Comparative life-history traits in a fig wasp community: implications for community structure

MAHUA GHARA and RENEE M. BORGES Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India

Abstract. 1. Whether life-history traits can determine community composition and structure is an important question that has been well explored theoretically, but has received scant empirical attention. Life-history traits of a seven-member community of galler and parasitoid fig wasp species (Chalcidoidea), developing within the inflorescences (syconia) of *Ficus racemosa* (Moraceae) in India, were determined and used to examine community structure and ecology.

2. Gallers were pro-ovigenic (all eggs are mature upon adult emergence) whereas parasitoids were synovigenic (eggs mature progressively during adult lifespan). Initial egg load was correlated with body size for some species, and there was a trade-off between egg number and egg size across all species. Although all species completed their development and left the syconium concurrently, they differed in their adult and pre-adult lifespans. Providing sucrose solutions increased parasitoid lifespan but had no effect on the longevity of some galler species. While feeding regimes and body size affected longevity in most species, an interaction effect between these variables was detected for only one species.

3. Life-history traits of wasp species exhibited a continuum in relation to their arrival sequence at syconia for oviposition during syconium development, and therefore reflected their ecology. The largest number of eggs, smallest egg sizes, and shortest longevities were characteristic of the earliest-arriving galling wasps at the smallest, immature syconia; the converse characterised the later-arriving parasitoids at the larger, already parasitised syconia. Thus life history is an important correlate of community resource partitioning and can be used to understand community structure.

4. This is the first comprehensive study of life-history traits in a fig wasp community. The comparative approach revealed constraints and flexibility in trait evolution.

Key words. Agaonid, galler, host window, inquiline, lifespan, non-pollinating fig wasps, ovigeny, parasitoid, survivorship curves.

Introduction

Information on life-history traits is essential to an understanding of ecological community structure and the coexistence of multiple competitors (Bonsall & Mangel, 2004; Bonsall *et al*., 2004). Life-history traits such as fecundity, egg size, and longevity have been coupled with host availability and competitive ability within an $r-K$ strategy continuum to explain species succession and the structure of parasite communities (Price, 1973a,b, 1975; Askew, 1975; Force, 1975).

Correspondence: Renee M. Borges, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India. E-mail: renee@ces.iisc.ernet.in

Trophic positions and resource partitioning are also considered important in determining community composition (Naeem & Hawkins, 1994; Vincent *et al*., 1996; Bonsall *et al*., 2002; Giacomini *et al*., 2009). Communities can contain mutualists (interactants that confer net positive benefits on each other as a result of the interaction) and exploiters (species that exact costs on interactants without conferring any benefits). In communities comprising mutualists and exploiters, coexistence of the various interactants, especially exploiters vis-à-vis mutualists, is theoretically believed to be facilitated by traits such as dispersal ability of exploiters and parasitism rates (Bronstein *et al*., 2003; Wilson *et al*., 2003), which in turn are influenced by life history (Price, 1975). While theoretical explorations of the role of life history and ecology in determining the structure

of such communities abound (Golinski, 2006), empirical investigations of these features for real communities are few (e.g. Askew, 1975; Price, 1975). For example, life-history traits of insect species, especially of parasites, have usually been examined in isolated species without the specific perspective of a comparative study (Blackburn, 1991a,b; Harvey, 2005; Jervis *et al.*, 2008). Few studies have examined life-history traits of all members of a parasitic community (e.g. Askew, 1975), especially communities in which some parasites are also mutualists, and must necessarily have life-history traits constrained by the mutualism, e.g. developmental time in the case of brood-site parasites in nursery pollination mutualisms (Dufaÿ & Anstett, 2003). Examination of the role of life history in structuring such communities is often constrained by knowledge of community membership and natural history, e.g. whether community members are generalists or specialists would have considerable impact on the interaction between life history and ecology (Stearns, 1976; Kneitel & Chase, 2004) and consequently an important bearing on community structure.

The fig wasp community is an ideal community for an investigation of the interaction between life history and ecology of mutualistic and exploitative community members. This is because: (i) it represents a multitrophic interaction system with co-existing galler, inquiline and/or parasitoid species (Cook & Rasplus, 2003; Herre *et al.*, 2008), and (ii) it is one in which all members of the community, hosts and parasites, develop within the same tissue package (the fig syconium), are taxonomically closely related and highly specialised, and must necessarily complete their development at the same time, although development may be initiated at different times. In a community with such characteristics and constraints, a comparison of the life-history traits of members would afford valuable insights into the direction of trait evolution leading to resource partitioning from which community assembly might emerge.

Despite its intrinsic value as a model system to study community organisation (Cook & Rasplus, 2003; Herre *et al.*, 2008), the community of fig wasps occupying a single fig species has been scarcely investigated (Compton *et al.*, 1994; West & Herre, 1994; West *et al.*, 1996; Kerdelhué *et al.*, 2000; Elias *et al.*, 2008; Wang & Zheng, 2008). Although the lifespan of some fig wasp pollinators has been recorded (Kjellberg *et al.*, 1988; Dunn *et al.*, 2008), only one study has investigated life-history traits, such as longevity and fecundity, of fig wasps comprising a community occupying a single fig species (Compton *et al.*, 1994). There is currently neither a comprehensive study of the life-history traits of fig wasps, nor an understanding of how ecological factors such as access to water and carbohydrates may differentially affect their longevity and ecology.

We therefore investigated life-history traits in a reasonably speciose fig wasp community occupying a single fig species at a single geographical location, and asked the following questions: (i) Do the fig wasp species differ in longevity and fecundity? (ii) Is there an effect of body size on life-history traits? (iii) Is there an effect of nutritional regimes on adult lifespans? (iv) Do the species differ in their ovigeny index (ratio of number of mature eggs at eclosion to lifetime potential fecundity) and does it correlate with longevity? (v) Is there a relationship between longevity and the length of time hosts are available for oviposition? These life-history data were used to perform a hierarchical clustering of community members to determine the correspondence between ecology and life history of the member species.

Materials and methods

Natural history of the fig wasp community

Figs (*Ficus*, Moraceae) and their pollinating fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) interact via a highly species-specific nursery pollination mutualism (Cook & Rasplus, 2003; Marussich & Machado, 2007). The fig inflorescence is an urn-shaped receptacle called a syconium with an opening termed the ostiole; the syconium has hundreds to thousands of flowers lining its inner wall. Syconium development is divided into five phases (A–E) (Galil & Eisikowitch, 1968). In a typical monoecious fig species, the pre-receptive (A) phase consists of young syconia with immature flowers. In the B phase, pollinating wasps enter the syconium, pollinate some receptive female flowers and oviposit into others after pollinating them to form galls. Pollinators thus develop in potential seed sites. In the inter-floral (C) phase, seeds, and pollinators develop. In the wasp dispersal (D) phase, pollinator males and females eclose, mate, and the wingless pollinator males chew an exit hole for females who leave the syconium with pollen from male flowers to enter another receptive syconium (usually on another tree, since developmental phases of fig syconia are generally synchronised within a tree) to recommence the cycle. Males usually die within their natal syconium. After pollinators disperse, syconial properties (colour, odour) change (E phase) to attract seed dispersers (Borges *et al.*, 2008). During development, the syconium and syconial wall change from small, thin-walled syconia in A phase to large, thick-walled syconia in later phases.

