The Influence of Temperature on the Reproductive Success of a Fig Wasp and Its Host Plant

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***Abstract*—**Ambient temperatures influence many aspects of insect behavior and reproduction, and limit their distribution and abundance. Small, delicate insects such as the fig wasps (Agaonidae) that pollinate fig trees rapidly succumb to heat stress when outside figs. We compared survivorship and reproductive success of the fig wasp *Kradibia tentacularis* pollinator of the Asian fig tree *Ficus montana* in three glasshouses maintained at different temperatures after foundress females entered figs (means of 17°, 21° and 27°C). The range of temperatures to which the fig wasps were exposed reflected conditions under a tropical forest canopy and their general lack of responsiveness indicates that only relatively extreme temperature conditions will influence them once they have entered a fig. Temperatures when adult fig wasps are dispersing between figs are likely to have a stronger impact than when they are in the relatively buffered environment within their host figs.

***Keywords*—** Agaonidae; Climate change; *Ficus*; Oviposition; sex ratio; thermal tolerance

I. Introduction

TEMPERATURE is probably the abiotic factor with the largest single influence on the distribution and abundance of insects [2]. Predicted changes in climate suggest that many insect species will be exposed to higher median temperatures and extreme temperature events in the future, with consequences for their population dynamics, distribution and evolution [31]-[30]. Species involved in obligate mutualisms are likely to be particularly responsive to climate change, because of the strong interdependency between partners [20]- [10]-[14].

Fig trees are an example of obligate mutualists that have very wide ecological significance: more species vertebrates feed on their fruits than on those of any other plants [27]. The approximately 800 described species of fig trees (Ficus, Moraceae) are found mainly in tropical and subtropical regions, in habitats ranging from rainforests to deserts [6]. They are all pollinated exclusively by host specific fig wasps (Agaonidae), with each fig tree species dependent on one or a small number of fig wasp species. Adult female fig wasps enter the figs in order to lay their eggs inside the numerous female flowers the inner surface of these specialized inflorescences. A single wasp larva develops inside each of the galled ovules of female flowers, which will usually also have been pollinated. Monoecious fig trees have figs where fig wasp offspring and seeds develop in the same figs. This contrasts with fig trees that have a dioecious breeding system, where there are distinct male and female plants, characterized by having mature figs that contain either the next generation of fig wasps or seeds, respectively. Fig wasps enter female figs, despite being unable to reproduce there, because of reciprocal mimicry displayed by male and female figs [15]. Female fig wasps escape from their natal figs via holes chewed through the fig wall by the males [29]. They are small (typically less than 2 mm in length), do not feed, and short lived – most probably die within 24 hours of emergence if they fail to find a suitable fig to enter [43]. Fig wasps lose their wings when entering through the ostiole into a fig, preventing them from dispersing further to other trees.

Temperatures control many aspects of the biology of fig wasps. Variations in temperature have direct impacts on the insects and also act indirectly via their host plants. The fruiting and leafing phonologies of fig trees vary considerably between species, but most respond by initiating and maturing fewer crops at colder times of the year. The time that fig crops take to reach maturity (and therefore the generation times of the fig wasps) is highly variable among those fig trees that grow in seasonal environments, with some winter crops taking months to complete development that is completed in weeks during the summer [9]-[11]. Emergence times from natal figs differ between diurnal and nocturnal-flying species, and in the day-flying *Elisabethiella baijnathi* the time when this occurs is linked to temperature, with the wasps emerging earlier in the day during summer months [35]. The minimum temperature at which emergence takes place may be particularly significant, because fig wasps maintained below this critical temperature can develop through to pupation, but then eventually die within their galls (M Zavodna and SG Compton, unpublished).

