounds.

(iv) Interference competition. In a few *Ficus* species, foundresses have been observed to fight (Ramirez 1970; Gibernau *et al.* 1996; Moore & Greef 2003), and the loser suffers reduced fecundity. In other species, when syconia receive large numbers of foundresses, space in the cavity can be so limited that foundresses impede each other's movements, resulting in a loss of oviposition efficiency (S. Compton and J. Cook, personal observation). Because interference requires foundresses to overlap temporally, this is the one exception where sequential and simultaneous ovipositions are not equivalent.

(v) Local mate competition. It is well documented that local mate competition causes the offspring sex ratio to become more male-biased with increasing foundress number (reviewed in Herre *et al.* 1997). There is also some indirect evidence that male eggs are more likely to be laid in short-styled flowers. For instance, in *Ficus burtt-davyi*, Compton *et al.* (1994) found that the average style length of flowers with female offspring increased with foundress number, but the average style length of flowers with males did not increase. Similarly, Murray (1990) found that in dioecious *F. hispida*, the male pollinator sex ratio in the inner ovule layer was twice that in the outer layer (38.4% versus 18.7%). One possible advantage of using the inner ovule layer for males is to allow them to emerge more quickly and thus to begin searching for mates more rapidly (Murray 1990). If male eggs are indeed laid preferentially in short-styled flowers, then the value of short-styled flowers will increase as foundress number increases. Foundresses will then continue to search for short-styled flowers, even when rare, and overall oviposition efficiency will decrease.

(vi) Exiting the syconium. Finally, in a few fig species, including *F. microcarpa*, some foundresses can exit syconia before they have finished laying, and in *F. carica*, it has been demonstrated experimentally that exiting foundresses can enter and continue laying in a different syconium (Gibernau *et al.* 1996). Because exiting is costly (e.g. foundresses often get stuck permanently in the entrance when trying to exit), leaving should only be profitable when oviposition rates drop so low that any expected extra fitness gained from staying is outweighed by the benefit of finding an empty syconium. In the context of our model, this amounts to later foundresses failing to lay all their eggs in any given syconium.

We have no parameter estimates for any of these proposed mechanisms, but we can make some guesses as to their qualitative effects, revealing that the six mechanisms can be divided into three general classes based on how they act to slow down oviposition. Mechanisms (i), (ii), (iv) and (v) all lower the oviposition profile by increasing the advantage of being a lone foundress, but under these mechanisms, given a sufficiently large number of foundresses, every ovule will still receive an egg. However, this high number of foundresses might never be achieved in nature. By contrast, under mechanism (ii) some ovules will always remain egg-free, regardless of the number of foundresses. Finally, mechanisms (iv) and (vi) could potentially show threshold effects, with foundresses only interfering or attempting to exit above some critical density of foundresses.

To illustrate the contrasting qualitative effects of some of these mechanisms, we first define functions to describe their effects, and then employ least-squares regression to fit to the observed data (figure 5). We emphasize that just because these functions can fit the data (for the most part), we do not mean to imply that the mechanisms are operating. To do that requires measuring parameter values empirically. Also, we only consider each mechanism in isolation, but multiple mechanisms could be acting in any given species.

(i) *Fixed time of receptivity*

Mechanism (ii) causes each succeeding foundress to have a shorter and shorter effective lifespan. To demonstrate this effect, we assume that each succeeding wasp's lifespan is α% of the previous wasps', and solve for α, using $k = 10$. In *F. microcarpa*, declining lifespans strongly flatten the oviposition curve, which is to be expected since late-arriving foundresses have no time to oviposit (figure 5*a*). In *F. maxima*, the flattening effect is not as evident, but would be if we fitted larger numbers of foundresses (figure 5*b*).

