

RESEARCH ARTICLE

Rising temperatures threaten pollinators of fig trees—Keystone resources of tropical forests

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Abstract

Pollinating insects are decreasing worldwide in abundance, biomass, and species richness, affecting the plants that rely on pollinators for fruit production and seed set. Insects are often sensitive to high temperatures. The projected temperature increases may therefore severely affect plants that rely on insect pollinators. Highly specialized mutualisms are expected to be particularly vulnerable to change because they have fewer partner options should one partner become unavailable. In the highly specialized mutualism between fig trees and their pollinating fig wasp, each fig species is pollinated by only one or a few wasp species. Because of their year-round fruit production, fig trees are considered a keystone resource for tropical forests. However, to produce fruits, wild fig trees need to be pollinated by fig wasps that typically travel a long one-way trip from the tree donating pollen to the tree receiving pollen. In a few previous studies from China and Australia, increasing temperatures dramatically decreased fig wasp lifespan. Are these grim results generalizable to fig mutualisms globally? Here, we use survival experiments to determine the effect of increasing temperature on the lifespan of Neotropical fig wasps associated with five common Panamanian *Ficus* species. Experimental temperatures were based on the current daytime mean temperature of 26.8°C (2SD: 21.6–31.7°C) and the predicted local temperature increase of 1–4°C by the end of the 21st century. We found that all tested pollinator wasp species had a significantly shorter lifespan in 30, 32, 34, and 36°C compared to the current diurnal mean temperature of 26°C. At 36°C pollinator median lifespan decreased to merely 2–10 h (6%–19% of their median lifespan at 26°C). Unless wasps can adapt, such a dramatic reduction in lifespan is expected to reduce the number of pollinators that successfully disperse to flowering fig trees, and may therefore jeopardize both fruit set and eventually survival of the mutualism.

KEYWORDS

Ficus, fig wasp, global warming, life span, mutualism, pollination

TAXONOMY CLASSIFICATION

Applied ecology, Conservation ecology, Entomology, Global change ecology

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1 | INTRODUCTION

Worldwide, pollinators are decreasing in occurrence, diversity, and abundance (Hallmann et al., 2017; Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019; Van Swaay et al., 2015; Wagner et al., 2021; Zattara & Aizen, 2021). Causes for this decline include habitat loss, increased pesticide use, and global warming (IPBES, 2016; Kearns et al., 1998; Memmott et al., 2007; Vanbergen & Garratt, 2013). Nearly 90% of flowering plants depend on pollinators for fruit production and seed set (Ollerton et al., 2011), and the number of available pollinators directly influence the seed set of the plant (Ågren, 1996; Robertson et al., 1999). Losing pollinators therefore would have a great effect on plant communities and other organisms dependent on plants (Biesmeijer, 2006; Brosi & Briggs, 2013; Kearns et al., 1998).

Although plants themselves may tolerate rising temperatures, pollinators have quite different physiologies from plants and may be negatively affected by high temperatures (Angilletta & Angilletta, 2009; Suttle et al., 2007). Most pollinators are insects, and studies show that insects can be negatively impacted by high temperatures, having reduced lifespans, reduced fecundity, or increased thermoregulating behavior (Durak et al., 2020; Feder et al., 1997; Mech et al., 2018; Wynants et al., 2021). However, most studies on pollinators measure physiological constraints at maximum viable temperatures (Käfer et al., 2012; Maebe et al., 2021; Maia-Silva et al., 2021; Oyen & Dillon, 2018; Sánchez-Echeverría et al., 2019) rather than lifespan at elevated, realistic temperatures (Jevanandam et al., 2013; Nasir et al., 2019). Measuring the actual lifespan of pollinating insects is highly relevant as this can determine their capacity to perform pollination services. Here, we study the effect of temperature on pollinator lifespan, a direct correlate to pollinator dispersal success in the mutualism between fig trees and their pollinating fig wasps.

Fig trees are keystone resources in tropical forests globally because by fruiting asynchronously they produce ripe figs year-round. Up to 70% of rainforest birds and mammals eat figs (Shanahan et al., 2001). To produce fruits, wild fig trees need to be pollinated by fig wasps. Fig trees and fig wasps have been coevolving for 80–90 million years, with currently over 750 species of fig trees globally (Cruaud et al., 2012; Datwyler & Weiblen, 2004). Each species of fig tree can only be pollinated by one or a few species of fig wasps (Figure 1), and fig wasps can only lay their eggs in fig flowers (Herre, 1989; Herre et al., 2008; Wiebes, 1979). Fig wasp larvae develop inside galled fig flowers, and collect pollen from their natal fig before dispersing to a different tree to pollinate and lay their eggs (Herre et al., 2008).

Fig wasps are tiny (1–3 mm), extremely short-lived (2–3 days on average), and disperse long distances, in central Panama on average 6–14 km in a single one-way trip (Dunn et al., 2008; Harrison, 2003; Jandér et al., 2016; Nason et al., 1998). Most fig wasp species that pollinate large rainforest trees disperse passively with the wind above the canopy during the day, exposing them to full sunlight and



FIGURE 1 A female fig wasp (*Tetrapus americanus*), pollinator of *Ficus maxima*, has just emerged from her natal fig and is cleaning herself, getting ready for the long one-way flight to a flowering tree where she can lay her eggs. Photograph by Christian Ziegler (www.christianziegler.photography).

daytime temperatures (Harrison, 2003; Nason et al., 1998; Ware & Compton, 1994). Additionally, as tropical insects, they are expected to be more sensitive to temperature increases because they are likely to already perform close to their thermal maximum (Sunday et al., 2014). During their larval development, fig wasps are sheltered within fig fruits that, at least in some species, are actively cooled by the tree (Patiño et al., 1994). However, when the adult wasps leave their fig fruit to carry pollen and eggs to a new fig tree, wasps are exposed to the ambient temperature. Earlier studies of four Old world fig wasp genera (*Ceratosolen*, *Eupristina*, *Pleistodontes*, and *Valisia*) found that pollinator fig wasps can be extremely sensitive to increased temperatures resulting in dramatic decreases in lifespan (Aung et al., 2022; Gigante et al., 2020; Jevanandam et al., 2013; Sutton et al., 2018). Are these worrying findings generalizable also to New World pollinator fig wasps?

