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The effects of seasonal changes on the dynamics of a fig tree's pollination

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ABSTRACT

Fig trees and their pollinating wasps are mutually dependent on each other. Both partners' reproductive success is regulated by the capacity of fig wasps to enter receptive figs at an appropriate time for pollination and oviposition. Oviposition is dependent on successful female pollinator dispersal from one tree to another and although fig wasps are slow flyers and short-lived they can be carried long distances by the wind. The relative importance of local versus long-distance pollinator dispersal is unclear, as is how this may vary with season. In the highly seasonal environment of the Makana Botanical Gardens, Grahamstown, South Africa, we recorded fruiting phenologies of all the trees in a monoecious *Ficus burtt-davyi* Hutchinson population together with variation in the abundance of its pollinator *Elisabethiella baijnathi* Wiebes. By comparing captures of fig wasps flying in the air with the numbers that emerged locally, we also examined the independence of the fig tree population, which was separated from the nearest conspecifics by more than 1 km. The abundance of pollinators flying in the air and the number of fig wasps released by figs were correlated with temperature. During winter there were times when no pollinators were released locally; however, they were still caught in the traps, showing that the wasps had dispersed from elsewhere and that the population was not totally independent. These results highlight the ability of fig wasps to disperse between populations and the likely impact of seasonal fluctuations on fig tree gene flow.

1. Introduction

Fig trees (*Ficus,* Moraceae) are a very diverse genus of flowering plants, with more than 800 species found mostly in tropical and subtropical areas. The genus is characterised by its unique enclosed inflorescence, the fig (sometimes called a syconium) and by the highly specific association between fig trees and agaonid pollinating fig wasps (Janzen, 1979; Weiblen, 2002). The joint dependency of fig trees and fig wasps has resulted in their interaction being one of the most intensively studied mutualistic relationships.

Each fig usually contains hundreds or more tiny flowers. Their pollination depends on female fig wasps (Hymenoptera: Agaonidae) entering the figs in order to lay their eggs (Wiebes, 1979; Kerdelhue et al., 2000)). The female fig wasps enter the fig via the ostiole, a narrow aperture. This route is the only way that pollen transported by wasps can reach female flowers for pollination. Each fig tree species is pollinated by one or a small number of fig wasp species (Cook and Rasplus, 2003; Compton et al., 2009; Cruaud et al., 2012). Upon entering the figs, the female wasps pollinate and attempt to oviposit in the ovaries of female flowers (Kjellberg et al., 2001). One pollinator larva develops within each galled ovule by feeding on some of the (usually pollinated) female flowers, and each larva prevents the seed in that particular ovule from developing. The adult fig wasps emerge from the galled ovules at the same time as the seeds and male flowers mature. When adult female wasps leave the galls, they either actively collect pollen or become pollen-coated as they pass through male flowers (Kerdelhue et al., 2000). Females leave the fig through a hole created by the males in the fig wall and look for new receptive figs to enter, resuming the life cycle (Weiblen, 2002; Suleman et al., 2012).

In many monoecious *Ficus* species (where seeds and pollinator larvae develop in figs on the same trees) fig crop development is synchronised within each tree, though asynchrony leading to opportunities for some within-tree cycling of fig wasp populations occurs in some species (Smith and Bronstein, 1996; Bronstein and Patel, 1992; McPherson, 2005; Jia et al., 2008). Most adult female fig wasps must nonetheless disperse between trees to enter receptive figs on other trees (Ware and

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Compton, 1994 a,b; Compton et al., 2005) and the time between one crop and the next on any given tree can range from a few weeks or months to several years. Pollinating wasps are tiny insects with a body length of less than 2 mm that live for less than two days and do not feed (Kjellberg et al., 1988). Despite being slow, weak fliers (Compton, 2002), some female pollinating wasps can successfully colonise trees with receptive figs more than 100 km from their natal trees (Ahmed et al., 2009). This ability is critical to their reproductive success and that of their host trees, but genetic and behavioural studies suggest that the extent of dispersal by fig wasps varies greatly between species (Deng et al., 2020; Hatta et al., 2023).

