



Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: [www.elsevier.com/locate/actoec](http://www.elsevier.com/locate/actoec)

## Detecting the elusive cost of parasites on fig seed production

Simon T. Segar<sup>a,b,c</sup>, Ani Mardiasuti<sup>d</sup>, Philip M. Wheeler<sup>e</sup>, James M. Cook<sup>a,f,\*</sup>

<sup>a</sup> School of Biological Sciences, University of Reading, UK

<sup>b</sup> Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

<sup>c</sup> Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic

<sup>d</sup> Faculty of Forestry, Bogor Agricultural University, Bogor, Indonesia

<sup>e</sup> Open University, Milton Keynes, UK

<sup>f</sup> Hawkesbury Institute for the Environment, Western Sydney University, Australia

### ARTICLE INFO

#### Keywords:

Conflict  
Costs  
*Ficus*  
Mutualism  
Parasites  
Pollination

### ABSTRACT

Mutualisms provide essential ecosystem functions such as pollination and contribute considerably to global biodiversity. However, they are also exploited by parasites that remove resources and thus impose costs on one or both of the mutualistic partners. The fig/pollinator interaction is a classic obligate mutualism; it is pantropical and involves > 750 *Ficus* species and their host-specific pollinating wasps (family Agaonidae). Figs also host parasites of the mutualism that should consume pollinators or seeds, depending on their larval ecology. We collected data from a large crop of figs on *Ficus glandifera* var. *brachysyce* in a Sulawesi rainforest with an unusually high number of *Eukoebelea* sp. parasites. We found that these parasites have a significant negative correlation with fig seed production as well as with pollinator offspring production. *Eukoebelea* wasps form the basal genus in subfamily Sycophaginae (Chalcidoidea) and their larval biology is considered unknown. Our analysis suggests that they feed as flower galls and impose direct costs on the fig tree, but a strategy including the consumption of pollinator larvae cannot be ruled out. We also present baseline data on the composition of the fig wasp community associated with *F. glandifera* var. *brachysyce* and light trap catch data.

### 1. Introduction

Mutualisms are ubiquitous and important biotic interactions that underpin some key ecosystem functions, such as pollination and nitrogen fixation (Foster and Wenseleers, 2006; Leigh, 2010), and also drive the evolution of much biodiversity (Sachs and Simms, 2006; Wardle et al., 2004). However, they are also exploited by parasites, which impose immediate costs on at least one of the mutualists and influence the longer-term evolutionary trajectories of mutualisms (Yu, 2001). It is therefore crucial to understand the host specificity (Farache et al., 2018) and biology of these parasites and to conduct targeted studies to identify and quantify their costs.

The interaction between *Ficus* (Moraceae) and fig-pollinating wasps (Agaonidae) is a classic obligate mutualism, in which the fig and wasp require each other for reproduction and show very high reciprocal partner specificity (Janzen, 1979; Weiblen, 2002). Female pollinator wasps enter the enclosed *Ficus* inflorescences (figs) and pollinate the female flowers within. Each flower can either produce a seed or host the development of one pollinator or parasitic wasp. Flowering is asynchronous between fig trees in a population, which both sustains pollinator populations and provides an important year-round fruit supply

for frugivores (Shanahan et al., 2001). This is of global significance since the > 750 *Ficus* species are spread across all tropical continents (Berg and Corner, 2005).

Like other mutualisms, the fig/pollinator interaction is subject to parasitism. In particular, many species of non-pollinating fig wasps (NPFWs) also develop in fig inflorescences and, like the pollinators, are typically specialists on a single *Ficus* species (Cook and Segar, 2010). There are distinct guilds of NPFWs with different resource use strategies (Cook and Rasplus, 2003; Craud et al., 2011b; Kerdelhué et al., 2000; Segar et al., 2013; West et al., 1996). Small gall-inducers feed on fig flowers by galling them, having broadly negative effects on both seeds (through direct consumption) and pollinators (through competition). Seed eating appears to be an unusual strategy, but some inquiline will feed on seeds if necessary (Pereira et al., 2007), hence only an effect on seeds is expected. In contrast, members of the small cleptoparasite guild exploit the galls of pollinators or small herbivores and kill them. Small cleptoparasites and pollinators should be negatively correlated, with no predicted relationship between small cleptoparasites and seeds.