(ii) *Increasing handling time and local mate competition*

Mechanisms (i) and (v) are equivalent in that they both increase the desirability of inner-layer ovules relative to outer-layer ovules: the former increases the variation in handling times, and the latter increases the variation in egg quality. In addition, mechanism (v) is density dependent: inner-layer ovules become more desirable with increasing foundress number. To illustrate mechanism (i), we set $k_{\mathrm{inner}} = 10 \times \beta$, $k_{\mathrm{middle}} = 10$, and $k_{\mathrm{outer}} = 10 \times 1/\beta$, then vary β to fit the observed data. For mechanism (v), we set

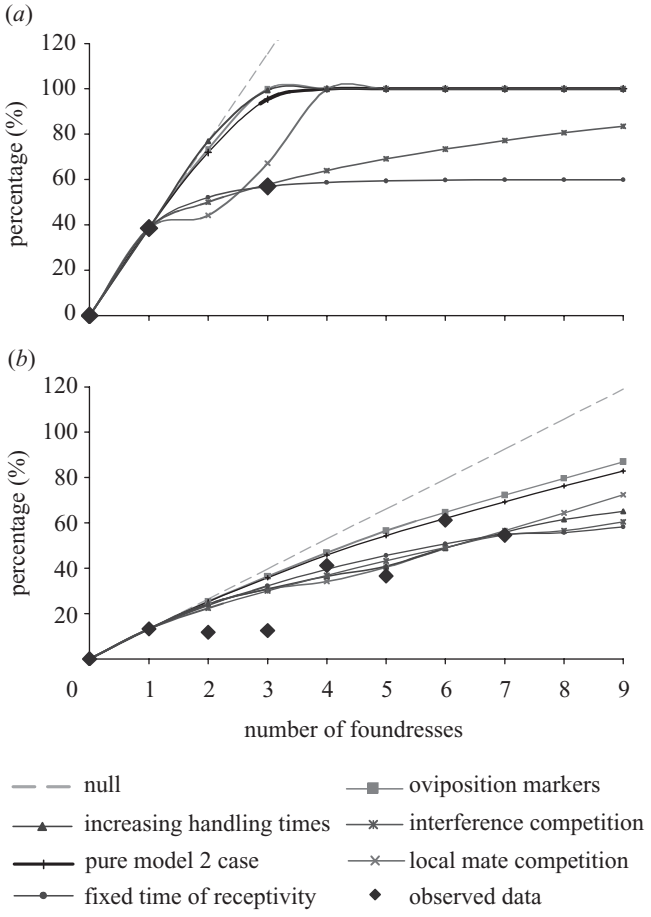

Figure 5. Oviposition profiles for model 3 mechanisms. (*a*) *Ficus microcarpa*. (*b*) *Ficus maxima*. See text and electronic Appendix C for details. Key: null, dashed grey line; increasing handling times, triangles; oviposition markers, grey circles; interference competition, dark-grey squares; pure model 2 case, black line; fixed time of receptivity, small dark-grey circles; local mate competition, light-grey squares; observed data, diamonds.

$k = 10$, $M_1 = (1/\gamma)^{F-1}$, $M_2 = 1$, and $M_3 = \gamma^{F-1}$, where F is the number of foundresses, and then vary γ to fit the observed data. In *F. microcarpa*, increasing handling time (mechanism (i)) does not decrease oviposition levels, but local mate competition (mechanism (v)) does reduce oviposition to near observed levels for $n \leqslant 3$ foundresses. In *F. maxima*, both mechanisms limit oviposition to the levels observed (figure 5*b*).

(iii) *Interference competition*

We illustrate mechanism (iv) with the Hassell & Varley (1969) function: $E = QF^{-\delta}$, where E is the *per capita* oviposition rate in the presence of F wasps, Q being the rate for a single wasp, and δ the constant quantifying the decline in oviposition rate with foundress number, which we vary to fit the observed data. In both species, interference competition can reduce oviposition to observed levels (figure 5), though with this function, the profile is not flat, as in mechanism (ii). However, it is possible that under different conditions, fighting can give a flat oviposition profile, as has been observed in *Ficus obtusifolia* (Herre 1989), for which genetic analysis has revealed that the majority of offspring are derived from only one foundress (Molbo *et al.* 2003).

