Historical constraints and heterospecific interference lead to maladaptive sex ratio changes in a pollinating fig wasp

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Accepted version of paper: Greeff JM, Mnguni SP, Warren M. 2025 Historical constraints and heterospecific interference lead to maladaptive sex ratio changes in a pollinating fig wasp. *Proceedings of the Royal Society B* **292**: 20250859.

Original available at: https://doi.org/10.1098/rspb.2025.0859

Electronic supplementary material is available online at:

https://doi.org/10.6084/m9.figshare.c.7857309.

Abstract

Natural selection's power is beautifully illustrated by sex ratio variation that seems near-perfectly adapted. However, the fit of sex ratios to optimal predictions is usually tested in oversimplified ecological settings. This creates a one-sided view of evolution, where details are ignored, and evolution appears to produce optimal solutions. Entertaining maladaptation as a potential explanation allows consideration of historical contingencies and trade-offs. These become important in realistic settings where traits may need to be multifunctional, and historical contingencies may channel evolution to suboptimal phenotypes. Evaluating traits' adaptive/maladaptive nature requires understanding the underlying mechanisms (the proximate causes). We studied clutch composition in a pollinating fig wasp where heterospecific females potentially interfere with sex ratio production and adjustment. Using an information-theoretic approach, we compared hypotheses and confirmed that heterospecific females disrupt *Ceratosolen arabicus* females' sex ratios. Given the high fitness costs of failing to adjust optimally, we argue this maladaptation stems from rudimentary mechanisms that fail in realistic conditions and are thus forced to be multifunctional, creating fitness trade-offs. Our findings highlight how historical constraints and ecological interactions may limit adaptation, challenging the assumption that selection always produces optimal traits. Furthermore, they emphasise the need to incorporate ecological complexity when testing evolutionary predictions.

Keywords: maladaptation, sex ratio, heterospecific interference, trade-off, historical constraint, pollinating fig wasp, *Ceratosolen arabicus*, *Ceratosolen galili*, *Sycophaga sycomori*, information-theoretic.

1. Introduction

A strength of the adaptationist programme is its ability to generate hypotheses [1,2]. However, it has been criticised for oversimplifying biological reality by reducing organisms into sets of independently evolving traits and for overlooking how evolutionary outcomes are contingent on past events [3]. Another shortcoming, more a product of its application than of the programme itself, is that species are frequently studied in isolation rather than as parts of a coevolving community [4–6]. To address these shortcomings, studies that address the adaptive nature of traits should focus on the wider ecological and historical contexts that underlie the traits.

Interpreting traits from an optimality perspective requires trait variation to be linked to its fitness effects [1]. While this can be done, a network of unidentified genetic and physiological constraints results in trade-offs that hinder our efforts to study traits in isolation and prevent traits from evolving independently. However, if we strategically assume that sufficient time has elapsed and enough mutations occurred for natural selection to have explored the entire phenotypic space and uncoupled constraints, then we can generate testable hypotheses [7]. Even though this is an unrealistically extreme position, taking this gambit allows us to interpret the failures of models' fits as the result of constraints [1,8]. In this manner, the optimality approach allows us to quantify both the constraints and variables that explain trait variation [1]. However, this '*inverse optimality*' cannot distinguish constraints from instances where selection has failed to generate the optimal phenotype [8]. Irrespective of the reason for a loss of fitness, it is useful to label these cases where fitness is lost as ‘maladaptations’ [9].

Although the fitness loss implied by maladaptation is infrequently quantified, there is a resistance to explicitly identify it as maladaptation and study it as a phenomenon in its own right [9–11]. An exception is the maladaptation caused by the mismatch between organisms and their environment caused by rapid anthropogenic changes [10,11]. An important aspect that is easily overlooked when focusing on adaptation rather than maladaptation is the historical context of adaptations. Since natural selection can only shape current variation, we should expect historical contingencies to direct adaptive evolution [12,13] away from the highest fitness peaks. Hence, rather than expecting organisms' phenotypic space to occupy global optima, they may occupy local optima, and organisms are likely to adopt simple strategies and heuristic rules derived from earlier adaptive solutions to related problems [14].

To appreciate the historical context of an adaptation, it is useful to have a good understanding of the proximal causes or mechanistic explanations of that adaptation. Maladaptation may arise when these mechanisms are disrupted. One such example is when mate recognition fails and mating efforts are directed towards the ‘wrong’ species, a phenomenon known as interspecific reproductive interference [15,16]. Species may also affect each other's reproduction by affecting their offspring's sex ratio [17–21]. Interspecific reproductive interference often results in positive density-dependent selection favouring the more common species [15]. Effects on the sex ratio may also have far-reaching eco-evolutionary ramifications because the sex ratio of a species is a crucial determinant of a population's growth rate [22].

Sex ratios stand apart from many traits because their direct link with fitness is clear, enabling mathematical models that make them an exemplar to study adaptation using the optimality approach [2,23–25]. The most well known of these is probably Hamilton's [26] local mate competition (LMC) model, which predicts, and thus explains, extremely female-biased sex ratios as fewer mothers (foundresses) oviposit on a patch. This theory applies when male offspring compete locally for matings within natal patches while female offspring disperse after mating. Then, a female-bias sex ratio reduces competition among a foundress's sons [26] and increases her remaining sons' mating opportunities [27]. Predicted, and observed, sex ratios become more female-biased as fewer foundresses oviposit on a patch [23,28]. In the extreme situation of a single foundress, she should produce just enough sons to fertilise all her daughters [26].