Much larger wasp species also occur, and the large gall-inducers make large galls from flowers or fig wall tissue. Finally, the large wasps are also attacked by specialist large parasitoids or cleptoparasites that

\* Corresponding author. Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia.  
E-mail address: [James.Cook@westernsydney.edu.au](mailto:James.Cook@westernsydney.edu.au) (J.M. Cook).

<https://doi.org/10.1016/j.actao.2018.03.002>

Received 31 January 2017; Received in revised form 11 February 2018; Accepted 6 March 2018  
1146-609X/ © 2018 Elsevier Masson SAS. All rights reserved.

kill them (West et al., 1996). To date few manipulative experiments have been conducted on these large non-galling species and often their exact larval biology, whether they are parasitoids or cleptoparasites, is unknown. Indeed, trophic role in fig wasps is likely to be evolutionarily labile with endo- and exo-parasitoids existing in the same genus (Yadav and Borges, 2017), and this deserves to be studied in more detail. The typical pattern across fig species is that the large gall-inducers and their parasitoids/cleptoparasites are far less common than the smaller wasps (Segar et al., 2014, 2013). In addition, the large and small wasp faunas appear to operate as separate modules within the community (in at least some systems) with each set of gall-inducers having its own set of size-matched parasitoids/cleptoparasites (Compton et al., 1994; Segar et al., 2014, 2013).

Most NPFW species belong to five subfamilies (Sycoryctinae, Sycophaginae, Otitesellinae, Sycoecinae, and Epichrysomallinae) of chalcid wasps associated exclusively with *Ficus*. Several studies have attempted to quantify the costs of parasites on various fig/pollinator mutualisms. Strikingly, when a significant cost has been found, it has usually involved reduced pollinator, not seed, production (Segar and Cook, 2012). A simple negative effect on pollinator numbers provides evidence of pollinator predation, while flower galls may also reduce pollinator numbers through competition for galls, as well gall numbers through direct consumption. It has been reported that several NPFW species across a range of higher taxa, including species of Sycoryctinae (Kerdelhué et al., 2000), Sycophaginae (West and Herre, 1994), Otitesellinae (West et al., 1996) and Epichrysomallinae (Peng et al., 2010), can have a negative correlation with pollinator numbers. This cost technically falls on both mutualists, since the female pollinator wasps that die would also have contributed to fig male reproductive function by carrying pollen. However, there is less evidence that NPFWs consume flowers. This is not surprising for the most species-rich wasp subfamily (Sycoryctinae), since it is believed to consist mainly of parasitoids and cleptoparasites.

In contrast, larval ecology has diversified greatly in the large subfamily Sycophaginae (Cruaud et al., 2011b), resulting in geographic and taxonomic disparities in trophic role. Indeed, while some species are small cleptoparasites (Elias et al., 2012; Kerdelhué and Rasplus, 1996; Wang and Zheng, 2008) others (sometimes congeners, e.g. in *Idarnes* and *Sycophaga*) have also been shown to compete with pollinators for galls (Elias et al., 2012; Galil and Eisikowitch, 1969) or consume seeds (Pereira et al., 2007). Others still fill the niche of large gall-inducers (Cruaud et al., 2011b). We expect that this variation in larval ecology is an important factor determining the detection of flower galling by fig wasps in this subfamily. By using correlations between seeds and wasps it is possible to shed further light on larval ecology.

In this study we take advantage of a crop of figs that was infested with *Eukoebelea* sp. wasps to statistically examine correlations between these parasitic wasps, fig-pollinating wasps and seeds. A recent phylogeny reveals that *Eukoebelea* is the basal genus of the pantropical Sycophaginae subfamily (Cruaud et al., 2011a), but no *Eukoebelea* species has been studied in detail. Therefore insights into the ecology of this genus can help us to understand the diversification of feeding regime in the subfamily, the ancestral state is currently thought to be ovary galling (Elias et al., 2017). One reason is that these Australasian *Eukoebelea* wasps have low abundance and patchy occurrence in studies of figs from the section Malvanthera, which are their host plants. For example, there was a mean of only 0.7 wasps per fig (across 8 crops and 255 figs) in *F. rubiginosa* (Segar et al., 2014) and of only 1.3 in *F. obliqua* (across 18 crops and 149 figs) (Segar and Cook, 2012), precluding informative statistical exploration of their effects. However, we sampled a single large crop of fruits in another malvantheran fig species, *F. glandifera* var. *brachysyce*, (Fig. S1). We took advantage of the unprecedented numbers of *Eukoebelea* sp. wasps, and small numbers of those species which mask their effects, to identify their correlation with seed (female function) and pollinator numbers (male function), and to