3. DISCUSSION

We present a simple model that shows how pseudointerference and style-length variation can help to explain why wasps do not oviposit in all ovules. Pseudointerference contributes because as ovules fill up with eggs, more time is wasted looking for the remaining empty ovules (figure 1). Style-length variation contributes because the first foundress oviposits preferentially in the flowers with shortest styles (figure 2). Subsequent foundresses, with the same lifespan, are forced to oviposit down longer styles, which have longer probing and handling times. Thus, subsequent foundresses suffer slower and slower oviposition rates, and total oviposition must be less than that predicted by a straight-line null model (figure 3). In short, the first foundress's realized fecundity overestimates the average foundress's realized fecundity because the first foundress gets all the easy ovules. More formally, variation in resource payoff (here, search and handling times) produces a 'pre-emptive' or 'despotic' distribution of oviposition success (Pulliam & Danielson 1991).

It is worth emphasizing that the more style lengths vary, the less important is the stabilizing role of pseudointerference. This can be seen most easily by imagining that the first foundress lays in almost all the inner ovules. The second foundress then switches to accepting longer styles, which reduces her oviposition rate, but initially also moderates the effect of pseudointerference, since outer ovules start with few eggs. (This is what causes some of the curves to be sigmoidal in figure 5.) As a result, we find that if foundresses were to use oviposition markers, which eliminate pseudointerference, oviposition levels would not materially increase (see electronic Appendix C; figure 5).

For *F. maxima*, style-length variation alone appears sufficient to explain seed production within the normal range of foundress numbers (figures 3*b* and 5*b*), and other mechanisms can further reduce oviposition levels (figure 5*b*). For *F. microcarpa*, additional mechanisms (model 3; figure 5*a*) are needed to allow the host plant to guarantee seed production. The proximate reason for the difference between species is that in *F. microcarpa*, the first foundress lays in a very high percentage of ovules (38.5%), which results in her being given a long calculated lifespan (see model 1 for estimation procedure). This therefore allows subsequent foundresses, which are assumed to enjoy the same long lifespan, enough time to fill most or all of the remaining ovules, even though oviposition is slower. The simulations in model 3 suggest that the most probable additional mechanisms guaranteeing seed production are fixed time of receptivity, local mate competition or some variant of interference competition (figure 5*a*). In addition, foundresses could exit the syconium before filling all the ovules (as reported by Gibernau *et al.* (1996) for this species).

Our modelling approach extends the utility of the 'insufficient eggs', 'unbeatable seeds' and 'short ovipositor' hypotheses. In *F. microcarpa*, oviposition levels are still (slightly) egg-limited at three foundresses, even though 2.6 foundresses carry enough eggs to fill all ovules (figure 3*a*), and in *F. maxima*, 7.6 foundresses oviposit in only 68–89% of ovules, depending on the value of k, even though that number of foundresses carries enough eggs to fill 100% of ovules ($7.6 \times 13.2\% = 100\%$; figure 3*b*). We also find that variation in style length and/or quality ($M_{1,2} > M_3 > 0$),

producing 'undesirable' ovules, is sufficient to reduce or even eliminate oviposition in outer-layer ovules (figures 2 and 4), making it unnecessary to assume that outer ovules are 'unbeatable' ($M_3 = 0$). Finally, there do exist some *Ficus* species in which foundress ovipositors are shorter than a large proportion of styles, preventing oviposition in long-styled flowers (Nefdt & Compton 1996). We propose that long ovipositors are costly (as suggested by Ganeshaiah *et al.* 1995), both to make and because handling time is necessarily increased. Thus, in some cases, perhaps when egg limitation is strong, there could be selection for short ovipositors, trading off length for efficiency (see Ganeshaiah *et al.* 1995). We note in passing that taken to the extreme, this trade-off can be thought of as a way to make outer ovules 'unbeatable'.

(a) *Phylogenetic perspectives*

Our approach can help us gauge the contribution that a variety of plant and wasp traits make to mutualism stability. In fact, as different sets of stabilizing mechanisms are likely to act in different fig lineages (Herre 1999), *Ficus* and wasp phylogenies (Machado *et al.* 2001; Jousselin *et al.* 2003; Cook & Rasplus 2003) could allow us to trace the evolution of these mechanisms. For example, the reason that the first foundress is able to oviposit in a larger proportion of ovules in *F. microcarpa* than in *F. maxima* is because *F. microcarpa*'s syconia are about one-twelfth the size of (and thus contain fewer ovules than) *F. maxima*'s syconia, but foundresses in *F. microcarpa* are only approximately twice as small as in *F. maxima*. Thus, the ratio of wasp fecundity to ovule number is much higher in *F. microcarpa*. In other words, the wasp–seed conflict should generally be more difficult to resolve in *Ficus* species with small syconia.

