Non-pollinating wasps distort the sex ratio of pollinating fig wasps

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In fig wasps, mating occurs among the offspring of one or a few foundress mothers within the fig, from which the mated females disperse to found new broods. Under these conditions, males will compete with each other for mating, and such local mate competition can result in female-biased sex ratios. In addition to pollinating wasps, non-pollinating wasp species are also associated with figs and develop in flower ovaries or parasitize the larvae of primary galling wasps. While studying the fig wasp *Pegoscapus tonduzi*, which pollinates *Ficus citrifolia* in Brazil, we examined the influence of non-pollinating fig wasps on the sex ratio of species that pollinate *F. citrifolia* to determine whether the presence of non-pollinating wasps resulted in a distorted sex ratio. There was a positive relationship between the sex ratio of *P. tonduzi* and the number of non-pollinating wasps that was independent of the number of foundresses and brood size. In addition, the number of non-pollinating wasps correlated negatively with the number of pollinating females, but was not significantly related to the number of pollinating males. This finding suggested that non-pollinating wasps had a direct effect in distorting the sex ratio of *P. tonduzi* broods. Our results indicate that the secondary sex ratio may not precisely reflect the primary sex ratio when there is a high infestation of non-pollinating fig wasps.

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Sex allocation has been the subject of theoretical and empirical studies in several groups of organisms (Werren 1980, Charnov 1982, Frank 1985, Herre 1985, 1987, Martins et al. 1999, West et al. 1999, 2000a, 2000b). Fisher (1930) showed that in large, randomly mating populations, frequency-dependent selection will lead to equal parental investment in the two sexes and, generally, an even sex ratio. Hamilton (1967) later pointed out that in many organisms mating occurs among the offspring of one or a few foundress mothers in isolated subpopulations (broods) from which the mated females disperse to found new broods. Under these conditions, local mate competition (LMC), in which males compete with each other for matings, will result in female-biased sex ratios. However, the same population structure that favors LMC also increases inbreeding and mother–offspring relatedness because of mating among siblings (Frank 1985, Herre 1985). In haplodiploid organisms, the haploid males derive all of their genome from the unfertilized eggs of the diploid mother such that inbreeding increases the relatedness of mothers to daughters to a greater extent than that of mothers to sons. This asymmetry in relatedness can result in female-biased sex ratios, independently of any effects of LMC (Herre 1985).

Several studies have reported female-biased sex ratios in fig wasps, and these insects have been considered as a model to study LMC (Hamilton 1979, Frank 1985, Herre 1985, 1987, West and Herre 1998), although some theoretical assumptions may be violated (Kathuria et al. 1999, Kinoshita et al. 2002, Moore et al. 2002). Studies of the sex ratio of pollinating fig wasps usually assess the

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secondary offspring sex ratios, e.g. the proportion of males that actually reach adulthood. Although mortality during offspring development may distort the primary sex ratio allocated by the mother (Green et al. 1982), the secondary sex ratio of fig wasps is considered to be a good reflection of the primary sex ratio since larval mortality is apparently not high (Kathuria et al. 1999).

Some non-pollinating wasps exert a negative effect on the offspring of pollinating wasps (West and Herre 1994, Kerdelhué and Rasplus 1996, West et al. 1996, Kerdelhué et al. 2000). Non-pollinating fig wasps may also develop at relatively high densities in the figs of some fig species (Kerdelhué et al. 2000, R. A. S. Pereira, unpubl.). High densities of non-pollinating wasps could distort the sex ratio of pollinating species if non-pollinators interfere with LMC or preferentially cause the mortality of one sex of the pollinators. If sex-related effects occur, a negative relationship between the females of pollinating species and non-pollinating wasps would be expected, with little or no relationship between pollinating males and non-pollinating wasps.

In this paper, we examined the effect of non-pollinating fig wasps on the sex ratio of a fig wasp species that pollinates *F. citrifolia* in Brazil. We also assessed the influence of a distorted sex ratio on studies of sex allocation based on the secondary sex ratio since foundress pollinating wasps may not consistently produce secondary sex ratios because of non-random mortality.

Biology of fig-wasp interactions

Each species of fig is pollinated by a single, species-specific pollinating wasp (Ramírez 1970). However, exceptions to this strict one-to-one association between figs and their pollinators appear to be more common than previously believed (Cook and Rasplus 2003). When the fig flowers are receptive, mated, pollen-bearing, female pollinating wasps (foundresses) arrive at the tree and several of them enter the enclosed inflorescence (or fig) through a bract-lined pore known as the ostiole. The foundresses then pollinate the receptive uniovulate flowers and probe the flowers with their ovipositors in an attempt to lay eggs in the ovaries (Galil 1977). Sex determination in fig wasps is haplodiploid so that females can control the sex of their offspring by deciding whether or not to fertilize the eggs (Cook 1993). With few exceptions, the foundress wasps subsequently die inside the fig, and their bodies can be counted to determine the number of foundresses that potentially pollinated and laid eggs in each fig (Herre 1996).

During the following weeks, the fig seeds and the wasp larvae develop within the figs. Immediately before the final ripening of the fig, the wingless male wasps chew their way out of the galls in which they have developed and then crawl around inside the fig in search of galls containing conspecific female wasps. The males then chew open these galls and mate with the females. The females eventually emerge from their galls and gather pollen before leaving through a hole in the fig wall chewed by the male wasps (Galil 1977). In addition to pollinating wasps, non-pollinating wasp species are also normally associated with fig inflorescences and develop in flower ovaries or parasitize the larvae of primary galling wasps (Janzen 1979, Bronstein 1992).