To fill this knowledge gap, we quantified the effect of increased air temperature on the lifespan of Neotropical fig wasps. Using climate chambers, we performed survival experiments on wasp species from both existing Neotropical fig pollinator genera, *Pegoscapus* and *Tetrapus*. Our tested wasp species are species-specific pollinators of five common Panamanian *Ficus* species (but see Machado et al., 2005; Satler et al., 2020, regarding rare host sharing). We tested temperatures that ranged from the local current mean daytime temperatures to the local predicted daytime temperatures by the end of the 21st century (1–4°C higher depending on the different climate scenarios; IPCC, 2021) and beyond. Because our samples also contained some parasitic fig wasp genera, we opportunistically included also them in the study. If parasitic fig wasps respond differently than pollinators to increasing temperatures, the wasp community structure may change (Aung et al., 2022; Kordas et al., 2011). Specifically, we asked how increased air temperature affects the lifespan of (1) pollinator fig wasps and (2) parasitic fig wasps.

2 | MATERIAL AND METHODS

2.1 | Study site

The experiments were performed at the Smithsonian Tropical Research Institute's field station Barro Colorado Island (BCI) in central Panama, during the dry season in January–March in the years 2015, 2016, and 2017. The local climate is quite stable with daytime mean temperatures above the canopy of 26.9°C (2SD: 22.1–31.1°C) in the dry season and 26.8°C (2SD: 21.6–31.7°C) in wet season (Figure 2; Paton, 2020). All wasp individuals were collected within Barro Colorado Nature Monument.

2.2 | Study species

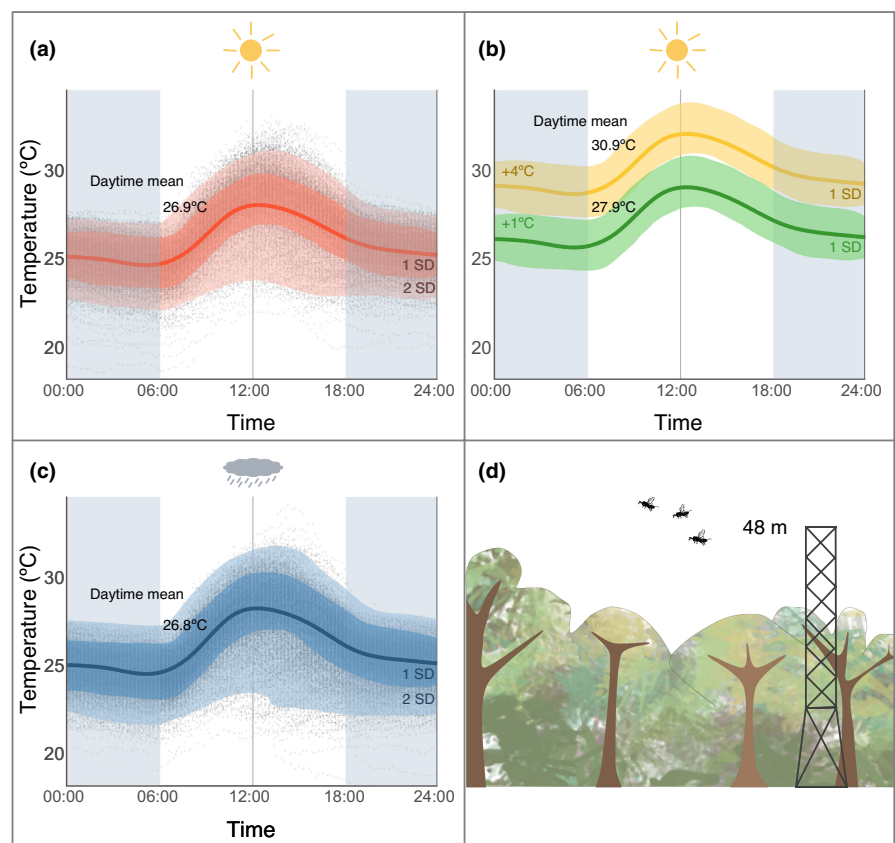
We quantified the lifespan of the fig wasps pollinating five common Panamanian fig species, representing the two genera of pollinator fig wasps present in the Neotropics: *Pegoscapus* (pollinators of *Ficus* subgenus *Urostigma*, subsection *Americana*) and *Tetrapus* (pollinators of *Ficus* subgenus *Pharmacosycea*, section *Pharmacosycea*) (Croat, 1978; Cruaud et al., 2012). Specifically, we studied *Pegoscapus tonduzi* (*Ficus citrifolia*), *P. hoffmeyer* A and B (*F. obtusifolia*), *P. gemellus* A and B (*F. popenoei*), *Tetrapus costaricanus* (*F. insipida*), and *T. americanus* (*F. maxima*) (Molbo et al., 2004; Wiebes, 1995). *F. obtusifolia* and *F. popenoei* are each pollinated by two cryptic fig wasp species that cannot be distinguished morphologically (Molbo et al., 2004;

Satler et al., 2020). For each fig species, one of the cryptic pollinator species is much more common than the other, and the wasps are sister species (*P. hoffmeyer* A and B) or closely related (*P. gemellus* A and B) (Molbo et al., 2004; Satler et al., 2020) so in this study, we did not try to separate them. Non-pollinating parasitic wasps were found on all fig species but only in two fig species were there a sufficient number of parasitic wasps in our samples to include them in the statistical analyses; *F. popenoei*: *Heterandrium* spp. and *Idarnes* “sensu stricto” (*Idarnes carme* spp. and *Idarnes flavicollis* spp. were combined and included; *Idarnes incerta* spp. were not included); and *F. insipida*: *Critogaster* spp. (Bouček, 1993; Cruaud et al., 2011; West & Herre, 1994) (see Appendix 1, Tables A1–A3 for an overview of the study species and sample sizes). Parasitic wasps were identified to genus level (Bouček, 1993). Lifespans and temperature responses of the different species within each genus might differ, so the results for the parasitic wasps should be interpreted with caution. Additional information about the biology of the parasitic wasp genera is included in Appendix 1, part A4.

2.3 | Survival experiment

To test the fitness effect of a temperature increase we quantified the lifespan of the wasps at 26, 28, 30, 32, 34, and 36°C (except for *P. hoffmeyer* [*F. obtusifolia*] where the highest temperature tested was 34°C). We selected 26°C as the baseline temperature in the survival models because the mean diurnal temperature of the air above the

FIGURE 2 Current and projected temperatures above the canopy at Barro Colorado Island. Temperatures were measured every 15 min at 48 m above the ground in the forest of Barro Colorado Island, Panama (Paton, 2020). The mean \pm 1 SD and 2 SD are indicated. (a) Data for the dry seasons 2002–2017, (b) projected dry season mean temperature \pm 1 SD under local predictions for 2100 (best and worst climate scenario; IPCC, 2021), (c) data for the wet seasons 2002–2017, (d) the measurement station on the Lutz-tower at 48 m is above the 40 m canopy, and at a relevant height for dispersing fig wasps (Harrison, 2003; Hubbell et al., 2014).



canopy at BCI is around 26°C (Paton, 2020). The experimental temperatures 26, 28, and 30°C fall within one standard deviation of the current diurnal temperatures (Figure 2). The experimental temperatures 32, 34, and 36°C reflect the regionally projected temperature increase scenarios of 1–4°C by the end of the 21st century (IPCC, 2021). The daytime relative humidity of the air above the canopy at BCI ranges between 83% and 94% with higher values during the wet season (Paton, 2020). In our survival experiments, we used a constant relative humidity of 85% to mimic local natural conditions, and because low relative humidity can decrease wasp lifespan (Dunn et al., 2008).