help clarify their controversial larval biology (Cruaud et al., 2011b). As outlined above, small gall-inducers are predicted to correlate negatively with both seeds and wasps, while small cleptoparasite numbers should correlate only with pollinator numbers. We also present data on the abundance of each species of non-pollinating fig wasp (NPFW) found in this, as yet undescribed, community of insects and provide supplementary data on the wasps collected at light in the study tree.

## 2. Materials and methods

The impact of parasitic wasps is often subtle, especially if numbers are low, and it can be masked by between-crop variation in resources available to individual fig-fruits (West et al., 1996). These differences in “productivity” of individual figs are manifested through differences in fig size and the numbers of flowers developing inside. We used a single large crop of figs from *Ficus glandifera* var. *brachysyce* (Fig. S1). Importantly, the crop had high abundance of the focal parasite species, offering a strong signal:noise ratio when trying to infer its effects on the mutualism. We collected 52 late D-stage figs (just before wasp emergence) from within the canopy of a hemi-epiphytic rainforest tree on Buton Island (Sulawesi, Indonesia) and allowed the wasps to emerge into individual collecting pots. We then measured the diameter of each fig to the nearest 0.01 mm and dissected it under a microscope at 10–60 $\times$ . Fig ovule contents were identified and recorded as: wasp (identified to genus and then morpho-species); seed; exited (with an emergence hole); or undeveloped. We also installed a light trap in the canopy of our focal tree (see Supplementary Information) and ran it for 150 h, which provided data on locally abundant pollinating and non-pollinating fig wasp species.

We performed two multiple-linear regression analyses with i) seed number and ii) pollinator numbers as the respective response variables and the two explanatory variables *Eukoebelea* number and fig diameter. We included fig size as a covariate as this is also correlated with the total number of wasps and seeds produced (“productivity” - Cook and Power, 1996). We performed stepwise deletion of nonsignificant terms using F-tests. All analyses were conducted in R v 3.2.4 (R Development Core Team, 2016) and all models were fitted using type II sums of squares. We tested the null hypothesis that the estimated slopes of models (i) seeds = *Eukoebelea* and (ii) pollinators = *Eukoebelea* were not significantly different from each other by comparing the slopes of the two models with different response variables (Sokal and Rohlf, 1995). All models were checked for heteroscedasticity, non-normality of residuals, and influential observations both graphically and by using the Non-Constant Variance (NCV) Score test (homoscedasticity) as implemented in the R package ‘car’ (Fox and Weisberg, 2011) and the Shapiro Wilk tests (normality of residuals).

## 3. Results

### 3.1. The effect of parasites on the mutualism

A single undescribed species of *Eukoebelea* represented 85% of all parasitic, or non-pollinating, fig wasps and had a significant negative effect on both seeds and pollinators (Table 1 and Fig. 1). The relationship between *Eukoebelea* sp. parasites and both mutualists (fig seeds and pollinating wasps) was significantly negative, and therefore likely to have a biologically meaningful effect on overall fitness. The slopes of simplified models i) seeds = *Eukoebelea* and ii) pollinators = *Eukoebelea* were not statistically different ( $t = 0.732$ ,  $p = 0.466$ ). We found constant variance of the residuals when plotted against the fitted values and this hypothesis was not rejected by NCV Score tests, the distribution of the residuals of each model was not significantly different from normal. All data are uploaded as ‘data in brief’ and can be downloaded from Mendeley Data ([dataset] Segar et al., 2018).

Download English Version:

<https://daneshyari.com/en/article/8846480>

Download Persian Version:

<https://daneshyari.com/article/8846480>

[Daneshyari.com](https://daneshyari.com)