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Climate warming and the potential extinction of fig wasps, the obligate pollinators of figs

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Figs (*Ficus*) have a reciprocally obligate mutualism with tiny, short-lived (1–2 days) fig wasps (Agaonidae). The small size and short life of these pollinators is expected to make them more vulnerable to climate change than their larger and longer-lived hosts. We experimentally tested the thermal tolerances of four species of adult female fig wasp from equatorial Singapore. The results suggest that an increase of 3°C or more above the current temperatures experienced across much of the equatorial tropics would markedly decrease the active adult lifespan of all four species. Fig plants are the centre of an intricate web of specialist and generalist animals. Unless fig wasps can acclimate or adapt to warmer temperatures in time, these responses may disrupt the mutualism, potentially affecting multiple trophic levels.

1. Introduction

The potential impact of anthropogenic climate change on plant–pollinator mutualisms remains poorly understood, particularly in the tropics [1]. Specialized pollination relationships, in which a plant species has few alternative pollinators, are expected to be more vulnerable than generalized ones [2,3]. In the extreme case of obligate, one-to-one relationships (one pollinator to one plant), neither species will survive climatic conditions that are unsuitable for the more sensitive partner [2]. The figs (*Ficus*, Moraceae) are a pantropical genus of 755 species of woody plants and their ecological importance as a food resource for diverse tropical frugivores has been well documented [4,5]. They have reciprocally obligate pollination relationships with tiny (1–2 mm), short-lived (1–2 days adult lifespan), fig wasps (Agaonidae). The different physiologies of the two partners are expected to respond very differently to climate change, destabilizing the mutualism in the short-run and possibly leading to co-extinctions in the long-run [3,6]. Numerous vertebrates (more than 1200 spp.) consume at least some figs, while some birds, bats and primates depend on them for a large fraction of their diets [5]. In addition, some fig species are important pioneers for reforestation efforts, while both planted and spontaneous fig species play a significant role in supporting urban wildlife [7,8]. Given the ecological importance of fig plants, it is important to understand the vulnerability of their pollinators.

This study was carried out in equatorial Singapore, which has a climate of extreme equability, with negligible seasonality in either rainfall or temperature [9]. Singapore experiences mean daily and mean maximum temperatures of 27°C and 31°C, respectively, with an extreme range (since 1929) of 19.4–36.0°C [9]. These conditions are expected to select for a narrow range of thermal tolerance and thus a high sensitivity to the predicted warming in the lowland tropics [10].

2. Material and methods

Four species of adult female fig wasps collected from Singapore were used: *Valisia malayana* (pollinator of *Ficus grossularioides*), *Ceratosolen constrictus hewitti* (*F. fistulosa*), *Ceratosolen appendiculatus* (*F. variegata*) and *Eupristina verticillata* (*F. microcarpa*), all in the family Agaonidae. Syconia (4333 wasps, 240 syconia) were haphazardly collected and adult female fig wasps left to emerge at room temperature for 1 h 30 min, so that they were the same age and to minimize acclimation. Experiments were run in a Sanyo growth chamber MLR-351H and were ended when all wasps had died or became irreversibly immobile. No data were censored. Kaplan–Meier survival analysis was used to obtain median lifespan duration (LD) estimates, and Cox's proportional hazard model with hazard ratios was used to obtain mortality rates (MRs). Temperature treatments for *V. malayana*, *C. c. hewitti* and *E. verticillata* were 25°C, 26°C, 28°C, 30°C, 32°C, 34°C, 36°C and 38°C at 85% relative humidity. Survival was recorded at 2 h intervals, except that above 36°C the pollinators died in less than 2 h so their states were recorded earlier. *Ceratosolen appendiculatus* temperature treatments were 26°C, 28°C, 30°C, 32°C and 34°C at 85% relative humidity and survival was recorded at 0, 6, 12 and then at 12 h intervals. *Valisia malayana* was also tested at 60% and 85% relative humidity at 32°C, 34°C, 36°C and 38°C, with survival recorded at 2 h intervals. Syconia on the same tree but different branches were used for within-species comparisons. Wasps from six syconia of *V. malayana*, two of *C. c. hewitti* and four of *C. appendiculatus* were tested at 28°C and 85% relative humidity, and survival recorded at 0, 6, 12 and then at 12 h intervals. All data have been deposited in Dryad (<http://dx.doi.org/10.5061/dryad.hj7h2>), see electronic supplementary material.