This development cycle is subject to parasitism by other chalcidoid wasps, all of which are not necessarily agaonids, but are still more closely related (Cook & Rasplus, 2003) than are other pairs of insect parasites and hosts. These non-pollinating fig wasps (NPFWs) are also highly host specific (Jousselin *et al.*, 2008; however see Marussich & Machado, 2007). NPFWs usually oviposit into the syconium from the outside using long ovipositors. They are flower gallers, inquilines, or parasitoids of the pollinating fig wasps or of each other, and also attack syconia at various developmental stages (Proffit *et al.*, 2007; Elias *et al.*, 2008; Wang & Zheng, 2008). Thus, several wasp species compete for brood space in the syconium. The details of the type of parasitism are scarcely known and the hosts of most parasites remain speculative and inferential (Cook & Rasplus, 2003; Herre *et al.*, 2008). Winged NPFW females leave the syconium in the D phase through the exit hole chewed by pollinator males. Pollinators and NPFWs use, at long distances, volatile compounds produced by syconia to locate figs appropriate for oviposition (Grison-Pigé *et al.*, 2002; Proffit *et al.*, 2007). The nature of the short-distance cues used by externally ovipositing NPFWs to locate potential hosts within syconia is still unknown.

Study site and fig community composition

The fig wasp community of *Ficus racemosa* L. (Section: Sycomorus) from South India (Indian Institute of Science campus, Bangalore, Karnataka, 12°58′N, 77°35′E) was chosen for the study. The community comprises one pollinating wasp species (*Ceratosolen fusciceps* Mayr: Agaonidae) and six species of NPFWs (*Apocryptophagus stratheni* Joseph, *Apocryptophagus testacea* Mayr, *Apocryptophagus fusca* Girault, *Apocryptophagus agraensis* Joseph, *Apocrypta* sp. 2, *Apocrypta westwoodi* Grandi) (Fig. 1). Since the Agaonidae are not monophyletic (Rasplus *et al.*, 1998), *Apocryptophagus* (subfamily Sycophaginae) and *Apocrypta* (sub-family Sycoryctinae) have not yet been assigned family status within the superfamily Chalcidoidea. Although the pollinator is a mutualist of the fig pollination system, it is also a parasite since its eggs develop at the cost of fig seeds. All species differ in their timing of oviposition across syconium development (Fig. 1) but leave the syconium concurrently. *Ceratosolen fusciceps*, *A. stratheni*, *A. testacea*, and *A. fusca* are gallers (Proffit *et al.*, 2007; Wang & Zheng, 2008) whereas *A. agraensis* is either an

inquiline or a parasitoid (M. Ghara, pers. obs.; Wang & Zheng, 2008), while *Apocrypta* sp. 2 and *A. westwoodi* are parasitoids (Proffit *et al.*, 2007; Wang & Zheng, 2008).

Life-history variables

Wasps were collected immediately on leaving D phase syconia and immobilised at 4 °C. After dissection in physiological saline under a stereomicroscope (Zeiss Stemi 2000-C), their ovaries were stained with acetocarmine to reveal immature and mature oocytes. The number of mature and immature oocytes was counted to estimate potential fecundity (Jervis *et al.,* 2005). Initial egg load was determined as the number of mature eggs present at emergence (Jervis *et al.*, 2008). Eggs were photographed using a digital camera Clemex Captiva (version 3.5.025) attached to the stereomicroscope. Egg dimensions (length and width) were measured from these images using ImageJ software (version 1.40g). Egg volume with and without the pedicel was calculated using the formula $V = 1/6\pi LW^2$ where L is length and W is width of the egg (Blackburn, 1991b; Giron & Casas, 2003). Volume of the cylindrical pedicel was estimated as $\pi r^2 l$, where $r = $ (width of pedicel)$/2$, and l is length of the pedicel. Ovigeny index (OI) was calculated as initial egg load divided by lifetime potential fecundity (Jervis *et al.*, 2001). For confocal microscopy, ovaries dissected in 1X PBS (phosphate buffered saline) were stained with propidium iodide and examined under a Zeiss LSM 510 microscope following Dedeine (2001). Body weight was measured using freshly eclosed wasps. *Apocryptophagus stratheni* males could not be found in any sampled syconia; hence the fresh weight for males of this species is not available. Hind tibia length was used as a surrogate for body size (Jervis *et al*. 2005; J.-Y. Rasplus, pers. comm.)

Adult lifespan under different nutritional regimes

Syconia ($n = 81$) in wasp dispersal (D) stage were collected from five *Ficus racemosa* trees. Wasps were allowed to exit naturally, or by providing assistance to NPFWs in syconia which had no developing pollinator males. Wasps were housed, under a 12:12 h light:dark regime at room temperature, in groups of 10–15 within aerated and regularly changed plastic tubes. Wasps were maintained under three feeding treatments: (a) starved (control), (b) water only, (c) sucrose 10% (w/v) solution. Water or sugar was provided daily by soaking in a ball of cotton. The exit day from the syconium was considered as day 0; wasps were censused every 24 h until 100% mortality occurred. At mortality, individuals were preserved in 70% alcohol for biometric measurements. Adult survivorship curves were plotted for each species and treatment.

Generalised linear models (GLMs) were used to examine the effect of nutritional regime (treatment) and body size as well as their interaction on longevity. Negative binomial error structures were employed for *A. fusca*, *Apocrypta* sp. 2, and *A. westwoodi*, and quasi-Poisson error structures for *A. testacea* and *A. agraensis* owing to overdispersion (Crawley, 2007). Treatment was a categorical predictor while body size was a continuous predictor variable.
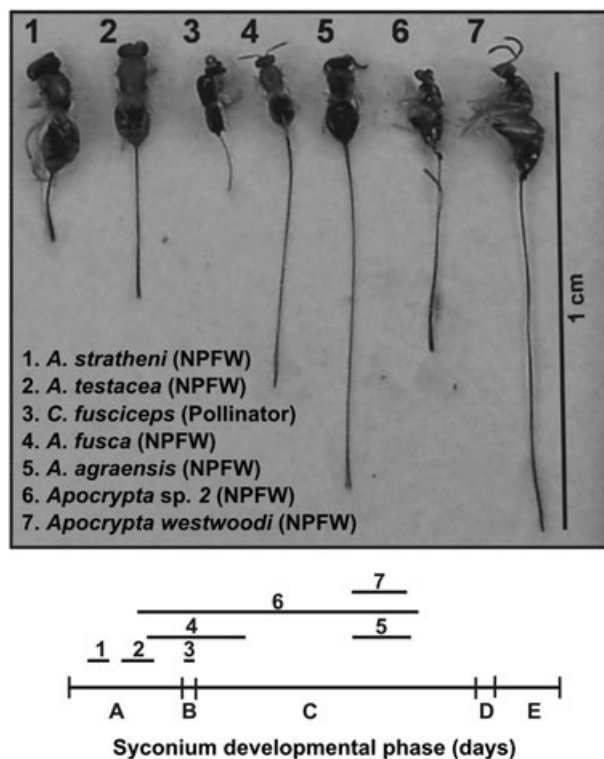