Fruiting in monoecious species is typically asynchronous at the population level so at any one time only a proportion of the trees are releasing fig wasps or have receptive figs ready to be pollinated. The distances between them will vary according to both local tree densities and the proportion of mature trees with figs at appropriate stages of development. Under exceptional circumstances, where host trees are present at low densities or few are fruiting, the nearest suitable figs may be kilometres away from a tree where fig wasps are being released, requiring them to travel long distances if they are to reproduce (Compton et al., 2005). In seasonal environments the abundance of fig trees with suitable receptive flowers within the dispersal range of the fig wasps will vary depending on the time of year when they emerge, because crop frequency and crop size are often temperature related. Monoecious fig tree species vary in their responses to seasons. A decline in reproductive activity may be the most common response to cooler seasons, but this is not always the case (McPherson, 2005; Chen et al., 2015) The ditances that fig wasps disperse may therefore vary seasonally, as well as over shorter time periods, as the maximum distances the pollinators can travel when they are flying will be determined by prevailing wind speeds, which can vary according to season and time of day. The chances of emerging pollinators being able to reproduce (and the rates of pollination of figs on host trees) are therefore expected to vary seasonally, influencing the population dynamics of fig wasp populations as may be the extent of long distance gene flow in the plant and insect populations.

The behaviour and ecology of adult and immature pollinator fig wasps while they are inside host figs has been studied intensively, but much less is known about the behaviour and survivorship of fig wasps when they are travelling between figs. In rainforest habitats fig wasps associated with monoecious strangler figs were found to disperse between hosts after entering the air space above the general rainforest canopy, where they encountered winds that could carry them long distances (Compton et al., 2000). Flight heights were concentrated in the air space immediately above the general canopy, and consequently the fig wasps dispersed closer to the ground when flying above logged forest than above primary forest (Compton et al., 2005). In contrast, dispersal of pollinators associated with dioecious fig tree hosts in rainforests appears to be more localised, with more flights closer to the ground (Harrison, 2003; Harrison and Rasplus, 2006). Under these conditions their behaviour may be more akin to that of small flies dispersing in still air (Leitch et al., 2021). A scheme based on models of the long-distance dispersal of aphids suggested that their initial long-distance dispersal phase from natal figs was followed by a return towards ground level and by upwind local orientation towards trees with receptive figs that were releasing attractant volatiles (Compton, 2002). It is unknown whether the ending of long distance flights is dictated by their duration or exhaustion, or is a more directed response to volatiles released from host trees.

Direct observations of the flight behaviour of the *Elisabethiella baijnathi* Wiebes pollinator of the South African veld fig F. burtt-davyi Hutchinson found that adult females emerge from natal figs in the morning, fly upwards and are then carried downwind (Ware and Compton, 1994a). Traps placed around trees with receptive figs showed that pollinators downwind of the trees were flying closer to the ground than those upwind, suggesting that the insects were responding to the volatiles released from receptive figs by descending close to the ground, where lower air speeds can allow them to fly upwind (van Noort et al., 1989; Ware and Compton, 1994a, 1994b). Here we describe how *F. burtt-davyi* and its pollinators respond to their highly seasonal environment. We recorded seasonal variation in the tree's frequency of fruiting, the sizes of its crops and how long the crops were present on the trees. During the same time period we monitored the impact of this seasonal variation on the local population of its exclusive pollinator by recording the numbers of fig wasps entering and emerging from their natal figs and the numbers of fig wasps that were flying in the air, away from host trees. We had two main questions 1) Are pollinators being released from trees within the population throughout the winter? And 2) Does dispersal into the population from elsewhere result in some pollinators being present regardless of whether or not local releases are taking place?

2. Materials and methods

2.1. *The study species*

The veld fig, *Ficus burtt-davyi*, is a monoecious fig tree distributed from the Eastern Cape of South Africa to Mozambique (Burrows and Burrows, 2003). It is a member of the *Ficus* Subgenus *Urostigma*, Section *Galoglychia.* Inland, it is found among rocks as a small free-standing tree or shrub. Along the coast, it can be a creeping shrub or strangler fig. It is deciduous, and although individual trees can vary slightly in leafing patterns, there are distinct seasonal trends in leaf production and loss. Most leaves senesce and fall during autumn and early winter (February to July) (Compton, 1993; Ross, 1994). There is more variation in the times when young leaves are present, but new leaf production is concentrated between August and November (South African spring) (Compton, 1993).