This perspective allows us to make a couple of predictions. (i) Large syconia should be the ancestral state in *Ficus*; and (ii) evolutionary transitions from large to small syconia (as would be expected in shifts to drier habitats) should be accompanied by the evolution of additional mechanisms to maintain stability. These could include the model 3 mechanisms suggested above, as well as smaller ovule size (to 'step down' foundress fecundity and lifespan; Herre (1989)), a very small syconium cavity (to impede foundress movement at high numbers) and increased variance in style length and ovule quality (to increase the advantage of being the first foundress and thus, to exacerbate the trade-off between ovipositor length and efficiency).

Accordingly, in three independent evolutionary transitions from dioecy to monoecy in *Ficus*, style-length variation more than doubles (G. Weiblen, unpublished data). In dioecious *Ficus*, 'male' trees produce syconia with only short-styled flowers, allowing all ovules to receive wasp eggs. 'Female' trees produce syconia with only long-styled flowers, precluding oviposition. Dioecy therefore resolves the seed–wasp conflict found in monoecious species (Machado *et al.* 2001; Weiblen *et al.* 2001). In light of our models, any evolutionary transition to monoecy from dioecy would necessarily be accompanied by an increase in style length variation.

(b) *Testing the models*

Although the stabilizing mechanisms we have proposed (models 1–3) are biologically distinct from each other, they cannot reliably be differentiated statistically using the oviposition profiles alone (compare, for example, the overlapping curves in figure 5*b*). Instead, in addition to the phylogenetic comparisons listed above, testing the model will require a combination of detailed observation and experiment, with a priority being to measure for several *Ficus* species: ovule number (N), foundress lifespan within the syconium (T), probe time (t), the ratio of oviposition to probe time (k), and style-length variation. These estimates can then be used to predict style-length usage and oviposition profiles for comparison with measured values.

Lifetimes can be measured by the simple expedient of introducing foundresses to multiple syconia and opening subsets at regular intervals. Probe and handling times can be estimated by direct observation since foundresses continue to oviposit after the syconium has been opened. In some wasp species, oviposition can be distinguished either by a pumping action of the gaster (Nefdt & Compton 1996), or, in many wasp species, by the active pollen-spreading behaviour that follows the successful implantation of an egg.

Similarly, the mechanisms proposed in model 3 can also be tested experimentally. If there is a fixed time of style receptivity, delayed introductions of a second foundress should result in lower total offspring production. For example, Kinoshita *et al.* (2002) found that in *Ficus erecta*, the total oviposition of two foundresses was *ca.* 150–200% of one foundress if introduced within 30 min of each other, but the longer the delay between foundresses, the less the second foundress was able to oviposit. At 24 h, the second foundress laid only half or less what the first foundress did. However, these results are only illustrative because *F. erecta* is dioecious. The existence of either increasing handling time or interference competition can be tested by direct observation. The potential stabilizing effect of local mate competition can be gauged by measuring the separate style-length distributions of male and female offspring (Murray 1990; Nefdt & Compton 1996) across syconia with different numbers of foundresses.

(c) *Host coercion as a theory of mutualism*

Our most important take-home message is that it is not necessary to invoke any of the mechanisms traditionally suggested as being important for the stability of mutualisms, such as vertical transmission, reciprocity or partner selection (Axelrod & Hamilton 1981; Bull & Rice 1991; reviewed in Herre *et al.* 1999; Yu 2001). These mechanisms work by coupling the benefits and costs of cheating, such that one cannot enjoy the former without suffering the latter, but the mechanisms require partners to be able to recognize cheating behaviour or cheaters themselves, or they assume viscous populations.