Adult female fig wasps do not eat or drink. Outside of figs, they are rapidly incapacitated when exposed to air temperatures above 30°C [24] and longevity declines above 25°C [19].The more rapid deaths of adult female fig wasps in response to higher temperatures are likely to be the result of more rapid dehydration as well as heat stress, though [19] could not confirm this in their experiments. The darker coloration typical of day flying fig wasps, compared with night-flying species, suggests that they nonetheless display adaptations to reduce water losses [12] and among the other

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insects that inhabit figs, a non-pollinating fig wasp Walkerella sp. (Pteromalidae) has a specialist male morph adapted for mating outside the figs that is darker in color and more resistant to desiccation than typical males [34]. Although darker fig wasps are not necessarily more resistant to dehydration [36], thermal tolerances may nonetheless limit the distributions of some fig wasps to sub-sets of the distributions of their host plants, with the day-flying *Ceratosolen galili*, a fig wasp that fails to pollinate its host figs, absent from the western desert areas of the range of *F. sycomorus*, unlike its night-flying congener *C. arabicus* [12]-[36]. Differing thermal tolerances may also explain seasonal variation in the relative abundance of the pollinator of *F. altissima* and an undescribed congener that utilizes the same host plant but fails to pollinate it [25].

Fig wasps are clearly highly vulnerable to dehydration when in transit between natal and receptive figs, but once they have found and entered receptive figs they are in a more benign environment. Humidities inside healthy figs will be consistently high, and larger figs also lose heat through transpiration, allowing foundress figs wasps to survive in figs where high ambient temperatures would otherwise quickly cause mortalities [24]. However, the survivorship of foundresses within figs at a wide range of temperatures does not necessarily mean that the number of flowers they pollinate, or the number of eggs that they manage to lay, are independent of temperature. Under warmer summer conditions, the pollinators of *F. racemosa* lay fewer eggs, but generate the same number of seeds as in the winter [32]. [33] argued that this results in contrasting summer and winter temperatures stabilizing the mutualism between fig trees and fig wasps, because it results in seasonal variation in the balance between seed and pollinator offspring production. They related the performance of the foundresses to temperature and humidity by removing the females shortly after they had entered receptive figs and monitoring survivorship under varying conditions. As with experiments utilizing females that had recently emerged from their natal galls, longevity was found to decline with temperature, suggesting a likely cause for the observed seasonal effects.

Here we describe experiments that more directly relate temperature to the longevity, behavior and reproductive success of foundresses within figs maintained at different temperatures. Utilizing a small dioecious fig tree maintained under controlled conditions within three different temperature ranges we addressed the following questions: Do ambient temperatures influence the behavior and survivorship of adult females after they have entered receptive male figs to oviposit? Do the numbers of their offspring vary according to temperatures at the time when eggs were laid? And are the numbers of seeds in female figs similarly modified by temperature at the time that pollinators are active inside receptive figs?

II. Methods

Natural history

Ficus montana (subgenus Sycidium) is a small dioecious shrub growing up to 2m tall, with a tropical distribution from Thailand and the Malay Peninsula southwards to Sumatra, Java and Borneo [6]. It grows in rainforest understory, in clearings, and in riparian situations [41] and is pollinated by *Kradibia* (*Liporrhopalum tentacularis*) Grandi, a daytime-flying fig wasp. The two species had been maintained at the experimental gardens of The University of Leeds, UK since 1995 [23]. They originated from the Centre for International Forestry Research (CIFOR) plantation, Bogor, West Java, Indonesia, and Rakata, Krakatau Islands, Indonesia.

The figs of *F. montana* are produced asynchronously by plants of both sexes throughout the year [28]. Mature figs on male plants contain pollen and the female pollinator offspring that will transport it, whereas mature figs on female plants produce only seeds. *K. tentacularis* females actively pollinate the flowers in female figs, even though they cannot lay eggs there [26]. The female flowers in its female figs have much longer styles and feathery stigmas that help prevent oviposition, but the mechanism preventing seed set in male figs is unclear [26]. Figs at the receptive (B) stage [42] release volatile blends that are attractive to *K. tentacularis* females. They squeeze through the ostiolar bracts, losing their wings and part of their antennae in the process. Once inside a male fig, they deposit a single egg in each galled ovule [16]. Larvae that develop in figs that have not been pollinated are less likely to survive. *K. tentacularis* foundresses often re-emerge from the receptive figs they enter, and walk to receptive figs nearby. Offspring sex ratios in *K. tentacularis* are female-biased, but the extent of this bias depends on clutch size, because females lay mainly male eggs initially, then mainly female eggs [26].

Glasshouse conditions

We used *F. montana* growing in three heated glasshouses with contrasting mean and maximum temperatures to provide low, medium and high temperature treatments. Temperatures were monitored during the periods when foundress fig wasps were ovipositing using 'tiny tag' data loggers (Meaco measurement and control, Newcastle under Lyme, England) situated within the plants, recording at 30 min intervals. Outside of these experimental periods, the plants and wasps were maintained under medium temperature conditions.