Fig. 1. Fig wasps of *Ficus racemosa*. (1) *Apocryptophagus stratheni*, (2) *Apocryptophagus testacea*, (3) *Ceratosolen fusciceps* (pollinator), (4) *Apocryptophagus fusca*, (5) *Apocryptophagus agraensis*, (6) *Apocrypta* sp. 2, (7) *Apocrypta westwoodi*. The schematic representation (not to scale) shows wasp arrival sequence across a syconium development cycle (A–E phases) for *F. racemosa* (approximately 60 days). The numbers in the schema correspond to those identifying each wasp species in the photograph. The bars represent the oviposition window (days).

Length of host window available for oviposition

The host window was defined as the time period (in days) for which a syconium was suitable for oviposition by a particular wasp species, as determined by the first and last observed oviposition attempts by NPFWs on the syconium during its development (schematised in Fig. 1). For pollinators, the host window was when they entered the syconium. Oviposition of each wasp species across syconium development (A–D phases) was recorded by scan sampling two bunches of syconia per tree on two focal trees. Individual syconia in each bunch were uniquely tagged and were scanned every alternate day at three sampling time points (09.00, 12.00 and 03.00 hours) to coincide with peak wasp activity (M. Ghara, Y. Ranganathan and R. M. Borges, unpublished). The number of individuals of each wasp species present on each syconium was noted. Thus oviposition in pre-pollination, pollination, and post-pollination phases was recorded for each syconium, for each wasp species. Data were then averaged across syconia. From observations on such marked syconia, the pre-adult lifespan for each wasp species was also estimated as the time between the first and last observed oviposition attempt by that species and the exit in D phase for all wasp species of a particular syconium.

Clustering community members by life history and ecology

The following life-history and ecological traits: length of host window, pre-adult lifespan, body weight, ovipositor length, longevity under various treatments, initial egg load and egg volume, were used to perform a hierarchical cluster analysis for all species using Euclidean distance and Ward's method. This method (Ward, 1963) uses ANOVA to evaluate distance between clusters and is considered to be very efficient, especially since it can determine clusters of small sizes, and thus at finer scales (Mojena, 2006). Clusters were built using the *pvclust* algorithm in R (version 2.8.1). Since all variables could not be measured for the same individual wasp, the cluster trees were generated using means for each trait and for each species. Since *A. stratheni* is rare, we did not have quantitative observations for host window and pre-adult lifespan; we therefore made educated guesses about these variables for this species based on opportunistic observations. All statistical analyses were performed using the software package R.

Results

Life-history variables

The pollinator *C. fusciceps* and all *Apocryptophagus* species were pro-ovigenic (ovigeny index = 1) with all eggs mature at eclosion (see Figure S1 and Table S1). The *Apocrypta* parasitoids were moderately synovigenic (ovigeny index < 0.5) as their ovarioles contained few matured eggs and many developing oocytes. *Apocrypta* ovarioles were polytrophic, with nurse cells or trophocytes within each follicle surrounding the developing oocyte (see Figure S1). Thus, *Apocrypta* have a continuous supply of eggs which mature over time. Initial egg load varied across species; *A. stratheni* and *A. testacea* had the largest (<250), while *A. agraensis* and *Apocrypta* had

the smallest (<60) (see Table S1). Eggs differed in morphology and yolk content across species (see Figure S1). Pollinator eggs were yolky with a filamentous pedicel, easily separated from the ovarioles. In all other wasps, eggs were firmly attached to ovarioles and only staining with acetocarmine made it possible to distinguish between the translucent non-yolky egg pedicel and the ovariole. Egg pedicel lengths, and thereby volume, were greatest for *Apocrypta*. All the *Apocryptophagus species* had similar egg pedicel lengths despite the fact that their ovipositor lengths varied, e.g. the ovipositor length of *A. agraensis* was nearly twice that of *A. testacea* and 1.5 times that of *A. fusca*. The size of mature eggs varied across species (see Table S1). *Apocryptophagus testacea* and *A. fusca* had the smallest total egg volume, and *Apocrypta* parasitoids the largest (see Table S1). Therefore, across most species, there appears to be a trade-off between egg number and egg volume.

Egg load and body size were not correlated in the pollinator *C. fusciceps* and galler *A. stratheni* (Kendall's $\tau = 0$ and -0.07, $P = 1$ and 0.9, $n = 14$ and 8 respectively). However, these variables were positively correlated in the other species (*A. testacea*: $\tau = 0.84$, $n = 15$, $P < 0.001$; *A. fusca*: $\tau = 0.62$, $n = 14$, $P = 0.002$; *A. agraensis*: $\tau = 0.7$, $n = 15$, $P < 0.001$; *Apocrypta* sp. 2: $\tau = 0.58$, $n = 15$, $P = 0.003$; *A. westwoodi*: $\tau = 0.64$, $n = 8$, $P = 0.03$). The potential lifetime fecundity of the synovigenic parasitoids increased significantly with body size (*Apocrypta* sp. 2: $\tau = 0.42$, $n = 15$, $P = 0.03$; *A. westwoodi*: $\tau = 0.64$, $n = 8$, $P = 0.03$). The lack of significant results in some cases, for example lack of correlation between egg load and body size in *C. fusciceps*, may have been caused by the unavoidably small sample sizes.

The fresh body mass of males of each species was much less than that of the females (see Table S1). Data on fresh weight of males of *A. stratheni* could not be collected because of unavailability of any male of this species.