To obtain the wasps used in the survival experiments, figs containing wasps were collected at dawn, within a few hours of when the wasps would naturally emerge from their figs. Figs were opened in the lab and wasps allowed to emerge into petri dishes; one petri dish per fig. To ensure that the wasps in the experiments were of similar age, we included only figs that upon opening were at the stage where several male wasps, but fewer than 20 female wasps, had emerged from their galls. Wasps were allowed to emerge for 2 h; we then removed the fig from the petri dish so that no further wasps would be added to the cohort of wasps. The number of wasps in each petri dish was on average 84.6 (range 34.5–149.8); full details in Appendix 1, Table A2. We aimed to test wasp cohorts originating from 20 independent figs per temperature treatment per fig species, but in some species (*F. obtusifolia*, *F. insipida*) we were restricted by the number of figs that were available at the correct developmental stage. In total, we tested wasps from 122 (*F. citrifolia*), 56 (*F. obtusifolia*), 120 (*F. popenoei*), 64 (*F. insipida*), and 116 (*F. maxima*) figs (Table A3). The petri dishes were sealed and kept in growth chambers (*Percival I-36LL* and *Percival Intellus*) that mimicked natural environmental conditions for the wasps (12-h light/dark regime and a relative humidity of 85%) (Paton, 2020). The only thing that differed between the different treatments was the temperature. To further ensure identical conditions, temperature and humidity were confirmed using an independent thermometer and hygrometer that were regularly transferred between the chambers.

The number of dead wasps was counted approximately every 4 h for the duration of the experiment. When death rate was very high, wasps were counted every 2 h or even every hour (in *F. insipida* 36°C, *F. popenoei* 28, 32, 34, 36°C, and *F. maxima* 34, 36°C) in order to capture the shape of all survival curves. A wasp was considered dead when it did not move, even after gentle tapping of the petri dish. The experiment ended when either all wasps were dead or all pollinator wasps were dead, except in *F. maxima* 28°C where five pollinator wasps remained alive at the end of the experiment, and *F. obtusifolia* 28°C (48 pollinators remained alive), 30°C (108 pollinators remained alive), and 32°C (eight pollinators remained alive). These were included in the analysis as right-censored individuals.

2.4 | Statistical analyses

To visualize differences in lifespan across treatments, survival curves for each treatment and wasp species were computed using

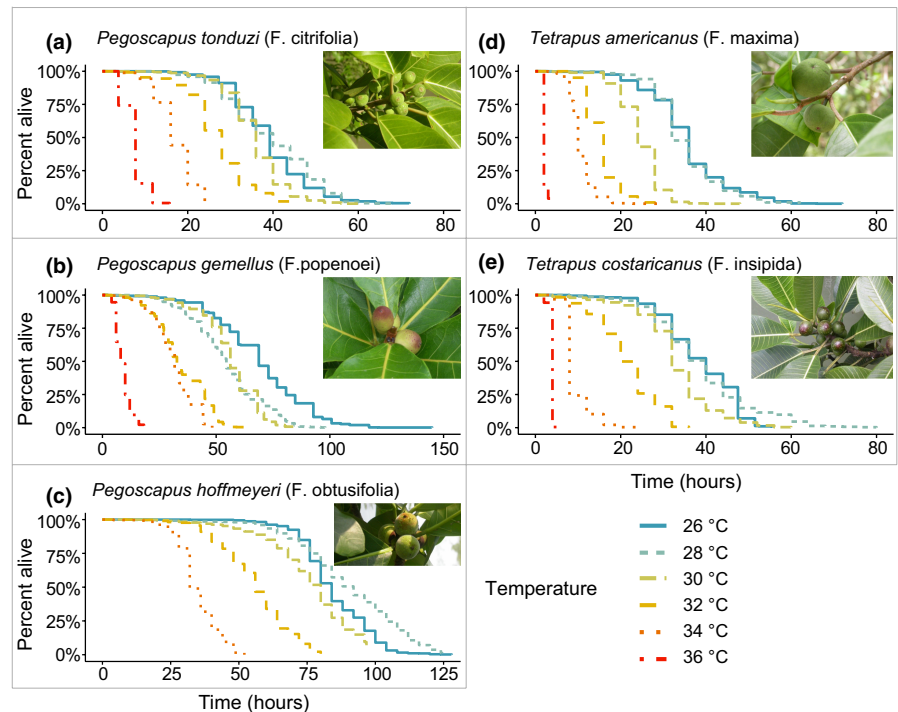
packages “survival” (ver. 3.1-12; Therneau & Lumley, 2020) and “survminer” (ver. 0.4.6; Kassambara et al., 2019) in R ver. 4.1.0 (R Core Team, 2021). To obtain the median lifespan across temperature treatments, the median lifespan duration and the 95% confidence interval were obtained using Kaplan–Meier survival analysis (package *survival*; function *survfit* and *surv_median*). We used a mixed effects Cox model (package “*coxme*”; Therneau, 2018) to model the effect of the temperature treatment on the survival probability of each species individually. The individual wasps inside each petri dish were not independent from each other because they shared their developmental environment (the fig) and were additionally potentially full sisters. We controlled for the variation between figs by including petri dish ID as a random factor in the survival model. We checked for all species if the random factor was significant by comparing the model with and without the random factor in an ANOVA; for all species, the random factor was significant ($p < .001$) except for *Heterandrium* ($p = .97$). The random factor was nevertheless included in all final models, as it corresponds to the experimental design. In the models for *Pegoscopus hoffmeyer*, *Tetrapus costaricanus*, *Pegoscopus gemellus*, and *Heterandrium*, the highest temperature treatment (34°C resp. 36°C) had to be excluded from the analysis because there was not sufficient variation within these treatments. In the survival models, we used 26°C as the baseline temperature as this is the temperature closest to the mean diurnal temperature except for the model of *Pegoscopus tonduzi* where a baseline temperature of 28°C was used due to a lack of enough variance in the 26°C treatment. Additionally, significant differences in lifespan between all pairwise temperature comparisons were investigated using Tukey contrasts with Bonferroni adjusted p -values, as implemented in the “multcomp” package (Bretz et al., 2010).