The figs of *F. burtt-davyi* reach about 15 mm in diameter and form in the leaf axils. Fruiting within a tree is synchronised, producing discrete crops. However, different trees bear fruit at different times of the year, resulting in various phases of fig development within the population at any one time. Crop sizes vary, ranging from just one fig to more than 20,000 (Compton, 1993). The fig wasp *Elisabethiella baijnathi* pollinates *F. burtt-davyi*, which is also a host to several other non-pollinating fig wasps (NPFW) (Compton and Nefdt, 1990; Compton, 1993). *E. baijnathi* is a day-flying insect and most emerging females leave their natal figs between 06.00 and noon, emerging earlier in the morning during summer (Ware and Compton, 1994a, 1994b). Observations in the laboratory found that a temperature of 15 or 16 °C was needed for *E. baijnathi* to take off from their natal figs but they can be seen flying in the field at considerably cooler ambient temperatures (Ware and Compton, 1994a).

Receptive figs of *F. burtt-davyi* release stage- and species-specific compounds via their ostioles that attract *E. baijnathi* females (van Noort et al., 1989). Female *E. baijnathi* foundresses do not routinely re-emerge from the first figs they enter, so each fig wasp can only pollinate one fig (Gibernau et al., 1996). Development times vary greatly depending on the season (Compton, 1993), and when the next generation of female fig wasps emerges from their galls they actively collect pollen before leaving their natal figs and dispersing in search of receptive figs.

2.2. *The study site*

The populations of *F. burtt-davyi* and its pollinator were monitored from September 1987 to January 1990 in the Makana Botanical Gardens (formerly 1820 Settlers Gardens), located in Grahamstown/Makhanda, South Africa. The gardens are located at 33°22′S, 26°29′E, around 60 KM inland from South Africa's southeast coast, at an altitude of around 550 m. Semi-arid conditions prevail locally, but despite the unpredictability of rainfall from year to year, there is usually more precipitation in the winter than summer months. The Botanical Gardens are about 2 km from the closest known population of *F. burtt-davyi*, located at the far side of the Rhodes University campus. The botanic gardens also contained a small number of *F. sur* Forssk. and *F. natalensis* Hochst. that were planted lower on the slopes away from the bulk of the *F. burtt-davyi* population, which was entirely comprised of individuals that had naturally colonised the area.

At the time of the study there were 105 *F. burtt-davyi* distinct shrubs or trees in the Botanical Gardens, though as a result of vegetative spread a small number were found to be genetically identical despite being located several metres apart (S. Ross & J. Nason, unpublished). The 105 plants were treated as separate individuals, but some of the smaller individuals never produced figs.

2.3. Meteorological data

Temperature records during the period of data collection were obtained from a meteorological station close to the gardens at the Rhodes University campus. The Rhodes University archive's daily measurements (http://oldwww2.ru.ac.za/weather/ARCHIVE/OLDSTATION/) were used to determine the seasonal variation in wind speeds in Grahamstown.

2.4. Fruiting phenology, pollination and fig wasp production of *F. burtt-davyi*

The population of *F. burtt-davyi* was observed at fortnightly intervals for a period of 29 months from September 1987 to February 1990, but with a break during September 1988. On each occasion we recorded the number of figs, their developmental stage, and their presence or absence on each tree. Initial crop sizes were estimated shortly after figs had been pollinated. Depending on crop size, samples of these figs were removed, and the number of pollinator foundresses present were counted. In total, samples of recently-pollinated figs were obtained from 149 crops on 64 trees.

Crop sizes were re-assessed when the next generation of figs wasps was being released or about to be released. A total of 93 crops matured (tiny crops often failed to produce any mature figs), from which 1014 figs were opened and the pollinators and NPFW counted. The crop durations were calculated from the time of crop initiation until the time when mature figs were recorded. For each crop the mean numbers of female pollinators per fig were multiplied by the size of the final crops to estimate the total number of female pollinator wasps discharged from each crop. Approximate weekly pollinator release rates were calculated by dividing total female pollinators by the number of weeks that mature figs were present on each tree. Average daily temperatures for each season were based on the average daily maximum and minimum temperatures across three month intervals.