The effect of nutritional regimes and body size on longevity

Adult survivorship curves ranged from the early mortality type I (*C. fusciceps*, *A. agraensis*, *A. stratheni*) to the late mortality type III (*Apocrypta* parasitoids) (Fig. 2). Interspecific differences in the curves were greatly exaggerated in the sucrose treatment. The GLM analysis indicated a significant effect of treatment on lifespan for all investigated species (Table 1). The pollinator *C. fusciceps* and *A. stratheni* were not included in the GLM analysis because *C. fusciceps* survived for only 24 h irrespective of the treatment and *A. stratheni* survived on average for only 1 day when starved, and with sucrose and water treatments it lived for a maximum of 2 days with more than 50% mortality in the first 24 h (see Table S1). *Apocryptophagus agraensis* also lived for an average of 2 days under all conditions. However, *A. testacea* and *A. fusca* lived for an average of 4 days without sucrose, while with sucrose their lifespan increased to a week (a maximum of 2 weeks in some individuals). The *Apocrypta* parasitoids lived for about 12 days with sucrose (a maximum of 3 weeks in some individuals); *Apocrypta* sp. 2 exhibited a four-fold increase and *A. westwoodi* a three-fold increase in lifespan with sucrose when compared to the starved control. Body size also had
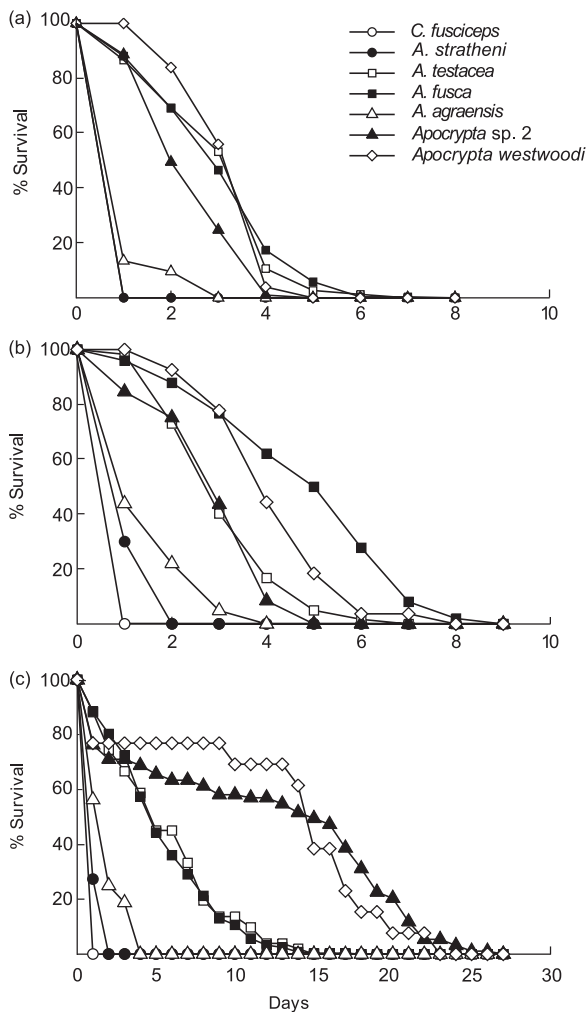
Fig. 2. Survivorship curves in the nutritional treatments. (a) Starved, (b) water, (c) sucrose.

an effect on longevity for all species except *A. westwoodi* (Table 1). Except for *A. fusca*, there was no interaction effect of treatment and body size on lifespan for any species.

Length of host window available for oviposition and pre-adult lifespan

Community members differed in their host windows and pre-adult lifespans. Host windows for *C. fusciceps* and *A. stratheni* were the smallest, followed by those for *A. testacea*, *A. fusca*, and *A. agraensis*, with the largest window for the parasitoid *Apocrypta* sp. 2 (Fig. 1, see Table S1). Pre-adult lifespans also followed the same species groupings, with similar ranges (see Table S1). The *Apocrypta* parasitoids and *A. agraensis* had the shortest pre-adult lifespans while *A. stratheni* and *A. testacea*, which oviposit into the syconia even before the pollinator, had the longest pre-adult lifespans (Fig. 1, see Table S1). Fresh mass of females at eclosion broadly corresponded with pre-adult lifespan, with the exception being *A. westwoodi* whose fresh mass was much higher relative to its pre-adult lifespan and to that of other species.

Cluster analysis of community structure

Hierarchical cluster analysis using life-history traits and oviposition host window as variables resulted in two main clusters with high AU (approximately unbiased) and BP (bootstrap) values (Fig. 3). The *Apocrypta* parasitoids and *A. agraensis* formed one cluster, while the other cluster comprised two groups: (i) the pollinator *C. fusciceps* and *A. fusca*, and (ii) *A. testacea* and *A. stratheni* (Fig. 3). This clustering did not change if ovipositor length was removed from the variable set, or when egg volume with or without the pedicel was used. The highest BP and AU values were obtained with the following variables: length of host window, pre-adult lifespan, fresh weight, ovipositor length, longevity under starvation, egg load and egg volume (without pedicel) (Fig. 3). This clustering did not change even when length of oviposition window (may be deemed an ecological variable) was removed from the analysis (results not shown). The clustering of *A. agraensis* with the *Apocrypta* parasitoids indicates that, unlike its congeners, it is unlikely to be a galler.

Discussion

Life-history traits and fig wasp ecology

Based on life history, the seven-member fig wasp community of *F. racemosa* in south India sorted into two main clusters, gallers and parasitoids. The life-history traits of these
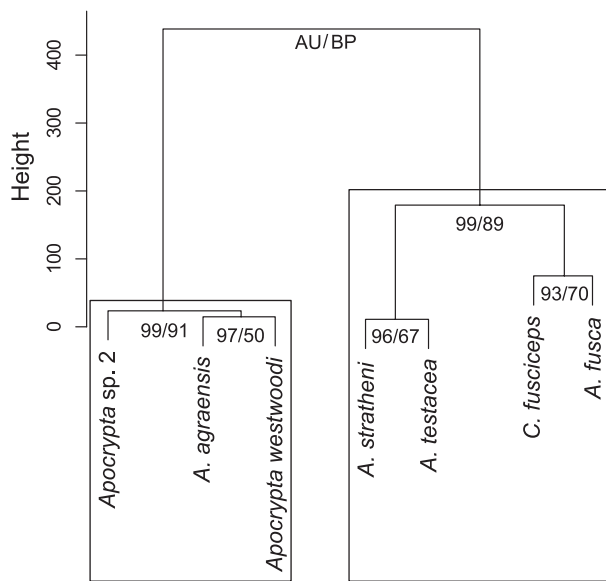
Table 1. GLM analysis of effect of nutritional treatment, body size, and the interaction between them on lifespan of wasp species.

Model	d.f.	*Apocrypta* sp. 2 χ^2	*A. westwoodi* χ^2	*A. fusca* χ^2	*A. testacea* F	*A. agraensis* F
Lifespan						
Treatment	2	233.83***	52.00***	130.04***	49.56***	5.38**
Body size	1	7.16**	1.81	13.77***	22.69***	8.56**
Treatment × body size	2	0.08	4.73	9.57**	0.04	0.62

*$P < 0.05$; **$P < 01$; ***$P < 0.001$.

Fig. 3. Hierarchical cluster analysis using life-history traits by Ward's cluster method, and showing AU (approximately unbiased) and BP (bootstrap) values. The boxes around the clusters indicate stable clusters in the analysis.