3 | RESULTS

3.1 | Pollinator response to temperature increase

For all pollinator species, we found a significant effect of temperature on lifespan (*P. tonduzi*: $\chi^2_5 = 14,709$, $p < .001$, *P. gemellus*: $\chi^2_4 = 8109.5$, $p < .001$, *P. hoffmeyer*: $\chi^2_5 = 381$, $p < .001$, *T. americanus*: $\chi^2_5 = 36,528$, $p < .001$, *T. costaricanus*: $\chi^2_4 = 2731$, $p < .001$). All tested pollinator wasp species had a significantly shorter lifespan in 30, 32, 34, and 36°C compared to the baseline 26°C ($p < .05$; Figure 3, Table 1; Appendix 1, Tables A5–A9). All pollinator species except *T. costaricanus* and *P. hoffmeyer* also had a significantly shorter lifespan in 28°C compared to 26°C ($p < .05$; Figure 3, Table 1; Appendix 1, Tables A5–A9), although the difference was no longer significant for *T. americanus* when testing all possible contrasts with Bonferroni adjusted p -values (Appendix 1, Table A8). The reduction in lifespan was stronger in higher temperatures. For example, whereas the median lifespan of *P. tonduzi* (*F. citrifolia*) was 39 h at 26°C, it was only 28 h (71%) at 32°C, 16 h (41%) at 34°C, and 7.8 h (20%) at 36°C (Figure 4). At 26°C, the median lifespan of pollinator fig wasps ranged from 36 to 84 h depending on species, whereas at 36°C it ranged from 2 to

FIGURE 3 The lifespan of fig wasp pollinators of five common Panamanian fig tree species was dramatically shortened at higher temperatures. The baseline temperature of 26°C reflects the mean diurnal temperature above the canopy in years 2002–2017 (Paton, 2020).



10 h (Figure 4). For some species (*Pegoscapus hoffmeyerii*, *Tetrapus costaricanus*, *Pegoscapus gemellus*), the highest temperature resulted in such a short lifespan that the reduced variation made it impossible to statistically model survival; these temperatures were therefore excluded from the final models.

3.2 | Parasite response to temperature increase

Due to a much smaller sample size of parasitic wasps, we could only include three parasitic wasp genera, from a total of two fig species, in the analyses: *Idarnes* (*F. popenoei*), *Heterandrium* (*F. popenoei*), and *Critogaster* (*F. insipida*). As for pollinators, increased temperatures dramatically reduced the lifespan of these parasitic wasps (Figure 5, Table 2; Appendix 1, Tables A10–A12). All parasitic genera had significantly shorter lifespan at temperatures higher than 30°C compared to at 26°C (Table 2; Appendix 1, Tables A10–A12). For example, the median lifespan of *Idarnes* decreased from 165.5 h at 26°C to only 24 h (15%) at 36°C (Figure 5). *Idarnes* had significantly shorter lifespan already at 28°C, whereas *Heterandrium* and *Critogaster* did not have a significant lifespan reduction until 32°C (Figure 5, Table 2). In all cases, the parasitic wasps on average lived longer than the pollinators of their respective host fig species (Figure 5).

4 | DISCUSSION

All studied fig wasp species showed a dramatic decrease in lifespan with increasing temperatures. Depending on the different CO₂ emission scenarios, temperatures in Panama are expected to rise 1–4°C by the end of the 21st century (IPCC, 2021). A 4°C increase

in temperature from the daytime mean 26–30°C reduced pollinator wasp median lifespan to 67% for some species. However, temperatures fluctuate during the day, and a 4°C increase could lead to daytime temperatures frequently reaching 33.8°C (1 SD above mean; Figure 2) (IPCC, 2021). This would severely impact fig pollinator lifespan, reducing the median lifespan to merely 20%–46% of the current lifespan.

Extreme weather events are also expected to increase under influence of global warming (IPCC, 2021; Kirtman et al., 2013). Exceptionally warm days, or even hours, would reduce wasps' lifespan dramatically. The median pollinator lifespan at 36°C was in our study reduced to merely 2–10 h (6%–19% of the baseline median lifespan), and in tropical Singapore to 1–4.5 h (4%–15% of baseline median lifespan) (Jevanandam et al., 2013). Pollinator fig wasps in temperate Australia, a more variable climate than the tropics, were slightly more tolerant to such high temperatures (50% median lifespan reduction at 35°C), but experienced a reduction to 14% median lifespan at 40°C (Sutton et al., 2018). Temperatures of 40°C already occur near the Australian study site approximately 5 days per year (Sutton et al., 2018). Extreme weather events such as these (36°C in tropics, 40°C in temperate regions) could both kill wasps while still inside the fig, and prevent dispersal of already emerged adults (Jevanandam et al., 2013; Sutton et al., 2018). Temperatures of 36°C are currently not occurring above the forest canopy in central Panama; the maximum measured temperature in 2002–2017 was 34.6°C (Paton, 2020). However, with a projected temperature increase of 4°C, temperatures above 36°C are expected to occur more frequently.

While all pollinator species showed a clear reduction in lifespan with increased temperatures, the reduction was particularly dramatic for those wasp species that had higher median lifespans at the