Hamilton [29] felt that this ‘section of evolutionary theory ... best proves the power and accuracy of the Neodarwinian paradigm’. While some share this optimism [23,30], others are more sceptical [31,32]. Even in pollinating fig wasps, which are often regarded as a quintessential example [23,33–35], significant problems exist [36–41]. One of the problems is the potential for interspecific interference with the pollinators' sex ratios: morphological studies show that many *Ficus* species host multiple pollinator species [42] and molecular data reveal that over a third host cryptic species [43] that are frequently closely related [43–47]. Additionally, nine genera of non-pollinating fig wasps from the family Pteromalidae (*Sycophaga, Crossogaster, Diaziella, Robertsia, Seres, Sycoecus, Lipothymus, Grasseiana,* and *Eujacobsonia*) lay eggs alongside pollinators [48,49]. Therefore, pollinating fig wasps provide a natural system for studying the effect of heterospecifics on the sex ratios produced by a focal species.

The sex ratio production and adjustment mechanism in pollinating fig wasps seems to be simple but robust [40]: foundresses lay mostly male eggs first, followed by mostly female eggs [41,50–52]. This decreasing probability of an egg being a male as it is laid later in the sequence of eggs, means that when some eggs cannot be laid due to competition between foundresses, the unlaid eggs would have been daughters. Therefore, the sex ratio (= fraction of offspring that are sons) will increase when there is competition that prevents the oviposition of entire clutches and will also increase more when more foundresses oviposit. We refer to this strategy as the slope strategy, reflecting the slope of the decrease in the probability of an egg being male, and it results in a change in sex ratio that is called the ladies-last effect. In essence, it is a reaction norm [53] that results in the wasps producing different sex ratios in variable environmental conditions. In about half of the studied species of pollinating fig wasps, the slope strategy is supplemented by a facultative adjustment through an increase in the number of sons when more than one foundress oviposits in a fig [40]. This adjustment requires that the intercept and/or the gradient of the slope increases. Besides pollinating fig wasps, the slope strategy has also been illustrated in wasps from the families Scelionidae [54–56] and Trichogrammatidae [56–58]. This ladies-last effect is certainly not universal because many species follow different strategies, such as males last or a random sequence [56]. It is clear that the ladies-last effect is potentially disrupted by competing heterospecific females. Considering these mechanisms and knowing the theoretical optimal predictions, generate alternative hypotheses: sex ratios are changed by heterospecific females, possibly differently by different species, and sex ratios remain unchanged in the presence of heterospecific females.

Evaluating these competing hypotheses requires a statistical framework that directly compares multiple explanatory models. The information-theoretic (I-T) approach allows such comparisons by treating the observed data as fixed and quantifying the relative support for each model in the candidate set, allowing for evidence-based model selection [59]. We prefer this approach over null hypothesis significance testing (NHST). NHST does not readily support direct comparisons between models and begins from the assumption that the null hypothesis is true even though in ecology, it is frequently obviously false *a priori* [60]. Furthermore, unlike the NHST, the I-T approach avoids the dichotomous decision-making of accepting or rejecting hypotheses based on an arbitrarily defined α level [59]. Instead, it evaluates all models in terms of their relative ability to explain the information in the data [59,61]. Here, we study a pollinating fig wasp, *Ceratosolen arabicus* (Mayr) that oviposits together with two other species, one closely related, *Ceratosolen galili* (Wiebes), and the other very distant, *Sycophaga sycomori* (Linneaus), to quantify and understand the effect of heterospecific interference on sex ratios and the resulting fitness loss using the I-T framework.

2. Materials and methods

(a) Relevant pollinating fig wasp biology

A female pollinating fig wasp enters a fig through a tight-fitting series of bracts called the ostiole [62]. In many species, this passage is so tight that the foundress's wings and part of her antennae break off [62]. In these species, a foundress lays all her eggs in the entered fig. In some other species, the ostiole is not as tight, and females may leave and lay eggs in a further fig [63].

The inside of the fig, the lumen, is lined with many uniovulate female flowers and fewer male flowers [62]. Once inside the lumen, the foundress lays a single egg in as many of the female flowers as she can [64], galling each flower she oviposited into [65]. The larvae hatch inside and consume the gall tissue, eventually pupating inside the gall. Males eclose first and females eclose with all their eggs developed [66].

Hamilton's assertion that females should produce just enough sons to mate with their sisters needs a slight adjustment in pollinating fig wasps, because males also fulfil roles beyond mating [62]. In summary, males compete by searching for galls containing females, chewing mating holes through female-containing galls’ walls and mating through these holes. In some species, they enlarge the mating hole so that the female may escape from the gall; in some of these, they may pull females out of their galls by tugging on their antennae. Then, males, either alone or collectively, chew an exit tunnel through the fig wall. In some species, males also distract ants on the outside of the figs, allowing more females to disperse [67]. A sufficient quantity of males is needed to fulfil all these functions, and the mean sex ratio for single-foundress figs for 39 species of pollinating fig wasps is 0.12 [40], suggesting that on average, each male is sufficient to liberate 7.33 females.

(b) Study species

The sycamore fig, *Ficus sycomorus* (Linneaus) hosts a pollinator, *C. arabicus*, and two other species that oviposit from the inside of the fig [68,69]. One is the non-pollinating fig wasp *S. sycomori*, and the other is the cuckoo fig wasp *C. galili* [68,69]. *Sycophaga sycomori* must have inhabited *F. sycomorus* for at least 4.5 million years when it diverged from *S. cyclostigma* [70]. *Ceratosolen galili*, a non-pollinating wasp from a pollinator lineage, has inhabited *F. sycomorus* for at least 750 generations (generation time = 6-7 weeks [68]; Wiebes [71] described a sample collected by Grandi in 1914), but probably for much longer. The two *Ceratosolen* species diverged about 40 million years ago [72,73]. Despite different flight times (*C. galili* fly mostly by day, *C. arabicus* mostly by night) [74], they co-occur frequently (*C. arabicus*: 15%, *C. galili*: 27%) [20]. Judged by *S. sycomori*'s black colour and normal-sized eyes, it probably flies by day (S. van Noort, 2025, personal communication). However, its males are less able to chew exit tunnels, and they can be expected to synchronise their exit with the *Ceratosolen* species that leaves first (J.M.G., 2008, personal observations).