2.5. Pollinating wasps in the air

Variation in the number of *E. baijnathi* flying in the gardens was assessed using passive sticky traps. Five black-painted vertical plastic poles with a diameter of 20 cm were placed among the *F. burtt-davyi* population in open spaces at least 50 m apart and 20 m from the nearest trees. Each trap was made of two transparent cellulose acetate sheets 10 cm wide and 42 cm long onto which pruning sealant had been sprayed (produced by Frank Fehr Ltd., Durban). The bottom edges of the sheets were 1.5 m above the ground surface. The traps were changed every week, and any fig wasps caught were identified and counted. The number of wasps caught on these passive traps depended on the number of wasps in the air and the speed of the air; therefore catch counts do not directly indicate aerial density but rather provide an estimate of the number of insects that were moving through a particular space.

2.6. Analysis of data

Crop duration, crop sizes and numbers of foundresses per fig were analysed using linear mixed models with the *nlme* package in R.2.12.2. Multiple crops were included from each tree, so tree ID was included as the random effect. Crop duration and numbers of foundresses were analysed in models including both initial crop size and the mean temperature during crop development as fixed effects. For initial and final crop sizes, the fixed factor was the mean temperature in the relevant month. Significance was assessed using t tests in the *summary* function. Assumptions were checked by examining diagnostic plots; crop sizes and numbers of foundresses were log-transformed before analysis.

Numbers of crops and numbers of aborted figs were analysed using Poisson generalized mixed models with the *lme4* package. Numbers of crops were analysed in models with the relevant temperature as the fixed effect, and tree ID as the random effect. Numbers of aborted figs were analysed in a model with initial crop size as the fixed effect, and crop ID as the random effect. Significance was assessed using z tests in the *summary* function. Dispersion parameters were <2.

3. Results

3.1. Seasonal climatic variation

The seasons in Grahamstown can be divided into summer (November to January), autumn (February to April), winter (May to July), and spring (August to October). The average daily temperature in Grahamstown varies depending on the season, being higher in the summer and lower in the winter. The average daily temperatures were highest in January/February (19–23 °C), with the highest daily maximum temperture of 29.4 °C in January 1989. During winter, the lowest daily average temperatures were around 9.0 °C in June and July, with a minimum of 2.0 °C in July 1988. In all three years the winter months had the highest mean daytime wind speeds, although there was not much seasonal variation.

3.2. Phenology of fig tree fruiting

During the 29-month study period, 64 of the 105 *F. burtt-davyi* trees produced at least one crop of figs. Small immature trees failed to reach maturity, and they did not yield any crops. The highest number of crops recorded from a single tree during the study period was seven. Some of the smallest crops did not include any figs that finished development. Although the number of trees bearing figs fluctuated substantially, figs were continuously present in the tree population throughout each year. There were no clear seasonal patterns, but the number of both new crop initiations and mature crops was lowest in the winter and spring (Figs. 1 and 2). These variations were reflected in statistically significant positive associations between daily seasonal temperatures and the number of crops starting and maturing ($z = 8.95$, $P < 0.0001$, and $z = 11.30$, $P < 0.0001$, respectively) with slope (SE) of 0.029 (0.0032) and 0.047 (0.0042).

Crop development from pollination to the first wasps of the next generation emerging lasted between 30 and 113 days (but as sample intervals were every 14 days, these numbers are approximate). The duration of crop development was inversely related to the mean temperature during the period that a crop was developing ($t_{59} = -9.25$, $P < 0.0001$), with crops that were started during warmer months needing less time to finish their development (slope (SE) = −3.67 (0.40), Fig. 5). Development times were not affected by the initial size of the crops ($t_{59} = 1.08$, $P = 0.28$).

The size of crops that were initated or matured in the same months varied substantially. The largest initial crop size was estimated to number 45800, in February 1988, while the smallest crop size started in the same month that year was 2200. The largest mature crop was found in October 1988, estimated at 30,324, whereas the smallest mature crop

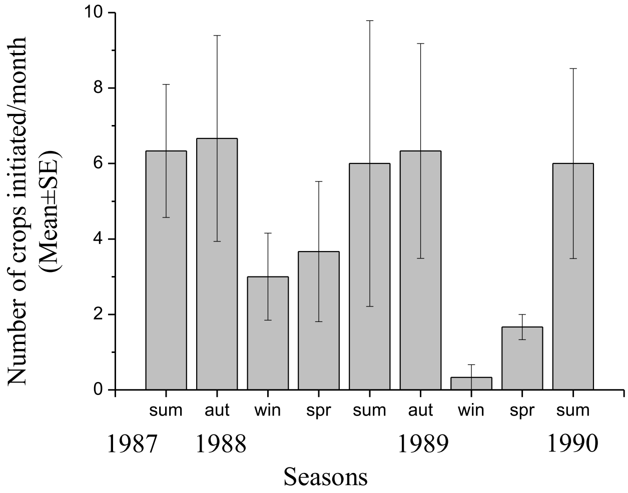

Fig. 1. Numbers of new crops of *Ficus burtt-davyi* initiated according to season.