	Treatment (°C)	coef	exp(coef) (\pm SE)	z	p
<i>Pegoscapus tonduzi</i> <i>Ficus citrifolia</i> Events = 6744 n = 6744	26	0.46	1.59e+00 (\pm 0.20)	2.27	.023
	30	0.81	2.25e+00 (\pm 0.16)	5.22	<.001
	32	3.23	2.52e+01 (\pm 0.16)	20.61	<.001
	34	6.00	4.05e+02 (\pm 0.13)	45.86	<.001
	36	10.84	5.10e+04 (\pm 0.17)	64.70	<.001
<i>Pegoscapus gemellus</i> <i>Ficus popenoei</i> Events = 6524 n = 6524	28	1.44	4.23e+00 (\pm 0.16)	9.25	<.001
	30	1.28	3.58e+00 (\pm 0.13)	10.01	<.001
	32	4.48	8.83e+01 (\pm 0.20)	22.28	<.001
	34	4.60	9.97e+01 (\pm 0.14)	33.00	<.001
<i>Pegoscapus hoffmeyer</i> <i>Ficus obtusifolia</i> Events = 7439 n = 7603	28	-0.32	7.29e-01 (\pm 0.45)	-0.70	.480
	30	1.32	3.73e+00 (\pm 0.48)	2.72	.007
	32	3.46	3.18e+01 (\pm 0.47)	7.39	<.001
<i>Tetrapus americanus</i> <i>Ficus maxima</i> Events = 14,259 n = 14,264	28	0.29	1.33e+00 (\pm 0.13)	2.20	.028
	30	2.67	1.44e+01 (\pm 0.09)	30.89	<.001
	32	5.03	1.53e+02 (\pm 0.11)	48.06	<.001
	34	7.23	1.38e+03 (\pm 0.10)	71.67	<.001
	36	14.72	2.46e+06 (\pm 0.22)	67.11	<.001
<i>Tetrapus costaricanus</i> <i>Ficus insipida</i> Events = 1999 n = 1999	28	-0.11	8.93e-01 (\pm 0.50)	-0.22	.820
	30	0.98	2.67e+00 (\pm 0.39)	2.52	.012
	32	2.59	1.33e+01 (\pm 0.40)	6.46	<.001
	34	5.42	2.27e+02 (\pm 0.52)	10.48	<.001

Note: For *Pegoscapus tonduzi* a baseline of 28°C was used instead of 26°C. Coefficient is the estimated logarithm of hazard ratio, exponential (coef) transforms the log hazard ratio to hazard ratio between the compared treatments.

baseline temperature 26°C (Figure 5). Although we here have tested too few species to reliably compare across species, a trend seems to be that wasps of the genus *Pegoscapus* (pollinating fig trees of section *Urostigma Americana*) have higher median lifespans than wasps of the genus *Tetrapus* (pollinating fig trees of section *Pharmacosycea*). This may reflect density of the host fig species in a natural forest, but we currently do not have sufficient data to test this hypothesis. Within a genus, larger wasp species seem to have longer median lifespans than smaller wasp species (Herre, 1989; Jandér et al., 2016) but additional species would be needed to test this hypothesis.

The parasitic wasps also showed a clear reduction in lifespan with increasing temperatures (Figure 5). The parasitic wasp genera we tested had a 47%–141% higher median lifespan at baseline temperature than did the pollinator of their host fig species, despite being of similar body sizes as the pollinator. At 34°C, parasitic wasp lifespan was reduced to 14%–20%. Because the parasitic wasp genera and pollinators we tested were affected similarly by increasing temperatures, our data do not suggest that temperature increase per se would be expected to lead to a dramatic change in fig wasp community composition. However, our lifespan data for the parasitic wasps should be interpreted with caution. We grouped the parasitic wasps according to genus, but the individual species within a genus might respond differently to increased temperatures. Also, due to practicalities of the experimental setup, we were unable to feed the

TABLE 1 Results of the mixed effects cox model, comparing survival of each pollinator species at the different temperature treatments with the baseline treatment of 26°C.

wasps during the lifespan assays. This is not an issue for pollinators as they are known to not eat, but some parasitic fig wasp genera are known to have extended lifespans if food (sucrose solution) is offered (Compton et al., 1994; Ghara & Borges, 2010). However, the difference in lifespan with and without food might not be dramatic. Van Goor et al. (2018, 2021) found a median lifespan of 168h when offering sugar water to the parasitic wasps *Idarnes flavicollis* ssp. of *Ficus petiolaris* at 22°C (J. van Goor personal communication, 2021). Additionally, a pilot study by Van Goor in Panama found median lifespans of *Idarnes carme* ssp. and *Idarnes flavicollis* ssp. of *F. popenoei*, at ambient temperature with food, to be 100–130h, compared to the median lifespan of 166h we found for *Idarnes* of *F. popenoei* at 26°C without food (J. Van Goor personal communication, 2021; Figure 5). Although our methods differ, therefore making direct comparison impossible, it seems that access to food may not dramatically prolong life for *Idarnes*, and our lifespan estimates for these parasites may be valid approximations.

A reduced lifespan of pollinator wasps is expected to reduce pollination levels and pollen dispersal of fig trees. Despite their short lives (2–3 days), fig wasps disperse large distances because fig trees typically grow in low densities, even for tropical trees (Mawdsley et al., 1998; Nason et al., 1996, 1998; Todzia, 1986; Ware & Compton, 1994). For example, in central Panama fig wasps commonly disperse 10 km, but on other continents occasional dispersal

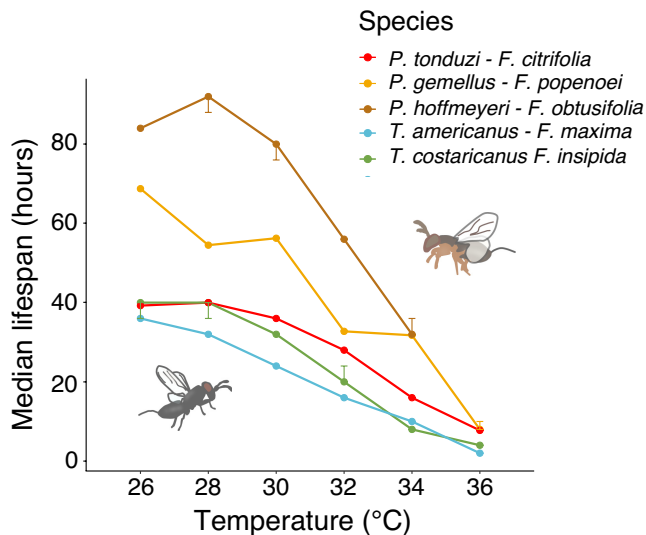


FIGURE 4 The median lifespan of pollinator fig wasps decreased with increasing temperatures (Kaplan–Meier survival analysis). Error bars represent 95% confidence intervals. Whereas lifespan maximum was either at 26 or 28°C for the different species, all tested pollinator fig wasps had significantly reduced median lifespans at 30°C and above.

distances up to 160km have been recorded (Ahmed et al., 2009; Nason et al., 1996). If fewer fig wasps successfully disperse to flowering trees, fewer of the figs will be pollinated thus producing fewer fruits for the frugivores (Herre, 1989; Jandér et al., 2016; Shanahan et al., 2001). Additionally, each fig inflorescence is likely to be pollinated by fewer foundress fig wasps, thus reducing overall seed numbers within each fig (Herre, 1989; Jandér et al., 2012; Jandér & Steidinger, 2017) and increasing inbreeding of the wasps (Herre, 1985; Herre et al., 2008; Molbo et al., 2004). Further adding to the problem, logging practices that reduce South American forest area with 2.6 million hectares per year cause forest fragmentation, thus further increasing distances between fig trees (Broadbent et al., 2008; FAO, 2020; Hansen et al., 2013; Mawdsley et al., 1998). Logging also increases the local temperature by biomass removal—the air above logged areas can be 5–10°C hotter than nearby intact forest environment (Blonder et al., 2018). Forest fragmentation therefore not only increases distances between trees, but might also reduce wasp lifespan even further. Forest fragmentation in combination with global warming could therefore be devastating for the continued pollination of fig trees.