Table 2. Life-history traits of the fig wasp community of *Ficus racemosa* reflecting their hierarchical clustering and sequence of arrival at the fig syconium for oviposition.

Life-history traits	Early-arriving gallers	Late-arriving gallers	Parasitoids (early and late-arriving)
Fig wasp species	*A. stratheni*, *A. testacea*	*C. fusciceps*, *A. fusca*	*A. agraensis**, *Apocrypta* sp. 2, *Apocrypta westwoodi*
Matured egg number	Largest	Intermediate	Smallest
Egg size	Intermediate and small	Intermediate and small	Intermediate and largest
Body size (fresh weight)	Largest and smallest	Smallest	Smallest and largest
Host window	Shortest	Intermediate	Shortest and longest
Adult lifespan	Short and intermediate	Shortest and intermediate	Short and longest
Pre-adult lifespan	Longest	Intermediate	Shortest and intermediate
Ovipositor length	Shortest	Intermediate (pollinator has shortest)	Intermediate and longest

**Apocryptophagus agraensis* is predicted to be an inquiline or a parasitoid.

species spanned a continuum from extremely short-lived pro-ovigenic gallers to extremely long-lived synovigenic parasitoids. The parasitoid cluster included a member of a genus believed to be strictly gallers (*Apocryptophagus*; i.e. *A. agraensis*), and corroborated data on this species in India (M. Ghara, pers. obs.) and in China (Wang & Zheng, 2008) in which its galler trophic niche was questioned. Therefore, in this wasp community, life history reflects trophic ecology. Here, for the first time in a fig wasp community, we also show how life-history traits can be used to explain the temporal ecology of parasitism, by demonstrating the correspondence between life-history traits and the arrival sequence for oviposition of this fig wasp community throughout the development of the syconium (Fig. 3, Table 2). The life history of wasps arriving early and late in syconium development also spanned a continuum between extremes with, for example, the largest number of eggs, the smallest egg sizes and the shortest longevity (with sucrose-feeding) being characteristic of the earliest-arriving wasps and the converse being features of the later-arriving wasps. Thus life history can be an important determinant of resource partitioning within a community of fig wasps, reaffirming the view that life history is fundamental to the understanding of community structure (Bonsall *et al.*, 2004).

The pollinator *C. fusciceps* is a pro-ovigenic short-lived galler, while among the NPFWs, the *Apocrypta* parasitoids are synovigenic and live longer compared to the pro-ovigenic gallers (see Table S1) consistent with the ovigeny index/lifespan trade-off demonstrated by Jervis *et al.* (2001). Synovigeny is typical of parasitoids across families while pro-ovigeny is rare (Jervis *et al.*, 2001); a pattern possibly related to host availability, which necessitates progressive egg maturation over parasitoid lifespan. However, while *A.*

agraensis is pro-ovigenic, its egg load was much lower than that of the other gallers and was similar to that of the *Apocrypta* parasitoids, possibly reflecting a non-galler trophic niche. Thus, while perhaps being phylogenetically constrained by egg development strategy (pro-ovigeny vs. synovigeny), *A. agraensis* produces fewer but larger eggs compared to at least two of its congeners *A. testacea* and *A. fusca* (see Table S1). A trade-off between egg number and egg size was therefore clearly evident in these fig wasp species as predicted by general life-history theory (Smith & Fretwell, 1974; Fox & Czesak, 2000) and as also found in several insects (Berrigan, 1991; Garcia-Barros, 2000). Furthermore, most species (except for the two earliest ones to arrive: *C. fusciceps* and *A. stratheni*) showed a positive intraspecific relationship between egg load (fecundity) and body size, clearly demonstrating resource constraints on egg numbers, as in other insects (Honěk, 1993; Bauerfeind & Fischer, 2008).

NPFW ovipositor lengths increased progressively with later arrival time, and consequent increase in syconium size during its development, as also observed in parasitic communities with species parasitising early or late host stages (Price, 1975; Compton *et al.*, 1994; Kerdelhué & Rasplus, 1996). Curiously, *A. agraensis* had the largest ovipositor length, very close to that of *A. westwoodi*, which was also the latest to arrive (Fig. 1; Table 2 and see Table S1). The long ovipositor of *A. agraensis* is borne on a female whose body mass is equivalent to that of the pollinator, which has the shortest ovipositor, and to that of *Apocrypta* sp. 2 which has the shortest ovipositor of the *Apocrypta* species (see Table S1). Hence the long ovipositor of *A. agraensis* may be costly in terms of maternal resource investment. This cost may be reflected in: (i) the

nearly four-fold smaller egg load in *A. agraensis* compared to the pollinator *C. fusciceps* and at least two of its congeners *A. stratheni* and *A. testacea*, and (ii) the smaller volume of its eggs compared to other co-arriving wasps. This smaller egg in such a late-arriving parasite must still facilitate rapid development and greater competitive ability. The pre-adult lifespan (30 days) of *A. agraensis* is equivalent to that of late-arriving *Apocrypta*. While ovipositor length in *A. agraensis* matches its ecology (since it is late-arriving it needs a long ovipositor to penetrate the thicker syconium wall), it is worth noting that egg pedicel length was not correlated with lateness of arrival, and was similar in all *Apocryptophagus* species. Egg pedicel length may correspond to ovipositor size, to facilitate yolk passage through thin long ovipositors during oviposition (Quicke *et al.*, 1994), but in *Apocryptophagus*, egg pedicel length appears to be a more conserved trait.

The wide host window for *Apocrypta* sp. 2 indicates that the developmental time (pre-adult lifespan) of this species is highly variable, and is consistent with the general lack of correlation between developmental time and lifespan within hymenopteran parasitoids (Eijs & van Alphen, 1999). Since it is not yet known whether these parasitoids are idiobionts or koinobionts, any relationships with this parasitic mode and life-history traits (Mayhew & Blackburn, 1999) cannot yet be examined. However, if pre-adult lifespan can be taken as an indication of parasitic mode (Blackburn, 1991b), then *Apocrypta* sp. 2 which has a longer pre-adult lifespan (maximum of 51 days) may be considered a koinobiont while the later-arriving and larger *A. westwoodi* may be considered an idiobiont parasitising a later and therefore larger host stage. The Chalcidoidea (to which fig wasps belong) are known to exhibit considerable variation in development and life history in accordance with their ecology (Pennacchio & Strand, 2006), which can even include seed-eating by fig wasps (Pereira *et al.*, 2007).

Longevity and nutritional regimes

The longevity of the community members (under sucrose feeding) matched their arrival sequence at the syconium (Table 2), the notable exception again being *A. agraensis*, which despite arriving very late at the syconium, had a very short adult longevity, similar to that of *A. stratheni*, the first NPFW to arrive.