(c) Co-occurrence

To determine how often *C. arabicus* occurs together with *C. galili* and *S. sycomori* we used the foundress count data on 1288 figs collected from 30 crops that were collected in the Kruger National Park, South Africa, between September 2005 and February 2006 [20]. We retained 853 figs that contained *C. arabicus* foundresses and tallied the number of figs with various combinations of foundresses.

(d) Clutch composition

We used the I-T approach to compare how well alternative hypotheses explain clutch composition data [59,61]. To demonstrate that this approach and the associated claims made here are legitimate, the usual NHST framework was also used (supplementary material). The clutch composition data that were modelled were: clutch size, number of daughters, number of sons and the sex ratios. We compared four alternative scenarios: A) heterospecific females have no effect on *C. arabicus*'s oviposition behaviour, B) *S. sycomori* and *C. galili* have the same effect, C) only *C. galili* affects *C. arabicus* and D) *S. sycomori* and *C. galili* affect *C. arabicus* differently (table 1). Scenario A is based on optimality models. If supported, it may indicate that the pollinating fig wasps' ability to lay an entire clutch is not affected by heterospecific females, and they did not trigger a facultative response. Scenario B might occur if pollinating fig wasp behaviour is influenced by another fig wasp, regardless of species. Scenario C may be expected because *S. sycomori* is less likely to compete with *C. arabicus* due to its longer ovipositor (allowing it to target flowers with longer styles), slower oviposition (J.M.G., 2005, personal observations) and its distant phylogenetic relationship to *C. arabicus*, which may prevent the triggering of a facultative response. Scenario D is a less extreme scenario than C and B and seems a plausible middle ground given the basis for scenarios B and C.

We conducted experiments to quantify changes in clutch composition at the Skukuza rest camp in Kruger National Park. Young figs were enclosed in fine mesh bags before they became receptive. Once receptive, each bag was removed briefly and newly emerged fig wasps were introduced by placing a single female near the ostiole with a small brush. In controls, only a lone foundress entered a fig. In treatment 1, a *S. sycomori* foundress was introduced about 30 minutes before a *C. arabicus* foundress and in treatment 2, a *C. galili* foundress was introduced about 30 minutes before a *C. arabicus* foundress. Figs were collected before the fig wasp offspring emerged and stored in individual jars. All fig wasps inside and outside the figs were counted under a dissection microscope in the laboratory.

We confirmed that the data were overdispersed by fitting generalized linear models with Poisson errors for counts and with binomial errors for sex ratios [75]. Therefore, we fitted negative binomial distributions to number of counts and beta-binomial distributions to the sex ratios (table 1). Both these distributions have an overdispersion parameter (k and θ respectively) in addition to the mean estimate (μ for counts and p for proportions) [76]. Although we were not primarily interested in the degree of overdispersion, we considered situations where: each species had its own overdispersion parameter; where treatment 1 and 2 had the same overdispersion parameter; where the control and treatment 1 had the same overdispersion parameter; and where all species had the same overdispersion parameter. This expanded our four scenarios to nine candidate models (table 1).

We used the optim command in R [75] to obtain parameter estimates that maximised the likelihood of the data given each model and distribution [76] (code available from repository). We alternated between the Nelder-Mead and BFGS methods of the optim command. For the sex ratios (proportions) we used the dbetabinom command in the emdbook package for R [76].

We calculated the Akaike Information Criterion (AIC) for the calculated maximum likelihood parameters of the models ($\hat{\theta}$) given the data, AIC = $-2\log\left(\mathcal{L}\left(\hat{\theta}\right)|\text{data}\right) + 2K$, with K being the number of parameters that were estimated and then corrected for sample size (n) by calculating AICc = $\text{AIC} + \ (2K(K+1))/(n-K-1)$ [59]. We then calculated the AICc differences (Δ_i) between each model i and the model with the smallest AICc and the Akaike weights or model probabilities as $w_i = \left(e^{-\frac{1}{2}\Delta_i}\right)/\left(\sum_j e^{-\frac{1}{2}\Delta_j}\right)$ [59]. Finally, we calculated an R^2

equivalent, $\mathcal{R}^2$, as explained by Anderson [59] to evaluate the fit of the model. The goal of the I-T approach is not to classify models dichotomously as rejected or failing to be rejected. Rather, models are evaluated on a continuous scale to assess how effectively each one utilises the information in the data, often expressed in terms of how many times more likely one model is than another [59]. We averaged model estimates by weighting each model's estimate by the model's Akaike weight. The importance of individual parameters can also be gauged by adding the Akaike weights of models that contain the parameter [59]. The code for analyses and figures is available on the repository.

(e) Fitness effect

Since a female lays all her eggs in one fig, for a single mother, as studied here, the number of daughters is proportional to the foundress's lifetime reproductive success. We thus used number of daughters as a proxy of fitness and compared the number of daughters of different treatments to calculate fitness consequences. To compare the fitness estimates of the three groups with each other, we assumed that control females behaved optimally. Then we can calculate the number of daughters that mothers could have had if their sex ratios did not change due to interference from heterospecific females.

3. Results

(a) Co-occurrence

The number of figs and the number of fig wasp foundresses in various combinations in the natural population are summarised in table 2. Of the figs containing *C. arabicus*, about 30% of figs contained *C. arabicus* foundresses in combination with one or both of the other two species where heterospecific interference could disrupt the sex ratio production and adjustment mechanisms. Forty seven percent of the pollinating wasps were in figs that contained more than one *C. arabicus* foundress and no other fig wasp species, and would require standard, conspecific sex ratio adjustment.