Highly specialized and obligate mutualisms are expected to be more vulnerable to the effects of rapid environmental change than relationships based on more generalist partners (Kiers et al., 2010; Vidal et al., 2021). In highly obligate mutualisms like the fig tree–fig wasp mutualisms, behavioral changes, plasticity, or rapid adaptation may be essential for the continuation of the mutualism. Behavioral changes of the pollinator fig wasps would be the fastest response, for example by emerging from figs earlier in the morning or by dispersing during the night like some species in Australia and East-Asia (Harrison, 2003). However, because wind speeds are lower at

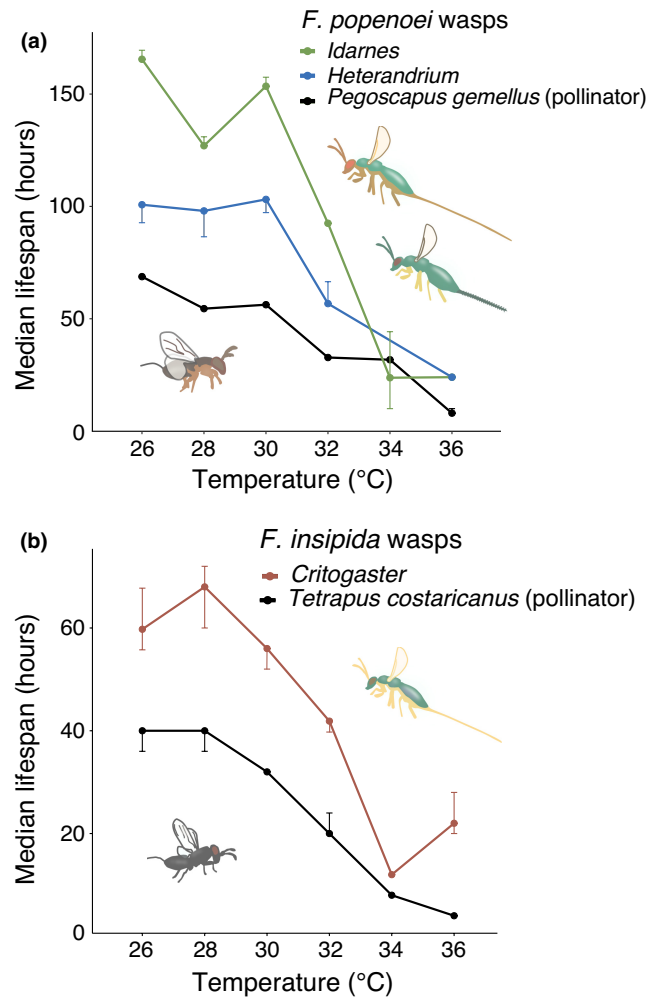


FIGURE 5 The median lifespan of pollinators and parasites of (a) *F. popenoei* and (b) *F. insipida* decreased with increasing temperatures (Kaplan–Meier survival analysis). Error bars represent 95% confidence intervals. Whereas maximum lifespan was either at 26, 28, or 30°C for the different species/genera, all tested parasitic wasps had significantly reduced median lifespans at 32°C and above. Wasp images are approximations for illustrative purposes.

night, this would likely compromise wasps' dispersal distances, and therefore the success rate of finding a flowering tree (Harrison & Rasplus, 2006; Kumagai et al., 2001; Paton, 2020). Rapid adaptation might be a possibility, favored by the short generation time of the wasps. However, several of these pollinator fig wasp species are highly inbred due to frequent sibling matings (inbreeding coefficient F up to 0.85; Molbo et al., 2004), reducing genetic variability. Nevertheless, in our experiments, as in Jevanandam et al. (2013), there were differences in wasp lifespan across different wasp sibling groups (wasp cohorts emerging from the same fig). This variation could be caused by either environmental or genetic factors, or a combination. If sufficient genetic variation is present, adaptation can be fast: studies of temperate mosquitoes showed that adaptation to heat can occur within as few as three generations (Foucault et al., 2018). However, tropical insects may be less capable of adapting as many already live at their thermal maxima, and ectotherm

TABLE 2 Results of the mixed effects cox model, comparing survival of each parasitic species at the different temperature treatments with the baseline treatment of 26°C.

	Treatment (°C)	coef	exp(coef) (±SE)	z	p
<i>Idarnes carme</i> spp. and <i>Idarnes flavicollis</i> spp.	28	2.503	1.22e+01 (±0.16)	15.73	<.001
<i>Ficus popenoei</i>	30	1.11	3.02e+00 (±0.20)	5.51	<.001
Events = 3750	32	4.51	9.13e+01 (±0.21)	21.51	<.001
n = 4220	34	9.34	1.14e+04 (±0.49)	18.90	<.001
	36	10.62	4.07e+04 (±0.35)	30.15	<.001
<i>Heterandrium</i> spp.	28	0.39	1.48e+00 (±0.56)	0.69	.490
<i>Ficus popenoei</i>	30	0.30	1.34e+00 (±0.85)	0.35	.730
Events = 40	32	2.49	1.21e+02 (±0.64)	3.89	<.001
n = 40					
<i>Critogaster</i> spp.	28	-0.96	0.38e+00 (±0.58)	-1.67	.096
<i>Ficus insipida</i>	30	0.45	1.57e+00 (±0.63)	0.72	.470
Events = 244	32	2.61	1.36e+01 (±0.62)	4.24	<.001
n = 262	34	6.38	5.93e+02 (±0.86)	7.39	<.001
	36	4.83	1.25e+02 (±0.64)	7.58	<.001

Note: Coefficient is the estimated logarithm of hazard ratio, exponential (coef) transforms the log hazard ratio to hazard ratio between the compared treatments.

thermal limits seem to evolve at a rate of only 0.8°C per million years (Bennett et al., 2021; García-Robledo & Baer, 2021; Sunday et al., 2014). Further studies on the possibility of tropical pollinators' adaptation to increasing temperatures would be valuable.