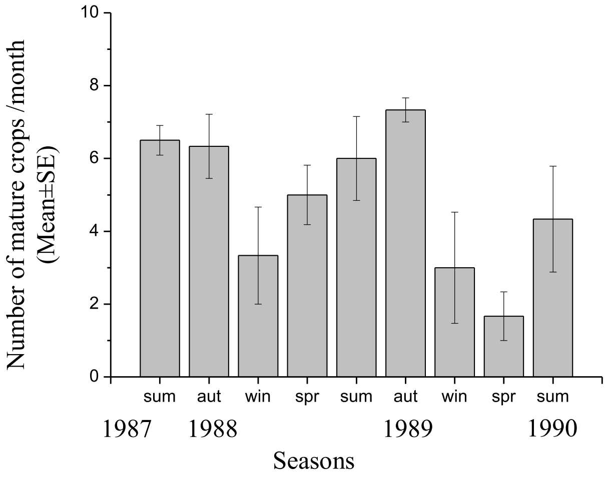

Fig. 2. Numbers of mature crops of *Ficus burtt-davyi* in relation to the season when they were initiated.

size in the same month was 521. Initial and mature fig crop sizes showed no obvious seasonal patterns and neither the initial nor final log-transformed crop sizes were significantly affected by mean temperatures during the months when they were recorded ($t_{60} = -0.19$, $P = 0.848$ and $t_{60} = 1.50$, $P = 0.138$, respectively).

3.3. *Numbers of pollinators released and in flight*

During the study period, fig wasps were being released almost continuously from one or more trees in the population, with the presence of mature figs on the trees, in which fig wasps were released or had recently been released, recorded in 56 of the 62 sample periods (Fig. 3). The highest estimated number of pollinators produced from a single crop was 1,642,260 females over an eight week period, with the smallest number of pollinator females from a single crop that successfully produced mature figs estimated as 192, released over two weeks (the figs on very small crops often all aborted).

Fig wasp production and the numbers of wasps flying in the air were greater during the summer months (Fig. 4). Within the study site an average of over 150,000 pollinators of *F. burtt-davyi* emerged each week during the summer months and around 100,000 pollinators emerged

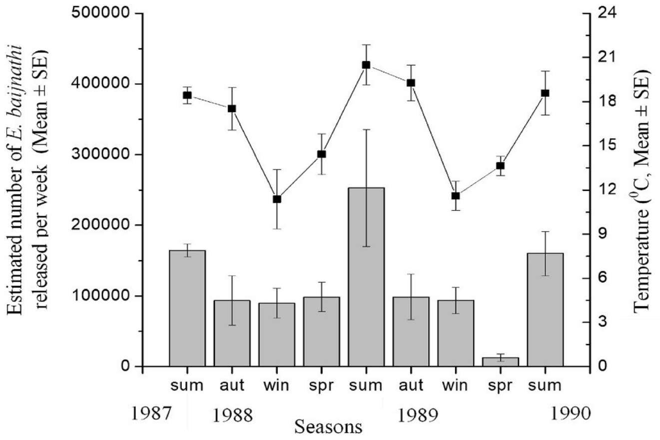

Fig. 3. Numbers of *E. baijnathi* females estimated to be released by the population of *Ficus burtt-davyi* trees (solid bars) and the average temperatures during the same periods (line).