(b) Clutch composition

We dissected 24 figs into which we had introduced fig wasps. Two of these figs contained no *C. arabicus* offspring suggesting that the females had not managed to enter the figs successfully. We thus recorded 22 clutches that contained *C. arabicus* females. Two of these clutches were more than 3 standard deviations smaller than the specific treatment mean and were deleted from the data set. The remaining 20 clutches consisted of 4,082 pollinating fig wasp offspring and contained 7 control figs, 6 figs containing a *C. arabicus* and a *S. sycomori* foundress, treatment 1, and 7 figs containing a *C. arabicus* and a *C. galili* foundress, treatment 2 (figure 1; table S3; raw data available at data repository).

The mean clutch size of lone *C. arabicus* foundresses was 240.9. This clutch size seems to be large enough to result in limited oviposition opportunities if a second foundress is added because the presence of either of the other species resulted in smaller *C. arabicus* clutches (figure 2a; table 3). Specifically, models where *C. galili* caused a reduction (c2-c9) were 755 times more likely than when it did not (c1); throughout, these calculations were based on more than the three decimals presented in table 3 (see repository). Models where *S. sycomori* caused a reduction in clutch size (c2, c3 and c6-c9) were almost 36 times more likely than ones where it did not (c1, c4 and c5). However, there was no convincing evidence that *C. galili* reduced clutch size more than *S. sycomori* (the combined weights of models where *S. sycomori* had the same effect as *C. galili* (c2 and c3) were almost identical to the combined weights of models where it had a reduced effect (c6-c9)). Note that the average overdispersion parameter estimate of treatment 2 (table 4, 89.85) was substantially less than for the control and treatment 1. *Ceratosolen galili* thus caused the largest overdispersion in *C. arabicus*'s clutch size. $\mathcal{R}^2$ for the best clutch size model compared to model 1 was 0.51 suggesting a reasonable fit.

The reduction in clutch size was due to a reduction in the number of daughters (figures 1 and 2b; tables 3 and 4: Models where *C. galili* caused a reduction (d2-d9) were more than 32852 times more likely than when it did not (d1)). Models where *S. sycomori* cause a reduction in clutch size (d2, d3 and d6-d9) were 105 times more likely than ones where it did not (d1, d4 and d5). The data contain some information suggesting that *C. galili* reduced *C. arabicus*'s number of daughters more than *S. sycomori* (figures 1 and 2b; table 3; Models d4-d9 were 11 times more probable than models d2 and d3). Once again, *C. galili* caused the biggest overdispersion in *C. arabicus*'s number of daughters. The $\mathcal{R}^2$ for the best number-of-daughters model was 0.76, suggesting a good fit.

In contrast to the number of daughters, the presence of another *C. galili* foundress increased the number of sons (figures 1 and 2c; tables 3 and 4: Models s4-s6 are 268 times more likely than model s1). However, the evidence in the data to support an effect of *S. sycomori* was not very convincing (figures 1 and 2c; table 3: Models s2, s3, and s6-s9 were only 1.2 times more likely than models s1, s4 and s5). Furthermore, three of the four best models estimated a common parameter for the control and treatment 1. The $\mathcal{R}^2$ for the best number-of-sons model was 0.46, suggesting a fair fit.

The sex ratio combines the effects of number of sons and daughters caused by the other two species. It is at least 175000 times more likely that *C. galili* increased *C. arabicus*'s sex ratio than not (figures 1 and 2d; table 3: Models r2-r9 versus r1). Similarly, but to a lesser extent, *S. sycomori* was almost 31 times more likely to increase *C. arabicus*'s sex ratio than not (figures 1 and 2d; table 3: Models r2, r3 and r6-r9 versus r1, r4 and r5). Even though the beta-binomial model was better than the binomial model, the smallest averaged estimated overdispersion was 243.36, suggesting a low level of overdispersion (table 4). The sex ratio of a single *C. arabicus* control foundress was 0.10, and increased to 0.16 in treatment 1 and to 0.25 in treatment 2 (table 4). The $\mathcal{R}^2$ for the best sex ratio model was 0.76, suggesting a good fit.

While all these conclusions were supported with a traditional NHST (electronic supplementary material), the I-T framework offers several further advantages that we enumerate on below and in the electronic supplementary material.

(c) Fitness effect

The two heterospecifics reduced the fitness of *C. arabicus* foundresses substantially (table 5). *Sycophaga sycomori* foundresses reduced *C. arabicus* foundresses' fitness by 24%. This was composed of a 19% loss due to a smaller clutch size and a 5% loss due to the inappropriate adjustment of the sex ratio (table 5). In the case of *C. galili* the total reduction in fitness was 39%, 27% due to competition and 12% due to the inappropriate adjustment of the sex ratio (table 5).

4. Discussion

Our analyses strongly suggest that the presence of *C. galili* foundresses, and to a lesser extent *S. sycomori* foundresses, affect the clutch composition of co-founding *C. arabicus* foundresses. First, both heterospecifics reduce the number of daughters through competition for oviposition sites. Second, *C. galili* triggers an inappropriate facultative increase in the number of *C. arabicus* sons. *Sycophaga sycomori* causes a smaller increase in the number of *C. arabicus* sons, but the evidence for this claim is weak. These changes combine to increase the sex ratio of a lone *C. arabicus,* which is 0.102 when it is on its own, to 0.157 in the presence of *S. sycomori*, and to 0.246 in the presence of *C. galili*. These changes constitute, respectively a 5 and 12% reduction in fitness and should thus be considered as maladaptations.

This maladaptation cannot be explained by weak selection because *C. arabicus* co-occurs with *C. galili* in 15.5% of figs in the Kruger National Park, and a 12% selection pressure in a population size exceeding millions is substantial [77]. Seven hundred and fifty generations (probably many more) should have been sufficient to lead to an evolutionary response given a selection pressure of 12%. We consider failure in the ladies-last effect and the facultative response in turn.