In conclusion, the projected local temperature increases in Panama could seriously decrease the lifespan of fig tree pollinators. By reducing the lifespan of fig wasps and therefore the chances of successful pollination of fig trees, increasing temperatures add an additional threat to this keystone resource of tropical forests. Anthropogenic ecosystem changes in the form of habitat destruction, fragmentation, and temperature increases, require species to cope with new situations. Particular attention should be paid to species in tight mutualistic relationships as they are vulnerable also to effects on their mutualistic partners.

AUTHOR CONTRIBUTIONS

Lisette van Kolschoten: Formal analysis (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Lovisa Dück:** Investigation (lead); writing – review and editing (supporting). **Martin I. Lind:** Formal analysis (equal); writing – review and editing (supporting). **K. Charlotte Jandér:** Conceptualization (lead); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (lead).

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CONFLICT OF INTEREST

All authors hereby state that we have no competing interests to declare.

DATA AVAILABILITY STATEMENT

Wasp lifespan data and R code are available on FigShare (DOI: <https://doi.org/10.6084/m9.figshare.20268552.v2>).

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APPENDIX 1

TABLE A1 Overview of the different species included in this study.

Tree	Tree species	Pollinator	Parasite
Subgenus <i>Urostigma</i> Section <i>Americana</i>	<i>Ficus citrifolia</i> (Molbo et al., 2004; Wiebes, 1995)	<i>Pegoscapus tonduzi</i>	<i>Idarnes</i>
	<i>Ficus obtusifolia</i> (Molbo et al., 2004; Satler et al., 2020; Wiebes, 1995)	<i>Pegoscapus hoffmeyerii</i> A <i>Pegoscapus hoffmeyerii</i> B	<i>Idarnes</i>
	<i>Ficus popenoei</i> (Molbo et al., 2004; Satler et al., 2020; Wiebes, 1995)	<i>Pegoscapus gemellus</i> A <i>Pegoscapus gemellus</i> B	<i>Idarnes</i> , <i>Heterandrium</i>
Subgenus <i>Pharmacosycea</i> Section <i>Pharmacosycea</i>	<i>Ficus insipida</i> (Molbo et al., 2004; Wiebes, 1995)	<i>Tetrapus costaricanus</i>	<i>Critogaster</i>
	<i>Ficus maxima</i> (Molbo et al., 2004; Wiebes, 1995)	<i>Tetrapus americanus</i>	<i>Critogaster</i>

Tree species	Figs (n)	Pollinator wasps (n)	Mean number of pollinator wasps per fig (range)	Parasitic wasps (n)
<i>Ficus citrifolia</i>	122	6744	55.28 (18–153)	1
<i>Ficus obtusifolia</i>	56	8391	149.84 (12–365)	6
<i>Ficus popenoei</i>	120	7260	60.50 (6–271)	4287
<i>Ficus insipida</i>	64	2208	34.50 (2–190)	262
<i>Ficus maxima</i>	116	14,264	122.97 (28–234)	159

Note: The number of parasitic wasps indicated here are those of the genera *Idarnes*, *Heterandrium*, and *Critogaster*; additional parasitic wasps genera were present but not included in the study.

TABLE A2 Summary of the overall sample sizes in this study. See Table A3 for the number of figs (i.e., wasp cohorts) and individual wasps in each temperature treatment.

TABLE A3 Number of figs (ie wasp cohorts) and individual wasps included in the analyses.

Tree species	Sample size (n)	26°C	28°C	30°C	32°C	34°C	36°C	Total
<i>Ficus citrifolia</i>	Figs	20	20	20	20	20	22	122
	Pollinators	957	1373	1342	852	1101	1120	6744
<i>Ficus obtusifolia</i>	Figs	10	15	11	13	15		56
	Pollinators	1140	3740	1540	1183	788		8391
<i>Ficus popenoei</i>	Figs	20	20	20	21	20	15	120
	Pollinators	1399	2813	1483	2341	1282	1881	7260
	Parasites <i>Idarnes</i>	320	472	730	1576	15	1107	4220
	Parasites <i>Heterandrium</i>	6	9	2	23	0	27	67
<i>Ficus insipida</i>	Figs	10	5	13	12	5	11	64
	Pollinators	440	360	576	496	293	318	2208
	Parasites <i>Critogaster</i>	40	54	31	28	7	104	262
<i>Ficus maxima</i>	Figs	20	20	20	20	20	20	116
	Pollinators	2146	2871	2623	1612	2330	2681	14,264

A4. | Biology of the parasitic wasp genera

Parasitic fig wasps, also referred to as non-pollinating fig wasps (NPFW), are wasp species that obligately rely on figs for their reproduction but do not provide any pollination services to the fig (Bouček, 1993; Bronstein, 1991; Marussich & Machado, 2007; West & Herre, 1994). New world parasitic fig wasps all oviposit from the external surface of the fig wall to reach the flowers or other tissues within (West et al., 1996). *Idarnes carme* spp., *Idarnes flavicollis* spp., and *Critogaster* spp. are in direct competition with the pollinator wasps over available flowers (Bronstein, 1991; Canesqui da Costa & Graciolli, 2010; Elias et al., 2008; Gordh, 1975; Marussich & Machado, 2007; Santinelo Pereira et al., 2007; West et al., 1996). *Idarnes carme* spp. lay their eggs in galls with developing pollinator wasps inside (Elias et al., 2008), whereas *Idarnes flavicollis* spp. gall the flowers (Elias et al., 2012). In contrast, *Heterandrium* spp. lay their eggs directly into the fig wall where they form galls (Bronstein, 1991; Elias et al., 2008; West et al., 1996). Parasitic fig wasps are generally less species specific than the pollinator wasps (Farache et al., 2018; Marussich & Machado, 2007).

TABLE A5 Multiple comparisons of all pairwise temperature treatments for the pollinator *Pegoscapus tonduzi* in *Ficus citrifolia*, using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	<i>z</i>	<i>p</i>
26°C – 28°C	0.461	0.203	2.28	.193
30°C – 28°C	0.809	0.155	5.22	<.001
32°C – 28°C	3.227	0.157	20.61	<.001
34°C – 28°C	6.004	0.131	45.86	<.001
36°C – 28°C	10.839	0.168	64.70	<.001
30°C – 26°C	0.348	0.216	1.62	.570
32°C – 26°C	2.766	0.178	15.57	<.001
34°C – 26°C	5.544	0.166	33.39	<.001
36°C – 26°C	10.379	0.196	52.86	<.001
32°C – 30°C	2.418	0.169	14.35	<.001
34°C – 30°C	5.195	0.134	38.78	<.001
36°C – 30°C	10.031	0.173	58.01	<.001
34°C – 32°C	2.778	0.133	20.93	<.001
36°C – 32°C	7.613	0.160	47.63	<.001
36°C – 34°C	4.835	0.124	38.98	<.001

Note: Significant contrasts are indicated in bold.