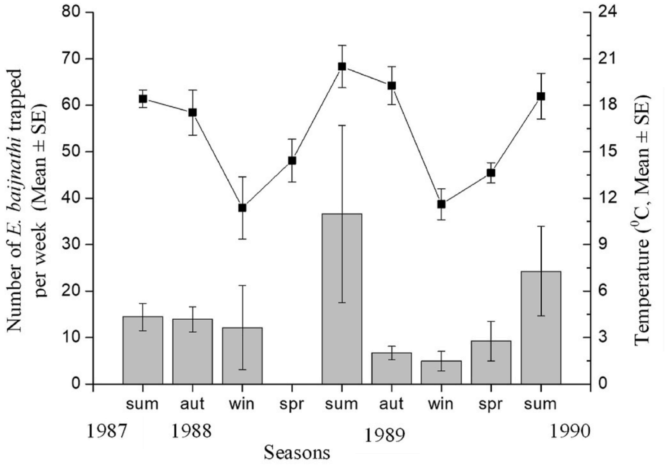

Fig. 4. The number of *E. baijnathi* females captured flying between trees each week (bars) and the mean temperatures in the same periods (line) (Data were unavailable for spring 1988).

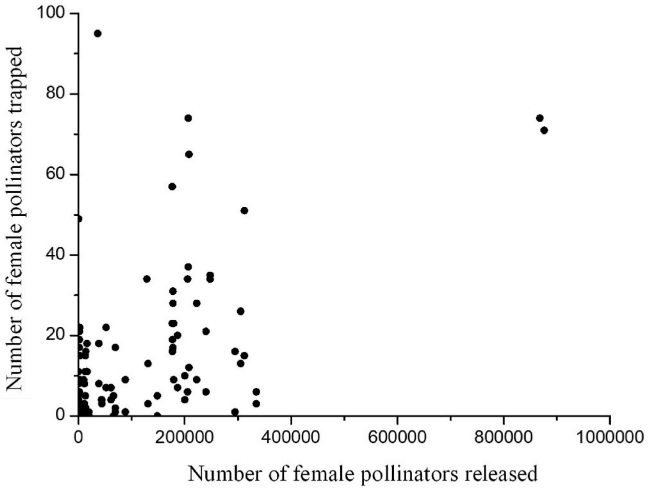

Fig. 5. The amount of *E. baijnathi* females captured in the air in relation to the number of local wasps released in Grahamstown (Data was unavailable for Spring 1988).

throughout the colder months. The number of wasps released each week was significantly correlated with the number of *E. baijnathi* captured flying that week though local releases explained only about half of the variance in trap counts ($P < 0.001$, Pearson's $R = 0.52$) (Fig. 5). Two periods when exceptionally high numbers of pollinators were released from the trees corresponded with two of the largest counts of fig wasps flying in the air, but the highest single trap count was recorded during a period when relatively few fig wasps were being released locally. An influx of fig wasps coming from outside the study area is a likely explanation.

There were nine weeks throughout the sampling period when no pollinators were present on the flight traps, during winter and early spring 1988 and 1989. Only two of these weeks were when the local trees were not releasing any pollinators (winter 1989). This suggests that when low numbers of pollinators were being released they were not necessarily detected on the traps. Conversely, fig wasps were still caught by the flight traps during periods when no pollinators were being released locally during ten weeks in the spring and early summer of 1989 (Fig. 6). This shows that the fig wasps flying within the study population had emerged from trees elsewhere and were the only possible pollinators of local trees at those times.

3.4. Foundress numbers

An average of 4257 ± 869 (mean ± SE) figs were available in each crop for pollinators to enter, ranging in size from 1 to 45,800 figs. Regardless of crop size, pollinators entered almost all the figs in each crop. The average number of pollinator foundresses that entered a fig was 1.5, ranging from 0 to 13 wasps, though 1269 of the 1967 figs (61.5%) contained just one pollinator. Temperature and crop size did not significantly affect the number of foundresses entering a fig (Fig. 7; $t_{55} = -1.09$, $P = 0.28$, $t_{55} = -0.94$, $P = 0.35$ respectively).

The bodies of pollinator females were found in almost every one of the developing figs, confirming that *E. baijnathi* is a species where re-emergence is very rare. Receptive figs that are not pollinated eventually fall off without developing further. Usually only small numbers of fallen figs had no pollinators (between 1 and 20 figs per crop), but one crop (with 20,500 figs initially) had over 100 figs that had not been entered by pollinators When this outlier is ignored there was a weakly positive relationship between the number of figs aborted due to not being pollinated and initial crop size ($z = 1.91$, $P = 0.056$) (Fig. 7).