Ladies-last effect: The most parsimonious explanation is that the intercept and/or gradient of the slope strategy have evolved in response to the average foundress numbers to yield the highest average fitness rather than the highest for each situation. This disruption of the passive effect is inevitable [40] and results in fitness compromises [78,79].

Facultative response: It is surprising that *C. galili* causes a facultative response in *C. arabicus*. Likewise, *C. arabicus* causes a facultative response in *C. galili* [20]. To remain distinct species, mating pairs must be able to identify their own species. However, ovipositing females seem unable to do so. This may be because a large part of their antennae break off on entering the fig [62]. Irrespective of the cause of this failure, it suggests that the mechanism does not allow for distinct adaptations for conspecifics and congenerics, forcing a fitness trade-off between being on their own, being with heterospecifics and being with conspecifics. To make these arguments, we assumed that LMC is the only factor influencing the optimal sex ratio in these pollinating fig wasps. Since each pollinating fig wasp develops in its own gall, it seems a reasonable assumption. In summary, the maladaptation seems to be caused by

C. arabicus's rather simple sex ratio production and adjustment mechanisms that are easily disrupted by the presence of a heterospecific foundress.

Similar production mechanisms are known from another chalcid wasp [57,58] and scelionid wasps [54,55]. Such simple mechanisms that may easily be disrupted by close or even more distantly related species might perhaps explain other heterospecific sex ratio disruptions [17–21]. Since natural selection proceeds by tinkering with current variation [80], we should expect such simple strategies to evolve, even though they incur fitness costs. These fitness costs result from compromised optimisation over various conditions [14] and from natural conditions being complex [81].

The passive effect allows sex ratio adjustments in various conditions when females have smaller clutches, whether due to arriving after the death of the first foundress [82] or due to other conspecific(s) ovipositing [78,79,83]. However, it will be multifunctional and represents a compromise between overshooting and undershooting optimal sex ratios. Hence, even though sex ratios will increase as LMC decreases along with model predictions, and even though selection probably will optimise the trade-offs, it is hardly the pin-point precision that has been claimed [23,34]. In fact, a case where it was argued that greater precision in sex ratio adjustments resulted from more frequent selection in a pollinating fig wasp [84] may be best interpreted as another example of a maladaptive sex ratio adjustment in the presence of a heterospecific (electronic supplementary material, figure S1). Specifically, the facultative response recorded in *Pegoscapus gemellus* (electronic supplementary material, figure S1) is invalidated by it being two cryptic species [34]. The claim that '... this part of evolutionary theory has even more power and accuracy than thought previously' [34] is thus misleading.

Many fig trees host more than one pollinating fig wasp species [42–47], and it is unclear why similar species do not competitively exclude each other [85]. Zhang and Hanski

[85] suggested that optimal sex ratio adjustment results in negative frequency-dependent selection that maintains multiple species in pollinating fig wasps. However, similar to interspecific reproductive interference [15], maladaptive sex ratio changes result in positive frequency-dependent selection and hence, the coexistence of multiple pollinator species is an unanswered question.

Here, we show how other species that oviposit from the inside, i.e. the lumen, of the fig can affect the primary sex ratio of pollinating fig wasps by interfering with the sex ratio production and adjustment mechanisms. In addition to this interference, parasitoids that oviposit from the outside of the fig can affect the secondary sex ratio of the pollinating fig wasps [86,87].

When explicit interactions are studied between species, e.g. predator-prey interactions, brood parasitism, competitive interaction, pollinator-plant interactions and cleaner-client relationships, the focus is automatically on more than one species. However, when evolution within a species is studied, unintended effects by heterospecifics may be important, but can be easily overlooked. These include the mate recognition system [15], sexual selection [88] and sex ratios [17–21].

An overly adaptationist approach may result in biased interpretations of data. For instance, the observation that *S. sycomori* does not elicit a clear facultative increase in the number of sons may be interpreted as evidence that the facultative component has adapted. However, it would be more parsimonious to conclude that an inappropriate trigger never existed in the first place. This is because *C. arabicus* possibly never sensed, nor had to sense, *S. sycomori* foundresses. Another potential example from the field of sex ratios may be the explanation for why *Nasonia vitripennis* uses few of the available cues to adjust its sex ratios [81,89]. Shuker & West [89] argued that fitness gains from additional information are minimal, so from an adaptationist perspective, the cost of using extra cues outweighs the benefits [81,89]. Alternatively, cue use may be constrained by the simple signals historically relied upon by foundresses. Even so, contrasting responses to alternative cues may illuminate the underlying mechanisms and hence shed light on the potential historical constraints and adaptive value of traits [79,89].

The maladaptation identified here probably stems from historical contingencies that resulted in an uncomplicated mechanism that cannot be modified to work optimally in different contexts. Therefore, the trait is necessarily multifunctional; at best, selection may optimise fitness averaged over all contexts [14,78]. To draw such a conclusion requires a pluralistic approach that combines the benefits of adaptationist [1] and spandrelist [3] programmes to make the most of evolutionary studies [90]. Such an approach becomes unforced when maladaptation is acknowledged [9–11]. If we do not, we will fail to distinguish between temporary variants that will eventually be fine-tuned by selection and variants that persist, despite their fitness costs, because of trade-offs and historical contingencies. Such a failure limits biologists to a view of evolution where time is the only obstacle to eradicating fitness loss. The risk is that the alternative view, that of evolution as a process hindered by history [12,91] and compromised by trade-offs where fitness losses are inevitable [92], becomes marginalised. To avoid such a biased perspective, the possibility of maladaptation must be entertained [9–11], the assumptions of optimality models should be tested directly [1,93], and alternative models should be systematically contrasted [3,59,94].