TABLE A6 Multiple comparisons of all pairwise temperature treatments for the pollinator *Pegoscapus gemellus* in *Ficus popenoei* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	<i>z</i>	<i>p</i>
28°C – 26°C	1.443	0.156	9.25	<.001
30°C – 26°C	1.275	0.127	10.01	<.001
32°C – 26°C	4.481	0.201	22.28	<.001
34°C – 26°C	4.602	0.139	33.01	<.001
30°C – 28°C	-0.168	0.155	-1.09	.793
32°C – 28°C	3.038	0.214	14.21	<.001
34°C – 28°C	3.159	0.152	20.77	<.001
32°C – 30°C	3.206	0.200	16.03	<.001
34°C – 30°C	3.327	0.127	26.12	<.001
34°C – 32°C	0.122	0.255	0.48	.988

Note: Significant contrasts are indicated in bold.

TABLE A7 Multiple comparisons of all pairwise temperature treatments for the pollinator *Pegoscapus hoffmeyer* in *Ficus obtusifolia* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	<i>z</i>	<i>p</i>
28°C – 26°C	-0.317	0.451	-0.70	.896
30°C – 26°C	1.316	0.484	2.72	.034
32°C – 26°C	3.458	0.468	7.39	<.001
30°C – 28°C	1.633	0.440	3.72	.001
32°C – 28°C	3.775	0.421	8.96	<.001
32°C – 30°C	2.142	0.456	4.70	<.001

Note: Significant contrasts are indicated in bold.

TABLE A8 Multiple comparisons of all pairwise temperature treatments for the pollinator *Tetrapus americanus* in *Ficus maxima* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	<i>z</i>	<i>p</i>
28°C – 26°C	0.288	0.131	2.20	.210
30°C – 26°C	2.668	0.086	30.89	<.001
32°C – 26°C	5.032	0.105	48.06	<.001
34°C – 26°C	7.230	0.101	71.67	<.001
36°C – 26°C	14.717	0.219	67.11	<.001
30°C – 28°C	2.380	0.097	24.54	<.001
32°C – 28°C	4.743	0.090	52.70	<.001
34°C – 28°C	6.942	0.095	73.27	<.001
36°C – 28°C	14.429	0.216	66.73	<.001
32°C – 30°C	2.364	0.088	26.86	<.001
34°C – 30°C	4.562	0.073	62.15	<.001
36°C – 30°C	12.049	0.208	57.81	<.001
34°C – 32°C	2.199	0.085	25.93	<.001
36°C – 32°C	9.686	0.210	46.09	<.001
36°C – 34°C	7.487	0.198	37.80	<.001

Note: Significant contrasts are indicated in bold.

TABLE A9 Multiple comparisons of all pairwise temperature treatments for the pollinator *Tetrapus costaricanus* in *Ficus insipida* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	z	p
28°C – 26°C	-0.114	0.507	-0.22	.999
30°C – 26°C	0.982	0.391	2.52	.085
32°C – 26°C	2.585	0.400	6.46	<.001
34°C – 26°C	5.424	0.518	10.48	<.001
30°C – 28°C	1.096	0.488	2.25	.159
32°C – 28°C	2.698	0.496	5.44	<.001
34°C – 28°C	5.537	0.595	9.31	<.001
32°C – 30°C	1.603	0.372	4.30	<.001
34°C – 30°C	4.442	0.496	8.96	<.001
34°C – 32°C	2.839	0.498	5.70	<.001

Note: Significant contrasts are indicated in bold.

TABLE A10 Multiple comparisons of all pairwise temperature treatments for the parasitic wasps *Idarnes carme* spp. and *Idarnes flavicollis* spp. in *Ficus popenoei* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	z	p
28°C – 26°C	2.503	0.159	15.73	<.001
30°C – 26°C	1.105	0.201	5.51	<.001
32°C – 26°C	4.514	0.210	21.51	<.001
34°C – 26°C	9.341	0.494	18.90	<.001
36°C – 26°C	10.615	0.352	30.15	<.001
30°C – 28°C	-1.398	0.185	-7.58	<.001
32°C – 28°C	2.011	0.186	10.82	<.001
34°C – 28°C	6.838	0.482	14.18	<.001
36°C – 28°C	8.111	0.335	24.21	<.001
32°C – 30°C	3.409	0.204	16.74	<.001
34°C – 30°C	8.236	0.493	16.72	<.001
36°C – 30°C	9.510	0.350	27.20	<.001
34°C – 32°C	4.827	0.489	9.87	<.001
36°C – 32°C	6.101	0.336	18.17	<.001
36°C – 34°C	1.273	0.536	2.38	.145

Note: Significant contrasts are indicated in bold.

TABLE A11 Multiple comparisons of all pairwise temperature treatments for the parasitic wasp *Heterandrium* spp. in *Ficus popenoei* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	z	p
28°C – 26°C	0.390	0.561	0.70	.896
30°C – 26°C	0.295	0.851	0.35	.985
32°C – 26°C	2.494	0.641	3.89	<.001
30°C – 28°C	-0.095	0.797	-0.12	.999
32°C – 28°C	2.104	0.547	3.84	<.001
32°C – 30°C	2.199	0.829	2.65	.038

Note: Significant contrasts are indicated in bold.

TABLE A12 Multiple comparisons of all pairwise temperature treatments for the parasitic wasp *Critogaster* spp. in *Ficus insipida* using Tukey contrasts with Bonferroni adjusted *p*-values.

Contrast	Estimate	SE	z	p
28°C – 26°C	-0.959	0.576	-1.67	.542
30°C – 26°C	0.448	0.627	0.72	.979
32°C – 26°C	2.608	0.615	4.24	<.001
34°C – 26°C	6.384	0.863	7.39	<.001
36°C – 26°C	4.827	0.637	7.58	<.001
30°C – 28°C	1.408	0.612	2.30	.185
32°C – 28°C	3.568	0.603	5.92	<.001
34°C – 28°C	7.344	0.855	8.59	<.001
36°C – 28°C	5.786	0.625	9.26	<.001
32°C – 30°C	2.160	0.593	3.64	.003
34°C – 30°C	5.936	0.846	7.02	<.001
36°C – 30°C	4.379	0.613	7.15	<.001
34°C – 32°C	3.776	0.762	4.95	<.001
36°C – 32°C	2.219	0.493	4.50	<.001
36°C – 34°C	-1.558	0.691	-2.25	.205

Note: Significant contrasts are indicated in bold.