The 24 h lifespan of the galler pollinator *C. fusciceps* in all treatments differs from the response of *Pleistodontes imperialis* (Hymenoptera: Agaonidae), the pollinator of *Ficus rubiginosa* in Australia, whose lifespan doubled with moisture (Dunn *et al.*, 2008). The longevity of the shortest-living and earliest-arriving gallers, *A. stratheni* and *C. fusciceps*, was unresponsive, even to water. Such pro-ovigenic species are probably 'capital' breeders with larval resources being the sole capital or resource for the entire egg clutch (Jervis *et al.*, 2005) and are thus likely to show Type III survivorship curves, as we found. Other galler insects are also pro-ovigenic, short-lived and non-feeding (Rosenheim *et al.*, 2007). However, in our study two gallers, *A. fusca* and *A. testacea*, showed an increase in lifespan with water and with sucrose.

The adult parasitoids exhibited a type I survivorship curve, in which most mortality occurred at older ages as in other synovigenic insects (Jervis *et al.*, 2001). We also found that the parasitoids lived longer on sucrose and water as expected (Quicke, 1997; Wyckhuys *et al.*, 2008), and in the wild might therefore depend on sources such as nectar and rotting fruit to augment their realised fecundity (Lee & Heimpel, 2008), and flight capacity (Wanner *et al.*, 2006). In the fig wasp community, it appears that the *Apocrypta* parasitoids and possibly some *Apocryptophagus* species are 'income' breeders for sugars, since their lifespan was increased by exposure to this source of nutrition (Jervis *et al.*, 2005).

Parasitoids in an African fig wasp community lived longer on a diet of sucrose while the gallers showed either no, positive, or negative effects of sucrose feeding (Compton *et al.*, 1994). In the African study and in ours, sucrose was the only carbohydrate source while under natural conditions wasps may utilise other sugars such as fructose.

Assembling the community

The hierarchical clustering method, which used life-history and ecological traits as input variables, grouped species which were similar with respect to their arrival times for oviposition in relation to syconium developmental stage (Figs 1 and 3; Table 2). These clusters were significant and stable even on removal of length of oviposition window from the analysis. Therefore, life-history traits separated gallers from parasitoids. Consequently, host availability and competition for hosts in these phases might be important selecting forces in the evolution of life-history traits, such as lifespan and egg load in this community as observed in some parasitoid communities (Askew, 1975; Price, 1975). In these communities, especially in the oak gall chalcid communities parasitising endophytic hosts (Askew, 1975), early-arriving parasites had higher egg production and smaller eggs, compared to late-arriving parasites that had lower egg production and larger eggs. Such strategies appear to be necessitated by host availability as well as the stage at which the host is attacked; early-arriving parasites were predicted to have high fecundity and low competitive ability (*r* strategists) and later-arrivers to have low fecundity and high competitive ability (*K* strategists) (Price, 1973a,b; Force, 1975). These contrasting strategies can be clearly seen in our fig wasp system with the largest number of eggs, smallest egg sizes and shortest longevities being characteristic of the earliest-arriving galling wasps at the smallest, immature syconia (with less internal crowding of wasps), while the converse characterised the later-arriving parasitoids at the larger, already parasitised syconia (with more internal crowding of wasps) (Table 2 and see Table S1).

In our system, for example, the rare galler *A. stratheni* is the first to arrive and oviposit into an A phase syconium, and thus encounters only intraspecific competition for galling sites. Each A phase syconium may provide hundreds of suitable sites, or an individual may even move between syconia for oviposition. Consequently, this species is expected to experience the least selection pressure for a greater lifespan, assuming that it can

reach a fig tree in A phase before it dies. Furthermore, the galls produced by *A. stratheni* within the syconium are the largest, probably because of the lack of competition for space and the fact that these large galls may arise from syconial wall hypertrophy as in the early-arriving *Aepocerus* and *Idarnes* (*incerta*) NPFWs in New World figs (Bronstein, 1991; West *et al.*, 1996). The pollinator *C. fusciceps* enters irreversibly into the syconium within which it must lay all its eggs. Thus, for this species also, the pressure should be to reach suitable syconia and to lay its eggs rapidly. After the arrival of each new wasp species, sites suitable for oviposition are subject to progressively increased intra- and interspecific competition. Consequently spatio-temporal variation in host availability, within and between syconia (within and across fig trees in the population), should determine the requirement for greater lifespan and dependence on external sources of nutrition. The NPFWs are also subject to predation and interference by predators such as ants (Ranganathan & Borges, 2009), and may therefore need to move between suitable syconia containing appropriate hosts or host stages, necessitating greater longevity. The trade-off between the ovigeny index and lifespan (Jervis *et al.*, 2001) is thus also ecologically relevant since pro-ovigenic fig wasps probably have abundant hosts and are shorter lived, while the progressive egg maturation of the longer-lived synovigenic late arrivers is probably necessitated by the search for their rarer hosts.

Fig wasp species with longer oviposition windows had longer lifespans except for *A. westwoodi*, which had a longer lifespan although its oviposition window was very small. One possible reason for this anomaly is that *A. westwoodi* may be a specialist (as suggested by Ulenberg, 1985, for the genus *Apocrypta*) that needs to search for longer and consequently to live longer to find specific hosts or host stages. Therefore, specialisation versus generalisation can also determine local host shortages and select for appropriate lifespans (Stearns, 1976; Roff, 1992). As mentioned earlier, *A. agraensis* was anomalous, since it had a very short lifespan despite arriving late in syconium development. The reason for its short lifespan might be that, unlike its congeners, it is not a galler, but instead is an inquiline or parasitoid of other wasp species that are abundantly available in the syconium (e.g. the pollinator; Wang & Zheng, 2008) and hence may not need to expend much time searching. A late-arriving inquiline strategy would evolve if females gain more in fitness by displacing developing larvae in already occupied sites (Ronquist, 1994). Further investigations are clearly needed, especially for the anomalous *A. agraensis*, and are underway.

While fig wasp communities appear to be unsaturated at local scales (Hawkins & Compton, 1992), this phenomenon can perhaps be better explored by knowledge of life-history traits as well as of trophic position and degree of specialisation of the community members which, when coupled with knowledge of syconial phenology at a population level, will help to explain fig wasp community structure. The fact that life-history traits correlated well with the arrival sequence of the fig wasps at the syconia during its development indicates that communities are not set up idiosyncratically, but are governed by individual-based assembly rules (Price, 1973b; Askew, 1975; Giacomini

et al., 2009). The observation that in all fig species examined so far, gallers with short ovipositors arrive early and parasitoids with longer ovipositors come later (e.g. West *et al.*, 1996; Kerdelhué *et al.*, 2000; Elias *et al.*, 2008), is indicative of a common structure across fig wasp communities. However, since all wasp species in this study did not occur in all syconia, some species were rare, and several species varied locally and seasonally in their presence at a population level (M. Ghara, unpublished), it is possible that the coexistence of seven members of this fig wasp community is only possible under conditions of such variability (Bronstein *et al.*, 2003; Morris *et al.*, 2003; Fraser *et al.*, 2008). Under such conditions, the life-history traits of community members will critically depend on and be driven by the spatio-temporal variation of host patches (Ellers *et al.*, 2000), as our results suggest.