3. Results

The LD for all four species decreased steadily with increasing temperature (figure 1a). At 27°C, the mean daily temperature in Singapore, the LD of our study species ranged from 11 to 24 h. At 31°C, LD decreased sharply from 6 to 18 h (figure 1a), and at 34°C, all four species survived 6 h or less. The MR of all species increased with temperature, but at different rates, with *E. verticillata* displaying the highest overall hazard ratio, with wasps 2.6 times more likely to die with every 2°C increase in temperature, compared with 1.4 times in *C. appendiculatus* (table 1). There was no significant difference in LD or MR between 85% (average for Singapore) and 60% (low for Singapore) relative humidity treatments ($n = 1504$, HR = 1.0, $p = 0.72$; figure 1b and table 1). There were significant between-brood MR differences for all three species tested: *V. malayana* ($n = 418$, Wald test = 132, d.f. = 5, $p < 0.001$), *C. c. hewitti* ($n = 315$, Wald test = 14, d.f. = 1, $p < 0.001$) and *C. appendiculatus* ($n = 268$, Wald test = 24, d.f. = 3, $p < 0.001$). Median LD estimates differed in *V. malayana* and *C. c. hewitti* but not *C. appendiculatus* (table 2).

4. Discussion

Much of lowland southeast Asia currently experiences mean daily temperatures of around 27°C and daily maxima in the 30–36°C range [11]. The IPCC's report [12] projects a regional warming of 2.2–3.0°C (25–75% quartile values from 21 models) for the moderate A1B greenhouse gas scenario by 2080–2099 and approximately 2.6–3.5°C for the A2 scenario. An increase in mean temperature of 3.0°C would result in a decrease in fig wasp LD in three of the four species with

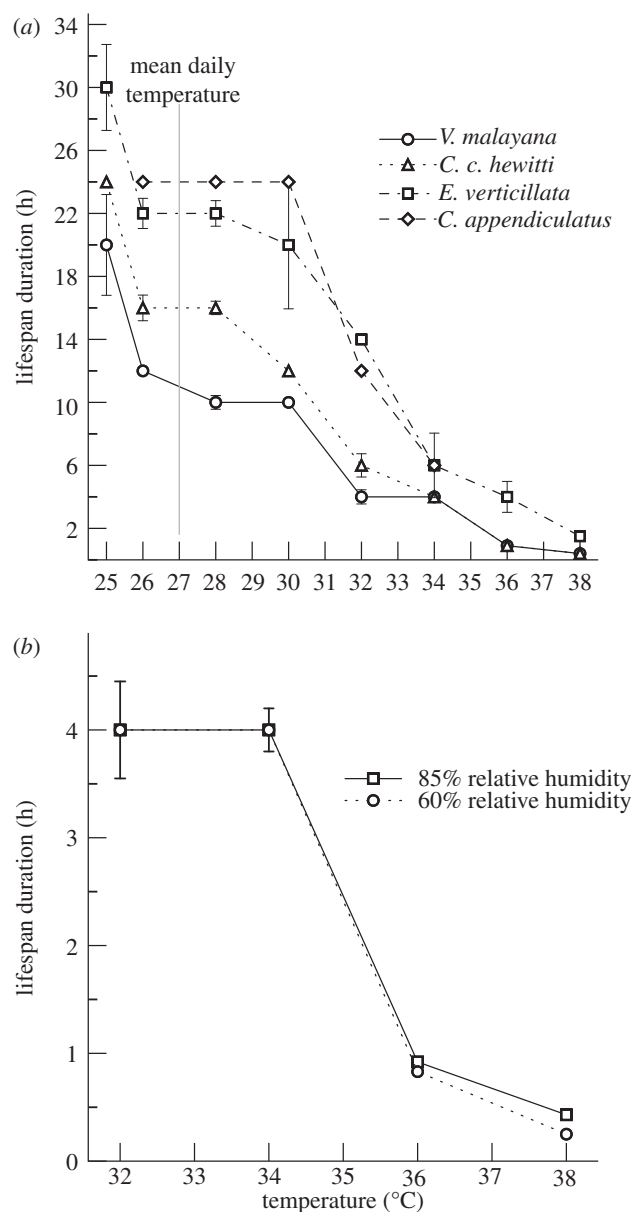


Figure 1. Median lifespan duration with 95% CIs for temperature treatments for (a) *Valisia malayana*, *Ceratosolen c. hewitti*, *Ceratosolen appendiculatus* and *Eupristina verticillata* at 85% relative humidity and (b) *Valisia malayana* at 60% and 85% relative humidity.

C. c. hewitti displaying the largest decrease at 25 per cent (figure 1a). However, mean daily temperatures are averaged over 24 h and daytime temperatures are more relevant for day-dispersing wasps that live less than 24 h. The mean daytime temperature (7.00–19.00) of Singapore for 2010 was 29°C [13] and an increase in 3.0°C, which is expected by 2100 [12], would reduce the LD of day-dispersing *V. malayana*, *C. c. hewitti*, *C. appendiculatus* and *E. verticillata* by 33–60% (figure 1a). Night-dispersing species will experience lower absolute temperatures, but a similar degree of warming [14].