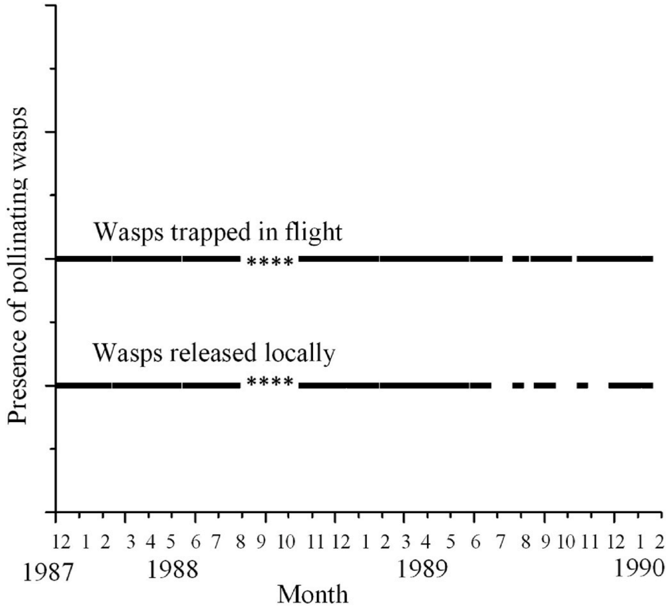

Fig. 6. The times that female *E. bajnathi* wasps were captured in flight corresponded with the times when wasps were released locally from their natal figs (solid lines show wasp presence, line breaks show when wasps were not trapped or were not being released; * a period when data were unavailable).

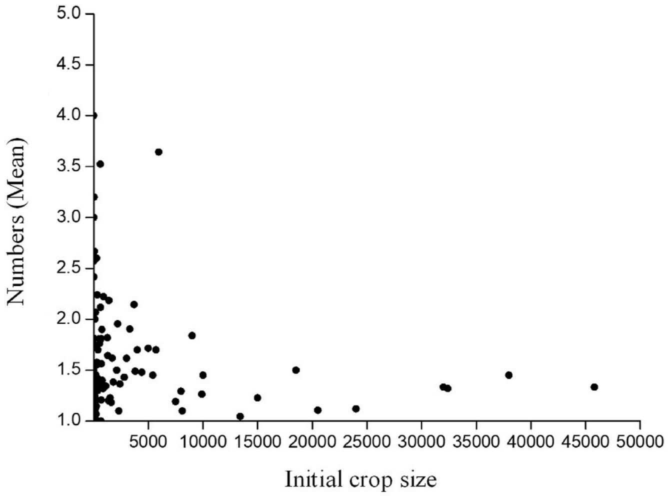

Fig. 7. The mean numbers of *E. baijnathi* females (foundresses) to enter a fig in relation to different sizes of the crops on the trees where the figs were present (only figs with at least one pollinator inside were included).

This suggests that the supply of pollinators was generally sufficient to meet the tree population's requirements, despite the great seasonal variation in the numbers of fig wasp emerging from their natal figs. This was partly a consequence of the ability of unpollinated receptive figs of *F. burtt-davyi* to remain viable for two weeks or more. The figs that were part of tiny crops were more likely to be entered by several pollinators, most of which may have failed to lay any eggs. More generally, the typically small number of foundresses in each fig was beneficial to the females, because they encountered limited or no competition for oviposition sites (and had space inside the figs to oviposit).

4. Discussion

Although most fig trees have tropical or sub-tropical distributions there are small numbers of monoecious extra-tropical species like *Ficus burtt-davyi* that are found at higher latitudes across the three southern continents, as well in temperate Asia (Avila, 1981; McPherson, 2005; Zhang et al., 2014) They and their associated fig wasps must necessarily face cold periods of the year when insect dispersal and pollination are more difficult, but they appear to lack some of the evolutionary responses displayed by dioecious *Ficus* species (Bronstien, 1989). *Ficus burtt-davyi* is one of the few monoecious fig trees with an exclusively extra-tropical distribution. The large population of 64 mature *F. burtt-davyi* we studied in the Makana Botanical Gardens released an estimated average of over one hundred thousand pollinator fig wasps each week, but pollinator releases nonetheless varied seasonally and there were brief periods in the winter months when no figs had released pollinators. At these times, traps placed within the population could still collect fig wasps, showing that they were dispersing into the site from elsewhere and that these females could potentially enter figs that might otherwise have remained unpollinated.