Since *F. racemosa* occurs over a large geographical area (from India through Australasia) it would be interesting to compare its fig wasp community composition with the life-history traits of the fig wasp community members across these geographical areas and to investigate if community membership is stable throughout this range. Geographical variation in life-history traits of community members based on spatio-temporal variation in host availability would provide critical insights into life-history evolution.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
DOI: 10.1111/j.1365-2311.2010.01176.x

Figure S1. Confocal images of eggs of fig wasps of *Ficus racemosa*.

Table S1. Life-history traits of fig wasps of *Ficus racemosa*.

Please note: Neither the Editors nor Wiley-Blackwell are responsible for the content or functionality of any supplementary material supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

References

Askew, R.R. (1975) The organization of chalcid-dominated parasitoid communities centred upon endophytic hosts. *Evolutionary Strategies of Parasitoids* (ed. by P. W. Price), pp. 130–153. Plenum, New York, New York.

Bauerfeind, S.S. & Fischer, K. (2008) Maternal body size as a morphological constraint on egg size and fecundity in butterflies. *Basic and Applied Ecology*, **9**, 443–451.

Berrigan, D. (1991) The allometry of egg size and number in insects. *Oikos*, **60**, 313–321.

Blackburn, T.M. (1991a) Evidence for a 'fast-slow' continuum of life-history traits among parasitoid Hymenoptera. *Functional Ecology*, **5**, 65–74.

Blackburn, T.M. (1991b) A comparative examination of life-span and fecundity in parasitoid Hymenoptera. *Journal of Animal Ecology*, **60**, 151–164.

Bonsall, M.B. & Mangel, M. (2004) Life-history trade-offs and ecological dynamics in the evolution of longevity. *Proceedings of the Royal Society of London Series B*, **271**, 1143–1150.

Bonsall, M.B., Hassell, M.P. & Asefa, G. (2002) Ecological trade-offs, resource partitioning, and coexistence in a host–parasitoid assemblage. *Ecology*, **83**, 925–934.

Bonsall, M.B., Jansen, V.A.A. & Hassell, M.P. (2004) Life history trade-offs assemble ecological guilds. *Science*, **306**, 111–114.

Borges, R.M., Bessière, J.-M. & Hossaert-McKey, M. (2008) The chemical ecology of seed dispersal in monoecious and dioecious figs. *Functional Ecology*, **22**, 484–493.

Bronstein, J.L. (1991) The nonpollinating wasp fauna of *Ficus pertusa* – exploitation of a mutualism. *Oikos*, **61**, 175–186.

Bronstein, J.L., Wilson, W.G. & Morris, W.F. (2003) Ecological dynamics of mutualist/antagonist communities. *American Naturalist*, **162**, S24–S39.

Compton, S.G., Rasplus, J.-Y. & Ware, A.B. (1994) African fig wasp parasitoid communities. *Parasitoid Community Ecology* (ed. by B. Hawkins and W. Sheehan), pp. 343–368. Oxford University Press, Oxford, U.K.

Cook, J.M. & Rasplus, J.-Y. (2003) Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology & Evolution*, **18**, 241–248.

Crawley, M.J.C. (2007) *The R book*. John Wiley & Sons, Chichester, U.K.

Dedeine, F., Vavre, F., Fleury, F., Loppin, B., Hochberg, M.E. & Bouletreau, M. (2001) Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 6247–6252.

Dufaÿ, M. & Anstett, M.-C. (2003) Conflicts between plants and pollinators that reproduce within inflorescences: evolutionary variations on a theme. *Oikos*, **100**, 3–14.

Dunn, D.W., Yu, D.W., Ridley, J. & Cook, J.M. (2008) Longevity, early emergence and body size in a pollinating fig wasp – implications for stability in a fig–pollinator mutualism. *Journal of Animal Ecology*, **77**, 927–935.

Eijs, I.E.M. & van Alphen, J.J.M. (1999) Life history correlations: why are hymenopteran parasitoids an exception? *Ecology Letters*, **2**, 27–35.

Elias, L.G., Menezes, A.O. Jr & Pereira, R.A.S. (2008) Colonization sequence of non-pollinating fig wasps associated with *Ficus citrifolia* in Brazil. *Symbiosis*, **45**, 107–111.

Ellers, J., Sevenster, J.G. & Driessen, G. (2000) Egg load evolution in parasitoids. *American Naturalist*, **156**, 650–665.

Force, D.C. (1975) Succession of *r* and *K* strategists in parasitoids. *Evolutionary Strategies of Parasitoids* (ed. by P. W. Price), pp. 112–129. Plenum, New York, New York.

Fox, C.W. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology*, **45**, 341–369.

Fraser, S.E.M., Dytham, C., Mayhew, P.J., Mouillot, D. & Anderson, B.J. (2008) Community structure in ichneumonid parasitoids at different spatial scales. *Oecologia*, **157**, 521–530.

Galil, J. & Eisikowitch, D. (1968) Flowering cycles and fruit types of *Ficus sycomorus* in Israel. *New Phytologist*, **67**, 745–758.

Garcia-Barros, E. (2000) Body size, egg size, and their interspecific relationships with ecological and life-history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, **70**, 251–284.

Giacomini, H.C., De Marco, P. Jr & Petrere, M. Jr (2009) Exploring community assembly through an individual-based model for trophic interactions. *Ecological Modelling*, **220**, 23–39.

Golinski, M.R. (2006) A review of theoretical approaches for studying the effects of interactions between mutualists and nonmutualists on community stability. *Bulletin of the Ecological Society of America*, **87**, 37–44.

Giron, D. & Casas, J. (2003) Mothers reduce egg provisioning with age. *Ecology Letters*, **6**, 273–277.

Grison-Pigé, L., Bessière, J.-M. & Hossaert-McKey, M. (2002) Specific attraction of fig-pollinating wasps: role of volatile compounds released by tropical figs. *Journal of Chemical Ecology*, **28**, 283–295.

Harvey, J.A. (2005) Factors affecting the evolution of developmental strategies in parasitoid wasps: the importance of functional constraints and incorporating complexity. *Entomologia Experimentalis et Applicata*, **117**, 1–13.

Hawkins, B.A. & Compton, S.G. (1992) African fig wasp communities: undersaturation and latitudinal gradients in species richness. *Journal of Animal Ecology*, **61**, 361–372.

Herre, E.A., Jander, K.C. & Machado, C.A. (2008) Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology, Evolution and Systematics*, **39**, 439–458.

Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.