A pluralistic approach that considers multiple hypotheses [95] may be enhanced and supported by an I-T analysis [59,61]. This framework insists on formulating competing hypotheses, and all the associated candidate models can be compared simultaneously, rather than via multiple pairwise tests. Each model is evaluated on its own merits by measuring its relative support from the data, and uncertainty in model choice is explicitly quantified through the Akaike weight metric. The inherent complexity penalty guards against over-fitting without arbitrary adjustments. Rather than enforcing a binary ‘reject/fail-to-reject’ decision, this approach operates on continuous gradients of evidence to give a more nuanced view of which biological factors matter most. Finally, the resulting model weights facilitate multi-model inference and averaging, allowing predictions or parameter estimates to draw on the entire set of models rather than hinging on a single ‘best’ choice. [59].

Ethics. This work did not require ethics.

Data accessibility. All data and code used in this study are available at [96].

Supplementary Material is available online [97].

Declaration of AI use. We did not use AI-assisted technologies to generate the content of this article. However, we used OpenAI's ChatGPT (GPT-4-turbo, accessed via ChatGPT in 2025) and Anthropic's Claude (Sonnet 4) to assist with shortening the text and improving grammar and clarity.

Author’s contributions. J.M.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, project administration, supervision, visualization, writing - original draft, writing - review & editing; S.P.M.: formal analysis, investigation, writing - original draft, writing - review & editing; M.W.: conceptualization, investigation, project administration, supervision, writing - review & editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project was funded by various grants from the National Research Foundation of South Africa: postdoctoral grant to MW and running costs by grants 65726 and 109270 to JMG. Any opinion, findings and conclusions or recommendations expressed in this material are those of the authors and therefore the NRF does not accept any liability in regard thereto. SPM received a postgraduate award from the University of Pretoria.

Acknowledgements. We thank SAN Parks for permission to do this work and for the accommodation they supplied and their logistical support, especially Hendrik Sithole and Thembi Khoza. We thank Xavier Brits and Karina Pentz for help with dissections, Willem Ferguson and Steve Compton for useful comments on the manuscript and Rian Pierneef for discussing the analyses. We are very grateful to the editor and two referees for pointing this manuscript in the right direction and for their many helpful suggestions. We are grateful to the NRF and the University of Pretoria for financial support. SPM thanks the University of Pretoria for a bursary and is grateful to the family that supported her.

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Table 1. The fitted models explaining *Ceratosolen arabicus* clutch composition. All figs contained a single *C. arabicus* foundress. t_0 figs were the control, t_1 figs contained an additional *Sycophaga sycomori* foundress and t_2 figs contained an additional *Ceratosolen galili* foundress. NegBin indicates a negative binomial distribution. The dependent variable, Y, stands for clutch size, number of daughters, number of sons or sex ratio. When the dependent variable is sex ratios, NegBin(μ, k) must be replaced by BetaBin(p,θ) for a beta-binomial distribution. See text for definitions of other variables.

scenario	model number	model
A	1	Y = NegBin(μ, k)
B	2	Y_i = NegBin(μ_i, k_i) i = 1 if t_0 and 2 if t_1 or t_2
B	3	Y_i = NegBin(μ_i, k) i = 1 if t_0 and 2 if t_1 or t_2
C	4	Y_i = NegBin(μ_i, k_i) i = 1 if t_0 or t_1 and 2 if t_2
C	5	Y_i = NegBin(μ_i, k) i = 1 if t_0 or t_1 and 2 if t_2
D	6	Y_i = NegBin(μ_i, k_i) i = 1 if t_0, 2 if t_1 and 3 if t_2
D	7	$Y_{i,j}$ = NegBin(μ_i, k_j) i = 1 if t_0, 2 if t_1 and 3 if t_2; j = 1 if t_0 and 2 if t_1 or t_2
D	8	$Y_{i,j}$ = NegBin(μ_i, k_j) i = 1 if t_0, 2 if t_1 and 3 if t_2; j = 1 if t_0 or t_1 and 2 if t_2
D	9	Y_i = NegBin(μ_i, k) i = 1 if t_0, 2 if t_1 and 3 if t_2

Table 2. The occurrence of *Ceratosolen arabicus*, *Ceratosolen galili* and *Sycophaga sycomori* combinations in 853 figs.

	single *C. arabicus*	*C. arabicus* > 1; others = 0	*C. arabicus* and *C. galili*	*C. arabicus* and *S. sycomori*	all three species
% of figs	40.9	28.7	12.3	15.5	2.6
% of wasps	24.2	46.6	12.4	13.6	3.3

Table 3. Summaries of the abilities of nine models to explain the information in the data; clutch size (c1-c9), number of daughters (d1-d9), number of sons (s1-s9) and the sex ratio (r1-r9). Only 3 decimals are given here but more were calculated (available in repository). Abbreviations are given in section 2. Text in bold is the best model for each trait.

scenario	model	rank	K	-log $\mathcal{L}$	AICc	Δ_i	w_i	model	rank	K	-log $\mathcal{L}$	AICc	Δ_i	w_i
A	c1	9	2	100.385	205.476	11.542	0.001	d1	9	2	102.861	210.428	18.960	3.0x10^{-5}
B	c2	4	4	93.133	196.932	2.998	0.095	d2	6	4	92.952	196.571	5.102	0.031
B	c3	**1**	**3**	**93.217**	**193.934**	**0.000**	**0.424**	d3	5	3	94.024	195.548	4.079	0.052
C	c4	8	4	96.194	203.056	9.122	0.004	d4	8	4	95.885	202.437	10.968	0.002
C	c5	7	3	96.204	199.909	5.975	0.021	d5	7	3	95.932	199.364	7.895	0.008
D	c6	6	6	90.625	199.712	5.779	0.024	d6	4	6	88.259	194.979	3.510	0.069
D	c7	5	5	92.039	198.363	4.430	0.046	d7	3	5	90.176	194.638	3.169	0.082
D	c8	3	5	91.226	196.738	2.804	0.104	d8	**1**	**5**	**88.592**	**191.469**	**0.000**	**0.398**
D	c9	2	4	92.050	194.766	0.832	0.280	d9	2	4	90.506	191.679	0.210	0.359