The seasonal variation in fig wasp activity in Grahamstown arose despite figs being present on a proportion of the trees throughout the year. It resulted from colder winter temperatures reducing the rate of initiation of new crops, the increased time that crops took to mature and consequently fewer crops completed their development. In contrast, the sizes of the crops showed no significant seasonal differences because of very large between-tree variation in crop sizes, and foundress numbers per fig overall were found to be independent of crop size. The slowing down of fruiting activity during colder months resulted in large seasonal differences in the numbers of *E. baijnathi* being released from the figs and this was reflected in a corresponding decline in the numbers of females trapped flying within the area during colder periods. Females that did emerge from their natal figs during colder periods would have found fewer receptive figs available in the area, and on average will have had to disperse further to reach them. Given that adult female fig wasps only survive for one or a small number of days, their chances of finding suitable figs in time may have been diminished during such periods, but the lower temperatures they experienced are also likely to have allowed them to live longer. Competition for suitable figs may have not been reduced during colder months because irrespective of season a majority of the figs were entered by a single foundress, and foundress numbers per fig did not vary significantly in relation to temperature: fewer pollinators were being released during colder periods, but there were also fewer figs waiting to be pollinated.

The smaller rate of crop maturation at colder times of the year resulted in a few periods when no pollinators were being released from any of the figs in the focal population. Despite this, small numbers of pollinators were still caught on the flight traps located within the area, even though there were no pollinators being released nearby. They may have arrived from the nearest known conspecific fig trees, about two km away, or from even further afield. The vegetation in the area comprised scattered, mostly small trees, bushes and low-growing herbaceous plants. Studies elsewhere suggest that the dispersing fig wasps will have been travelling within a few metres of the ground, where the wind could quickly have carried them over the relatively short distance to the nearest trees (Compton et al., 2005). Some species of fig wasps can disperse over much long distances between host trees (Thornton et al., 1996), but genetic studies suggest that smaller, dioecious species routinely disperse much more locally (Chen et al., 2011). Equivalent genetic data are not available for *F. burtt-davyi*, but in the Botanic Gardens its bushy/small tree growth form was closer to that of many dioecious species than to large monoecious strangler figs and its population genetic structure may reflect this.

Fig wasp females will enter receptive figs immediately after they have emerged from their natal figs, suggesting that receptive figs located on trees close to other trees that are releasing fig wasps at the same time are likely to be mainly or entirely pollinated by local sources. During colder months, when source trees were more scattered, and especially when no local *F. burtt-davyi* pollinators were being released, longer distance pollinator dispersal will not only have ‘rescued’ small numbers of figs, but will also have contributed to more extensive gene flow between fig tree populations during the winter months. *Ficus burtt-davyi* supports a small community of non-pollinating fig wasps in addition to its *Elisabethiella* pollinator that are ovule gallers or parasitoids (Compton, 1993). Their relative dispersal abilities and temperature tolerances are unknown, but evidence from other fig wasp communities suggests that some non-pollinators can disperse even more widely than their respective pollinators (Sutton et al., 2016). Non-pollinators are also more tolerant of temperature extremes (von Kolfschoten et al., 2022) and this combination may generate seasonal variation in fig wasp community composition that has consequences for seed and pollinator numbers inside the figs (Wang and Sun, 2009; Zhang et al., 2019).

Most species of fig tree are found in tropical areas, where seasonal variation in temperatures are smaller. Temperate dioecious fig trees in the northern hemisphere such as *F. carica*, *F. pumila* and *F. tikoua* have highly modified fruiting cycles where synchonised crop production is associated with pollinators spending months inside the figs as larvae (Berg and Corner, 2005; Zhao et al., 2014). This evolutionary strategy has not been followed by monoecious species, and the fruiting phenology of *F. burtt-davyi* is similar to that reported for species such as *F. macrophylla* and *F. rubiginosa* in Australia (McPherson, 2005). This apparently widespread slowing down, but not total cessation, of fig development during the winter months can maintain local pollinator populations but has consequences for species that require mature figs for food, such as frugivorous birds, reducing the likely ‘keystone’ significance of *F. burtt-davyi* and similar species during periods when other trees are not producing fruits (Compton and Greeff, 2020).

Author contributions

HGR and SGC devised the project. SGC collected the data. HGR carried out preliminary analyses and JJ and RJQ analysed the data. JJ and SGC wrote the manuscript.

Declaration of competing interest

The authors have no conflicts of interest to declare.

Data availability

Data will be made available on request.

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