Jervis, M.A., Heimpel, G.E., Ferns, P.N., Harvey, J.A. & Kidd, N.A.C. (2001) Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *Journal of Animal Ecology*, **70**, 442–458.

Jervis, M.A., Boggs, C.L. & Ferns, P.N. (2005) Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. *Ecological Entomology*, **30**, 359–375.

Jervis, M.A., Ellers, J. & Harvey, J.A. (2008) Resource acquisition, allocation, and utilization in parasitoid reproductive strategies. *Annual Review of Entomology*, **53**, 361–385.

Jousselin, E., van Noort, S., Berry, V., Rasplus, J.-Y., Rønsted, N., et al. (2008) One fig to bind them all: host conservatism in a fig wasp community unraveled by cospeciation analyses among pollinating and nonpollinating fig wasps. *Evolution*, **62**, 1777–1797.

Kerdelhué, C. & Rasplus, J.-Y. (1996) Non-pollinating Afrotropical fig wasps affect the fig–pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos*, **75**, 3–14.

Kerdelhué, C., Rossi, J.-P. & Rasplus, J.-Y. (2000) Comparative community ecology studies on Old World figs and fig wasps. *Ecology*, **81**, 2832–2849.

Kjellberg, F., Doumesche, B. & Bronstein, J. (1988) Longevity of a fig wasp (*Blastophaga psenes*). *Verhandelingen der Koninklijke Nederlandse Akademie Wetenschappen*, **91**, 117–122.

Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69–80.

Lee, J.C. & Heimpel, G.E. (2008) Floral resources impact longevity and oviposition rate of a parasitoid in the field. *Journal of Animal Ecology*, **77**, 565–572.

Marussich, W.A. & Machado, C.A. (2007) Host-specificity and coevolution among pollinating and nonpollinating New World fig wasps. *Moleclular Ecology*, **16**, 1925–1946.

Mayhew, P.J. & Blackburn, T.M. (1999) Does development mode organize life-history traits in the parasitoid Hymenoptera? *Journal of Animal Ecology*, **68**, 906–916.

Mojena, R. (2006) Ward's clustering algorithm. *Encyclopedia of Statistical Sciences*. John Wiley & Sons, Hoboken, New Jersey.

Morris, W.F., Bronstein, J.L. & Wilson, W.G. (2003) Three-way coexistence in obligate mutualist–exploiter interactions: the potential role of competition. *American Naturalist*, **161**, 860–875.

Naeem, S. & Hawkins, B.A. (1994) Minimal community structure: how parasitoids divide resources. *Ecology*, **75**, 79–85.

Pennacchio, F. & Strand, M.R. (2006) Evolution of developmental strategies in parasitic Hymenoptera. *Annual Review of Entomology*, **51**, 233–258.

Pereira, R.A.S., de Pádua Teixeira, S. & Kjellberg, F. (2007) An inquiline fig wasp using seeds as a resource for small male production: a potential first step for the evolution of new feeding habits? *Biological Journal of the Linnean Society*, **92**, 9–17.

Price, P.W. (1973a) Parasitoid strategies and community organization. *Environmental Entomology*, **2**, 623–626.

Price, P.W. (1973b) Reproductive strategies in parasitoid wasps. *American Naturalist*, **107**, 684–693.

Price, P.W. (1975) Reproductive strategies of parasitoids. *Evolutionary Strategies of Parasitoids* (ed. by P. W. Price), pp. 87–111. Plenum, New York, New York.

Proffit, M., Schatz, B., Borges, R.M. & Hossaert-McKey, M. (2007) Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. *Journal of Animal Ecology*, **76**, 296–303.

Quicke, D.L.J. (1997) *Parasitic Wasps*. Chapman & Hall, London, U.K.

Quicke, D.L.J., Fitton, M.G., Tunstead, J.R., Ingram, S.N. & Gaitens, P.V. (1994) Ovipositor structure and relationships within the Hymenoptera with special reference to the Ichneumonoidea. *Journal of Natural History*, **28**, 635–682.

Ranganathan, Y. & Borges, R.M. (2009) Predatory and trophobiont-tending ants respond differently to fig and fig wasp volatiles. *Animal Behaviour*, **77**, 1539–1545.

Rasplus, J.-Y., Kerdelhué, C., Le Clainche, I. & Mondor, G. (1998) Molecular phylogeny of fig wasps. Agaonidae are not monophyletic. *Comptes Rendus de l'Académie des Sciences de Paris*, **321**, 517–527.

Roff, D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, London, U.K.

Ronquist, F. (1994) Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). *Evolution*, **48**, 241–266.

Rosenheim, J.A., Jepsen, S.J., Matthews, C.E., Smith, D.S. & Rosenheim, M.R. (2007) Portrait of an ephemeral adult stage: egg maturation, oviposition, and longevity of the gall midge *Rhopalomyia californica* (Diptera: Cecidomyiidae). *Annals of the Entomological Society of America*, **100**, 549–561.

Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.

Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, **51**, 3–47.

Ulenberg, S.A. (1985) The phylogeny of the genus *Apocrypta* Cocquerel in relation to its hosts *Ceratosolen* Mayr and *Ficus* L. *Verhandelingen der Koninklijke Nederlandse Akademie Wetenschappen*, **83**, 149–176.

Vincent, T.L.S., Scheel, D., Brown, J.S. & Vincent, T.L. (1996) Trade-offs and coexistence in consumer–resource models: it all depends on what and where you eat. *American Naturalist*, **148**, 1038–1058.

Wang, R.W. & Zheng, Q. (2008) Structure of a fig wasp community: temporal segregation of oviposition and larval diets. *Symbiosis*, **45**, 113–116.

Wanner, H., Gu, H. & Dorn, S. (2006) Nutritional value of floral nectar resources for flight in the parasitoid wasp, *Cotesia glomerata*. *Physiological Entomology*, **31**, 127–133.

Ward, J.H. (1963) Hierarchical grouping to optimise an objective function. *Journal of the American Statistical Association*, **58**, 236–244.

West, S.A. & Herre, E.A. (1994) The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig–pollinator mutualism. *Proceedings of the Royal Society of London Series B*, **258**, 67–72.

West, S.A., Herre, E.A., Windsor, D.M. & Green, P.R.S. (1996) The ecology and evolution of the New World non-pollinating fig wasp communities. *Journal of Biogeography*, **23**, 447–458.

Wilson, W.G., Morris, W.F. & Bronstein, J.L. (2003) Coexistence of mutualists and exploiters on spatial landscapes. *Ecological Monographs*, **73**, 397–413.

Wyckhuys, K.A.G., Strange-George, J.E., Kulhanek, C.A., Wäckers, F.L. & Heimpel, G.E. (2008) Sugar feeding by the aphid parasitoid *Binodoxys communis*: how does honeydew compare with other sugar sources? *Journal of Insect Physiology*, **54**, 481–491.