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

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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).

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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 gallers, 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 a 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 monoeocious 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 gillers, inquilines, or parasitoids of the pollinating fig wasps or of each other, and also attack syconia at various developmental stages (Profit 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; Profitt 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 agaensis Joseph, Apocrypta sp. 2, and Apocrypta westwoodi Grandi) (Fig. 1). Since the Agaonidae are not monophyletic (Rasplus et al., 1998), Apocryptophagus (sub-family Sycomarginae) and Apocrypta (sub-family Sycoryctinae) have not yet been assigned family status within the super-family 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. agaensis 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 aceticarmine 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 $V = \frac{1}{6}\pi lW^2$ 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. agaensis owing to overdispersion (Crawley, 2007). Treatment was a categorical predictor while body size was a continuous predictor variable.
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 Apocrypta 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 parasites 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 τ = 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: τ = 0.84, n = 15, P < 0.001; A. fusca: τ = 0.62, n = 14, P = 0.002; A. agraensis: τ = 0.7, n = 15, P < 0.001; Apocrypta sp. 2: τ = 0.58, n = 15, P = 0.003; A. westwoodi: τ = 0.64, n = 8, P = 0.03). The potential lifetime fecundity of the synovigenic parasitoids increased significantly with body size (Apocrypta sp. 2: τ = 0.42, n = 15, P = 0.03; A. westwoodi: τ = 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 3 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
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

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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Apocrypta sp. 2</th>
<th>A. westwoodi</th>
<th>A. fusca</th>
<th>A. testacea</th>
<th>A. agraensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lifespan</td>
<td>d.f.</td>
<td>$\chi^2$</td>
<td>$\chi^2$</td>
<td>$\chi^2$</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>233.83***</td>
<td>52.00***</td>
<td>130.04***</td>
<td>49.56***</td>
</tr>
<tr>
<td>Body size</td>
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<td>7.16**</td>
<td>1.81</td>
<td>13.77***</td>
<td>22.69***</td>
</tr>
<tr>
<td>Treatment $\times$ body size</td>
<td>2</td>
<td>0.08</td>
<td>4.73</td>
<td>9.57**</td>
<td>0.04</td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01; ***P < 0.001.
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

<table>
<thead>
<tr>
<th>Life-history traits</th>
<th>Early-arriving gallers</th>
<th>Late-arriving gallers</th>
<th>Parasitoids (early and late-arriving)</th>
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</thead>
<tbody>
<tr>
<td>Fig wasp species</td>
<td>A. stratheni, A. testacea</td>
<td>C. fusciceps, A. fusca</td>
<td>A. agraensis*, Apocrypta sp. 2, Apocrypta westwoodi</td>
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<tr>
<td>Matured egg number</td>
<td>Largest</td>
<td>Intermediate</td>
<td>Smallest</td>
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<td>Intermediate and small</td>
<td>Intermediate and small</td>
<td>Intermediate and largest</td>
</tr>
<tr>
<td>Body size (fresh weight)</td>
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<td>Smallest and largest</td>
<td>Smallest and largest</td>
</tr>
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<td>Intermediate</td>
<td>Shortest and longest</td>
</tr>
<tr>
<td>Adult lifespan</td>
<td>Short and intermediate</td>
<td>Shortest and intermediate</td>
<td>Shortest and longest</td>
</tr>
<tr>
<td>Pre-adult lifespan</td>
<td>Longest</td>
<td>Intermediate</td>
<td>Intermediate and longest</td>
</tr>
<tr>
<td>Ovipositor length</td>
<td>Shortest</td>
<td>Intermediate</td>
<td>Intermediate and longest</td>
</tr>
</tbody>
</table>

*Apocryptophagus agraensis is predicted to be an inquiline or a parasitoid.
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 *Apoecrypta*. 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 *Apoecryptophagus* 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 *Apoecryptophagus*, egg pedicel
length appears to be a more conserved trait.

The wide host window for *Apoecrypta* 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. How-
ever, if pre-adult lifespan can be taken as an indication of par-
asitic mode (Blackburn, 1991b), then *Apoecrypta* 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 gall 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 galler, *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 gellers, *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 *Apoecrypta* parasitoids and
possibly some *Apoecryptophagus* 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 ovigency 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 gallor, 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, gellers 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.

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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

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

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**References**


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