Foundress behavior and survival

Pre-receptive (A phase) figs on male plants were placed in cotton bags to exclude pollinator females. When the figs were receptive (B phase), single foundresses were placed at their ostioles using a fine paint brush. After the foundresses had entered, the bags were replaced to prevent entry by additional pollinators. The foundresses had emerged the same morning from mature (D phase) figs collected from other male plants that had been placed in netting-covered pots, with the wasps allowed to emerge naturally. The experimental figs were opened 3, 6, 12 or 24 hours after foundress entry and we recorded how many of the fig wasps were dead (or moribund), alive and active, or had exited the figs.

Reproductive success

Figs on male and female plants were bagged and entered by single foundresses, as before. The bags were then returned around the figs to prevent entry of further pollinators, and subsequently to prevent oviposition by non-pollinating fig wasps that lay their eggs from outside the figs. After 48 hrs. (when all foundresses had died), the plants from the three temperature regimes were all housed together in the medium temperature greenhouse, where they remained for several weeks until the figs had matured. The contents of the figs (total female and male flowers, seeds, failed empty galled ovules ('bladders') and pollinator offspring were then recorded.

Analysis

Numbers of galls, empty galls and unpollinated flowers in male figs, and seed set in female figs, were expressed as proportions of the female flowers present in the figs. Temperature effects were analyzed by mixed-effects logistic regression, with temperature included as a continuous explanatory variable. To account for the non-independence of data from flowers in the same figs and figs on the same plant, plant and fig were included as random effects. Three male figs which produced no offspring (1 in each temperature group) were excluded from the analysis. Analysis was carried out in Stata 11.2 (Stata Corp, College Station, Texas).

III. Results

Glasshouse conditions

Maximum temperatures during the periods when foundress behavior and survival were monitored inside the figs were 22.7, 27.9 and 34.5 ^{o}C in the low, medium and high temperature regimes respectively. Temperatures during the 48 hours after pollinators were introduced into figs and offspring plus seed production were monitored are summarized in table 1.

Foundress behavior and survival:

No active foundress females remained in the figs 12 hours single individuals had been introduced, irrespective of temperature (Table 2). Some females died within the figs, but the majority re-emerged to seek out oviposition opportunities in other figs. The overall proportion of wasps that were dead or moribund varied from 1 of 32 wasps at medium temperatures to 5 of 32 wasps at low temperatures, but there was no significant variation across temperatures (Fisher's exact test, P = 0.29).

Reproductive success:

The proportion of female flowers in male *F. montana* figs that *K. tentacularis* females managed to exploit successfully varied between about 40% and 60% in different temperature treatments (Table 3), but there was considerable variation between individual figs within treatments and no significant relationship between the proportion of galls (galls/total flowers) and temperature treatment (Wald χ^2 = 1.77, df = 1, p = 0.18). Empty galls in *F. montana* figs are likely to be ovules where pollinators laid eggs, but their larvae failed to develop successfully [16]; the proportion of unsuccessful galls (empty galls/total flowers) decreased as temperature increased, but not significantly so (Wald χ^2 = 3.44, df = 1, p = 0.064). In female figs, where *K. tentacularis* cannot lay eggs (Table 4), there was no significant relationship between the proportion of seeds (seeds/total flowers) and temperature treatment (Wald χ^2 = 0.13, df = 1, p = 0.72).

IV. Discussion

Climate warming is expected to have deleterious effects on many plants and animals, including fig trees and the insects that pollinate them, and [19] have shown that a 3^{o}C temperature increase could have a significant impact on the survivorship of female fig wasps when they are dispersing between trees. Whereas female fig wasps are clearly highly susceptible to elevated temperatures after they have emerged from natal figs, or when they are removed from figs where they were ovipositing [33], we found that *L. tentacularis* females are more resilient while inside receptive figs, during the period when they are laying their eggs and pollinating the flowers of *F. montana*. A ten degree temperature range failed to elicit significant changes in foundress death rates or behavior, nor did it alter the numbers of offspring they produced or the numbers of seeds that they pollinated.