scenario	model	rank	K	-log $\mathcal{L}$	AICc	Δ_i	w_i	model	rank	K	-log $\mathcal{L}$	AICc	Δ_i	w_i
A	s1	9	2	75.547	155.800	9.415	0.003	r1	9	2	80.596	165.899	22.892	5.7x10^{-6}
B	s2	7	4	71.097	152.861	6.477	0.015	r2	6	4	70.429	151.524	8.517	0.008
B	s3	4	3	71.167	149.833	3.449	0.067	r3	8	3	72.871	153.243	10.236	0.003
C	s4	3	4	69.382	149.432	3.047	0.082	r4	7	4	70.773	152.212	9.205	0.005
C	s5	**1**	**3**	**69.442**	**146.385**	**0.000**	**0.378**	r5	5	3	70.774	149.047	6.040	0.026
D	s6	8	6	67.922	154.306	7.922	0.007	r6	4	6	65.158	148.778	5.771	0.030
D	s7	5	5	67.954	150.194	3.809	0.056	r7	3	5	65.484	145.254	2.247	0.173
D	s8	6	5	67.973	150.231	3.847	0.055	r8	2	5	65.229	144.744	1.737	0.223
D	s9	2	4	67.976	146.618	0.234	0.336	r9	**1**	**4**	**66.170**	**143.007**	**0.000**	**0.532**

Table 4. Average model estimates for the clutch size (c), number of daughters (d), number of sons (s) and sex ratios (r). Number estimates' column headings are μ (mean) and k (overdispersion) and sex ratio estimates' column headings are p (mean) and θ (overdispersion). Other abbreviations are given in section 2. Individual model estimates for each model are given in table S3.

trait	μ_{t0} or p_{t0}	k_{t0} or θ_{t0}	μ_{t1} or p_{t1}	k_{t1} or θ_{t1}	μ_{t2} or p_{t2}	k_{t2} or θ_{t2}
c	240.262	110.482	190.018	143.190	180.001	89.850
d	216.344	164.901	163.010	280.485	133.504	58.016
s	25.670	40.818	29.639	41.927	42.496	42.769
r	0.102	17029.717	0.157	798.928	0.246	243.359

Table 5. Fitness consequences of heterospecifics (*Ceratosolen galili* and *Sycophaga sycomori*) on *Ceratosolen arabicus*. Column two gives the mean observed number of *C. arabicus* daughters, column three the potential number of daughters (= the observed clutch size for treatment multiplied by the fraction of daughters in control figs) and column four to six the fitness costs of the treatments due to competition and sex ratio adjustment as percentages of the best strategy.

treatment	observed mated daughters	potentially mated daughters[a]	total fitness loss	fitness loss due to competition	fitness loss due to sex ratio adjustment
on own	216.6	216.3[b]	-	-	-
with *S. sycomori*	164.2	175.0	24	19	5
with *C. galili*	132.3	157.4	39	27	12

[a] If 0.102 (table 4) is the optimal sex ratio.

[b] Slight difference is due to small differences in averaging and likelihood estimates.