Reduced LD and increased MR for fig wasps, some of which disperse tens of kilometres to receptive host figs [15], would mean that wasps would have less time to locate a receptive host syconium and pollinate and/or oviposit in the hundreds of florets within it [16]. The potential consequences include: (i) declines in the populations of fig wasps; (ii) reduced pollination services leading to fig population declines; (iii) reduced fig populations reducing food abundance for frugivores, resulting in secondary population declines. Besides supporting a huge

Table 1. Temperature and humidity effects on mortality rate. Cox's proportional hazards model (hazard ratio, HR), regression coefficient (coeff.) and standard error (s.e.) for (a) *Valisia malayana*, *Ceratosolen c. hewitti*, *Ceratosolen appendiculatus* and *Eupristina verticillata* from 26°C to 38°C at 85% relative humidity and (b) *Valisia malayana* at 32°C, 34°C, 36°C and 38°C crossed with 60% and 85% relative humidity.

	no. of wasps	HR	coeff.	s.e.	p-value
(a) temperature					
<i>Valisia malayana</i>	1923	1.6	0.49	0.01	< 0.001
<i>Ceratosolen c. hewitti</i>	757	1.9	0.64	0.03	< 0.001
<i>Ceratosolen appendiculatus</i>	763	1.4	0.36	0.02	< 0.001
<i>Eupristina verticillata</i>	201	2.6	0.94	0.07	< 0.001
(b) humidity					
humidity 60% (baseline group)	689	1.0	0	—	—
humidity 85%	815	1.0	−0.02	0.06	0.72

Table 2. Median lifespan estimate and mortality rate of wasps emerging from different syconia at 28°C and 85% relative humidity. Median lifespan estimate (h) derived from Kaplan–Meier analysis. Cox's proportional hazards model (hazard ratio, HR), regression coefficient (coeff.), standard error (s.e.) and Wald test for *Valisia malayana*, *Ceratosolen c. hewitti* and *Ceratosolen appendiculatus*.

	no. of wasps	lifespan estimate (h)	mortality rate				Wald test
			HR	coeff.	s.e.	p-value	
<i>V. malayana</i>							
A (baseline group)	41	24	1.0	0	—	—	$W = 132, \text{d.f.} = 5, p < 0.001$
B	88	12	2.7	0.98	0.19	> 0.001	
C	37	24	1.3	0.30	0.22	0.20	
D	101	24	0.7	−0.43	0.19	0.02	
E	77	12	0.6	−0.51	0.20	0.01	
F	74	24	0.5	−0.79	0.20	> 0.001	
<i>C. c. hewitti</i>							
A (baseline group)	111	12	1.0	0	—	—	$W = 14, \text{d.f.} = 1, p < 0.001$
B	204	24	0.6	0.64	0.12	> 0.001	
<i>C. appendiculatus</i>							
A (baseline group)	41	24	1.0	0	—	—	$W = 24, \text{d.f.} = 3, p < 0.001$
B	62	24	0.6	−0.47	0.20	0.02	
C	87	24	1.1	0.10	0.19	0.60	
D	78	24	0.5	−0.61	0.20	< 0.001	

range of vertebrates, a single host fig can support up to 30, more or less host-specific, non-pollinating fig wasp species [17]. Sustained collapses in the fig–fig wasp mutualism could thus affect multiple trophic levels.

Pollinator species with a wide latitudinal range will have been exposed to higher thermal extremes over their evolutionary history than those that occur only in the equatorial lowlands, and might be expected to have a higher degree of thermal tolerance [10]. Indeed, the thermal tolerances of the four species of fig wasp studied here appear to correspond to the ranges of their host figs, with the least thermally tolerant, *V. malayana* (*F. grossularioides*), restricted to the aseasonal tropics, and the most thermally tolerant, *E. verticillata* (*F. microcarpa*) and *C. appendiculatus* (*F. variegata*), ranging from Queensland, Australia to south Japan [4]. *Ceratosolen c. hewitti* (*F. fistulosa*) has an intermediate range. Rainfall and humidity may also

influence wasp survival ([16,18] but see [19]), but the humidity treatments in this study did not affect LD and MR significantly.

Developing fig syconia are able to use evaporative cooling to avoid temperatures that would be lethal to fig wasp larvae [20]. Even within the same tree, however, syconia are exposed to different microclimates, whereas wasps from a single syconium may have several mothers. Individual wasps may, therefore, vary in both their opportunities for temperature acclimation during development and in the genetic component of thermal tolerance. We did not assess either in this study, but the significant variation in thermal tolerance among wasp broods from the same host tree suggests that one or both may be significant. The literature suggests that the ability of insects to acclimate to higher temperatures may be limited [21], but the short generation times of fig wasps (approx. one month) would favour rapid evolution if heritable

genetic variation in heat tolerance exists. It is also important to note that we assessed only the ability of wasps to move. Both pollination and oviposition are complex behaviours in fig wasps and their success may be more sensitive to warming. Moreover, in a Neotropical pseudoscorpion a 3.5°C warming had only a small impact on survival but rendered the females sterile [22].

The three genera of fig wasps we tested represent three widely divergent clades [23], suggesting that our results can be generalized to other fig wasps. This implies that fig populations,

not just in Singapore but in the entire aseasonal tropics, could be extremely vulnerable to anthropogenic global warming. Because of their ecological importance, any loss of fig species or reduction in their abundance would be of major conservation concern. We hope this study will encourage more research.

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