Our results narrow down the situations during the life cycle of fig wasps when heat stress is likely to be significant, but do not reduce the likely significance of increasing temperatures for the mutualism. Our experimental temperature range reflected temperatures that *F. montana* figs are likely to experience, but not extremes of temperature [13]. Even if brief, extreme events when the temperatures inside figs rise above 30^{o}C are highly likely to be detrimental to the fig wasps [24]. Some fig wasp species are more likely to be subject to heat stress than others, because habitat and the location of figs on plants will influence the temperatures to which female fig wasps will be exposed once they enter the figs. Understory plants, for example, experience less diurnal variation in temperatures than in the rainforest canopy, or plants growing in gaps or forest edges [5]-[13], and figs located on tree trunks may be less exposed that those located among the leaves.

Longer term, persistence of fig tree and fig wasp populations is linked to habitat fragmentation [22] and the dispersal abilities of the pollinators [8]. Host finding among fig wasps is surprisingly effective, and some fig wasps can disperse more than 100kms between natal trees and receptive figs [1], but the longer that females are in the air, the more susceptible they will be to dehydration and the effects of increased ambient temperatures. Some species of fig wasps disperse during the day, others at night, with fig wasps that disperse at night more common in tropical than temperate latitudes. Any increases in temperature are more likely to have a negative impact on day-flying species, and night-fliers may even benefit, if low temperatures limit when they can fly.

TABLE I
TEMPERATURES EXPERIENCED BY FOUNDRESS FIG WASPS DURING THE 48 HOURS AFTER ENTRY INTO FIGS.

TEMP.	Temperatures (^{o} C)	
	Mean + SD	Maximum
Low	17.0 + 0.58	18.1
Medium	21.4 + 2.20	27.4
High	26.7 + 4.79	38.1

TABLE II
. THE CONDITION AND BEHAVIOR OF SINGLE FOUNDRESS FIG WASPS INTRODUCED INTO RECEPTIVE FIGS MAINTAINED AT THREE DIFFERENT TEMPERATURES.

Temperature	Condition	Time (Hours after entry)			
		3	6	12	24
Low	Active	5	4	0	0
	Moribund	1	3	0	1
	Re-emerged	2	1	8	7
Medium	Active	7	6	0	0
	Moribund	1	0	0	0
	Re-emerged	0	2	8	8
High	Active	7	3	0	0
	Moribund	0	1	1	1
	Re-emerged	1	4	7	7

TABLE III
THE CONTENTS OF MATURE MALE FIGS THAT HAD EARLIER BEEN MAINTAINED AT THREE DIFFERENT TEMPERATURES FOR 48 HOURS AFTER ENTRY BY A SINGLE FOUNDRESS FIG WASP INTO THE FIGS WHEN THEY WERE RECEPTIVE.

Temperature	N plants	N figs	Contents (Mean ± SD)		
			Total flowers	Proportion seeds	Proportion unpollinated
Low	3	30	113.7 ± 22.8	0.71 ± 0.14	0.29 ± 0.14
Medium	3	25	107.8 ± 29.2	0.71 ± 0.19	0.29 ± 0.19
High	3	27	93.8 ± 23.0	0.67 ± 0.20	0.33 ± 0.20

TABLE IV
THE CONTENTS OF MATURE FEMALE FIGS THAT HAD EARLIER BEEN MAINTAINED AT THREE DIFFERENT TEMPERATURES FOR 48 HOURS AFTER ENTRY BY A SINGLE FOUNDRESS FIG WASP INTO THE FIGS WHEN THEY WERE RECEPTIVE.

Temperature	N Plants	N figs	Contents (Mean ± SD)			
			Total female flowers	Proportion successful galls	Proportion empty galls	Proportion unpollinated flowers
Low	6	24	97.1 ± 25.7	0.42 ± 0.25	0.37 ± 0.21	0.21 ± 0.14
Medium	4	29	108.4 ± 25.9	0.55 ± 0.20	0.30 ± 0.15	0.16 ± 0.14
High	4	25	114.8 ± 28.0	0.58 ± 0.21	0.23 ± 0.19	0.19 ± 0.18

ACKNOWLEDGMENTS

Thanks to Martin Lappage for invaluable help with maintaining the glasshouse populations of fig trees and fig wasps, and managing the temperatures to which they were exposed. We would also want to express appreciation to Salah Ghana for his advice and help on collecting figs.

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