Instead, it is more useful to view fig wasps as a kind of managed disease, with this disease's virulence measured as the rate at which the wasps convert ovules to offspring. The added complication is that the wasp offspring also provide a beneficial service: transporting pollen to other plants. Thus, to achieve a mutualistic outcome, *Ficus* must somehow manage the virulence of the foundresses so that not only wasp offspring (male function) but also seeds (female function) are produced.

Our models suggest that *Ficus* brings about this scenario primarily by adjusting fig morphology (most crucially,

style lengths and ovule size), thereby allowing the host plant to overcome selection on wasps to increase oviposition at the expense of seeds (see Herre 1989, 1999). Note that the proposed mechanisms do not require figs to recognize individual foundresses or to detect oviposition levels. Interestingly, Ganeshaiah *et al.* (1999) have recently shown that style-length variation in figs is greater than can be explained by simple ovule packing considerations, and they have independently suggested that this unexplained additional variation is an adaptation whose function is to regulate oviposition.

Our approach thus provides a mechanistic implementation of the idea that, in symbioses, the partner that controls the physical resources (as opposed to providing the services, such as pollination or nitrogen fixation) ultimately controls the relationship, regardless of relative evolutionary rates (Herre 1989; West & Herre 1994; Yu 2001; West *et al.* 2002*a*,*b*; Ferdy *et al.* 2002; Yu & Ridley 2003).

Subtle forms of host coercion are also being found in other mutualisms, potentially providing a roadmap to the development of a general theory. For example, plants that associate symbiotically with protective ants ('ant-plants' or myrmecophytes; Davidson & McKey (1993)) can sometimes be inhabited by ant species that do not invest in herbivore defence (Janzen 1975; McKey 1984). These parasitic ant species compete with mutualistic species for host plants. Explaining how ant–plant mutualisms persist therefore becomes equivalent to explaining why the parasitic strategy is less fit than the mutualistic one, despite the apparently higher cost of mutualism. Yu (2001) has proposed that part of the answer can be found in plant morphology, in that ant plants grow modularly, physically linking the production of each new domatium (a hollow plant structure colonized by ants, such as a stem chamber) to the successful protection of an attached set of new leaves (called 'hostage trading'). As a result, non-protecting ant species might save the cost of producing the workers needed to patrol leaves, but pay the large fecundity cost of living in fewer domatia, which puts them at a disadvantage in the competition for new plants.

In another more involved example, rhizobial endosymbionts of leguminous plants fix nitrogen in return for plant photosynthate. This system is open to invasion by parasitic genotypes that do not pay the large metabolic costs of fixing surplus nitrogen but consume photosynthate anyway. Denison (2000), West *et al.* (2002*a*,*b*) and Kiers *et al.* (2003) have shown that since the endosymbiont population is divided into multiple root nodules, provided each nodule is inhabited by a single genotype, hosts can select for high levels of nitrogen fixation by killing off or 'sanctioning' nodules (via reduced O_2 provision) inhabited by parasitic genotypes.

In a system similar to figs, Ferdy *et al.* (2002) argue that the morphology of globeflowers (*Trollius europaeus*) selects for mutualistic behaviour in specialist *Chiastocheta* flies. *Chiastocheta* flies are beneficial in that they pollinate, but they also lay eggs, and the larvae eat some fraction of the seeds. Ferdy *et al.* (2002) argue that because the uniquely enclosed corolla of *Trollius europaeus* increases the survivorship of the earliest laid eggs (protecting them from parasitism and the elements) and because subsequent larval competition for food is so intense, the flower ends up imposing selection on the flies to lay few eggs, thereby shifting the balance of pollination and seed predation to a net mutualistic outcome (see also Yu & Ridley (2003) for a review, and Shapiro & Addicott (2003) for a potentially similar phenomenon in yucca plants).

In these examples, host plants set up a competitive landscape that favours mutualistic species and/or the evolution of mutualistic behaviour. Although many questions remain unanswered, viewing hosts as capable of coercing or directing mutualistic behaviour in their visitors appears to be a fruitful path for studying how to stabilize mutualisms. We also suggest that the same approach might be applied to host–parasite interactions, the other side of the symbiosis coin.

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