Figures

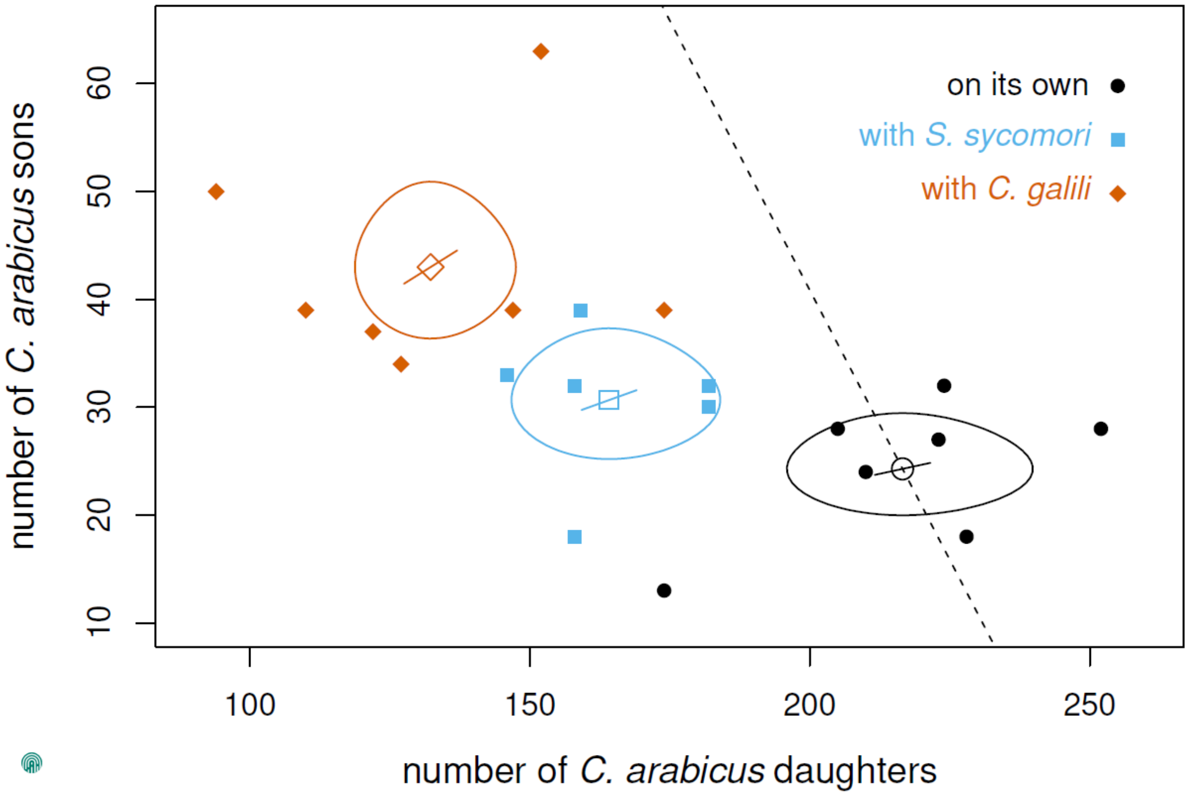

Figure 1. Brood composition of 20 clutches totalling 4082 wasp offspring (solid symbols). Open symbols are the maximum likelihood estimates for model 9 for the number of sons and the number of daughters. Ellipses are likelihood-based confidence limits for these estimates. The short lines running through the maximum likelihood estimates are sex ratio isoclines that are not parallel to each other, and that will intersect at the origin (0, 0) if extended to the left. The dashed line connects points where the clutch size equals the average of 240.9. All clutch-size isoclines are parallel to this line.

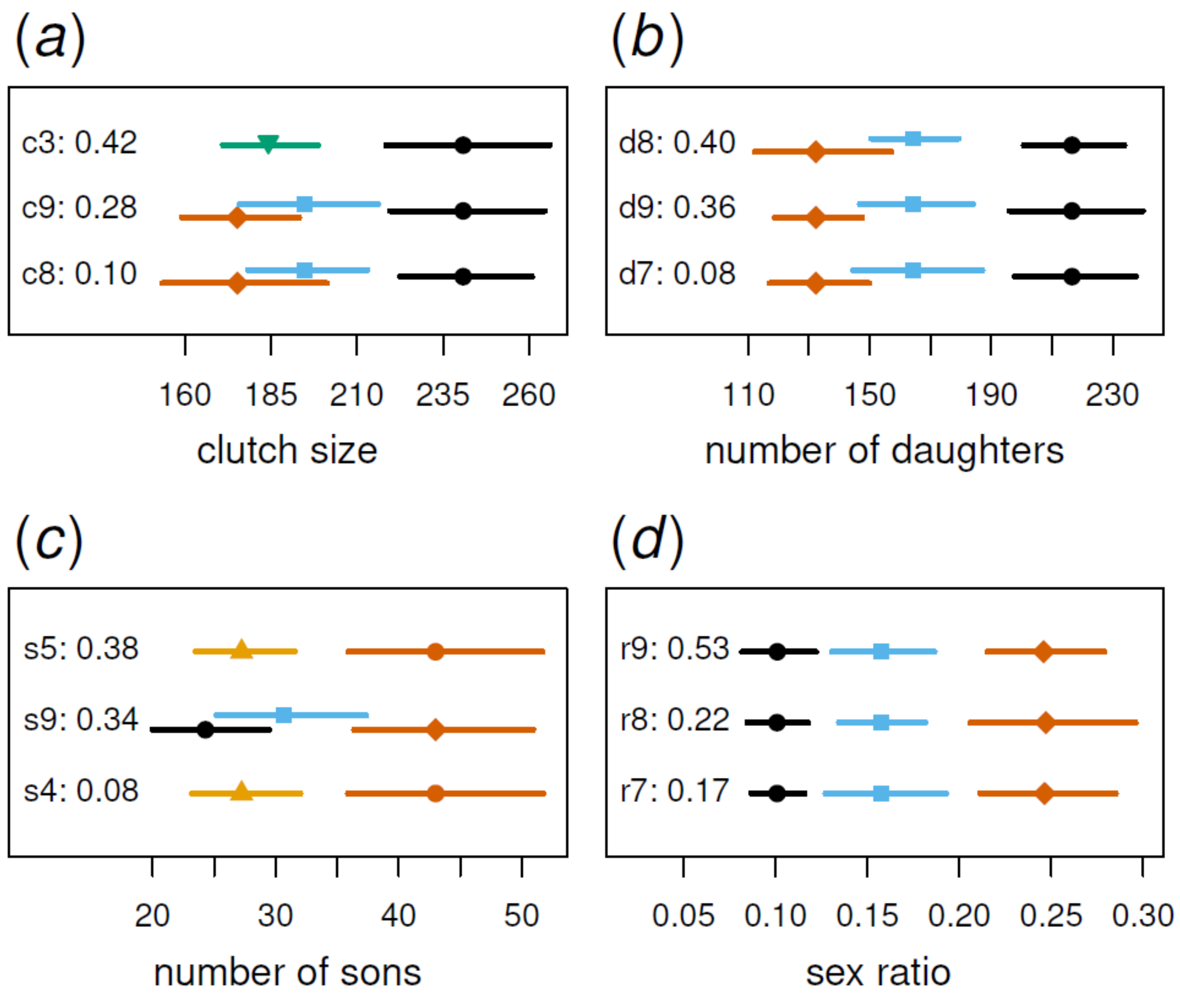

Figure 2. Maximum likelihood estimates and likelihood-based confidence limits (lines) for the three best models for each of (a) the clutch size, (b) the number of daughters, (c) the number of sons and (d) the sex ratio. Note that apart from the focal parameter, these confidence limits are based on parameters that are picked so that the likelihood is maximised. The model names and Akaike weights are given to the left of each set of estimates. Black and circles are for *Ceratosolen arabicus* on their own, sky blue and squares are for *C. arabicus* together with *Sycophaga sycomori*, and vermillion and diamonds are for *C. arabicus* together with *Ceratosolen galili*. Turquoise with a down-triangle is for when the model assumes that *S. sycomori* and *C. galili* affect *C. arabicus*'s clutch size in the same way, and orange up-triangle is when models assume that the number of *C. arabicus* sons produced when they are on their own is the same as when they are together with *S. sycomori.*