Material and methods

Study species

In Brazil, *Ficus citrifolia* is pollinated by *Pegoscapus tonduzi* (Chalcidoidea: Agaonidae) and is also associated with 14 non-pollinating chalcid wasp species (Pereira et al. 2000, referred to as *F. eximia*). Among these non-pollinating species, the genus *Idarnes* is the most represented, with three species having wingless males (two of the *carme* and one of the *flavicollis* group) and one species having winged males (*incerta* group); the levels of infestation by these species are often much greater than for *P. tonduzi*. Based on indirect evidence, all *Idarnes* species are thought to be phytophagous gallers (West et al. 1996). We have evidence that species within the *I. flavicollis* and the *I. incerta* groups are indeed gallers while species within the *I. carme* group are cleptoparasites (sensu Abdurahiman and Joseph 1978). Species of the *flavicollis* and *incerta* groups colonize figs immediately before, or simultaneously with, pollinating foundresses and are able to develop in experimental pollinator-excluded figs (R. A. S. Pereira and A. O. Menezes Jr., unpubl.). Species of the *I. carme* group colonize figs after pollination and oviposit in galls initiated by pollinating wasps.

Data collection and analysis

To study the *P. tonduzi* offspring sex ratio, 25–40 figs were sampled from each of eight *F. citrifolia* trees (total of 210 figs) in the surroundings of the State University of Campinas (22°54′S, 47°03′W) from April 1999 to August 2001. The figs were sampled near the wasp emergence phase before any wasp had left the fig. The fig diameter was measured to the nearest 0.1 mm, and each fig was then cut open and the number of foundresses counted. The fig halves were tied with a piece of wire, placed individually in plastic flasks, and all the wasps were allowed to emerge before being frozen. Later, the number and sex of each species of wasp were recorded for each

fig. In addition, the number of seeds was counted in one half of each fig.

Data from previous studies (nearly 450 figs from seven crops sampled from October 1992 to August 1993 on the campus of Londrina State University, 23°18′S, 51°09′W), and eight crops sampled from September 1996 to April 1998 near the campus of the State University of Campinas in which the number of foundresses was not recorded were included along with the present data. In this dataset, the fig diameters were also measured and the figs were cut into four equal parts, with the seeds being counted in one quarter.

Figs with a high proportion of males (0.5–1) were assumed to have been founded by sperm-depleted females (West et al. 1997, 1998). These figs, and figs with low a level of infestation (*P. tonduzi* broods with <30 insects), were not included in the analysis. The sex ratio (proportion of males) of *P. tonduzi* versus the number of non-pollinating wasps was analyzed using a linear model in the S-Plus 6.1© Insightful Co. statistical package (S-Plus 2001). Non-pollinating wasps were divided into three categories: *Idarnes* sp. 3 (*flavicollis* group), *Idarnes carme* group (two species lumped together) and "others" (all remaining wasp species, including a species of the *Idarnes incerta* group and the genera *Aepocerus, Eurytoma, Heterandrium, Physothorax* and *Torymus*). The *Idarnes* species in the *carme* group and the *Idarnes* sp. 3 (*flavicollis* group) were kept separate because of ecological differences between these two groups. To control for confounding variables, the model initially included the following co-variates: crop (factor variable, represented by the figs collected in one season from a single tree), fig volume (estimated by the fig diameter, assuming the shape of a sphere), the total number of seeds (the total number of seeds produced by each fig was obtained by multiplying the seed counts by two or four, depending on whether the counts were from one half or one quarter of a fig), and the *P. tonduzi* brood size (total number of *P. tonduzi* that emerged per fig).

Similar analyses were done separately with the number of females and the number of males of *P. tonduzi* as response variables to assess any sex-selective effect of non-pollinating wasps on the pollinating progeny. Crop assignment, fig volume, number of seeds and number of *P. tonduzi* belonging to the other sex (number of males when the response variable was the number of females and vice-versa) were included as co-variates in the model. The explanatory variables were retained in the model, depending on their statistical weight.

The sex ratio data were initially analyzed by assuming binomially distributed errors. However, the ratio of the residual deviance to the residual degrees of freedom was around five, indicating considerable overdispersion and suggesting that the assumption of binomial errors was inadequate (Crawley 1993). Consequently, we analyzed

the data by assuming normal errors. The sex ratios were arcsine square root transformed and counts of *P. tonduzi* offspring were square root transformed (Zar 1996). In all of the analyses, the residuals showed no obvious patterns and plots of the ranked residuals against the standard normal deviates were close to straight lines, thus supporting the assumption of normal errors.

In the data subset in which the foundress number was quantified (210 figs), the previous analyses included foundress number as co-variate to control its confounding effect on the sex ratio and brood size.

Results

Sex ratio vs non-pollinating wasps

The characteristics of the sampled figs are shown in Table 1. The mean proportion of males in the *P. tonduzi* broods was significantly higher in figs infested by non-pollinating wasps (≥ 10 individuals, Fig. 1). After controlling for crop differences, the brood sex ratio showed a significant positive relationship with the number of *P. tonduzi* and with the number of wasps belonging to the *carme* and *flavicollis* groups of the genus *Idarnes*, whereas for the other non-pollinating species lumped together the relationship was almost positively significant (Table 2). Fig volume and the number of seeds were not significantly related and were excluded from the final model. In all subsequent linear model analyses, the inclusion of "crop" as a co-variate was also significant. Consequently, the variable "crop" was retained in all models in order to control for crop differences.

In the data subset for which the foundress number was quantified (210 figs), none of the non-pollinating species categories were significantly related to the *P. tonduzi* sex ratio (Table 3a). However, even when foundress number was excluded from the model, there were no significant

Table 1. Characteristics of the *Ficus citrifolia* figs.

| Variables	No. of fig crops sampled	No. of figs sampled	Mean ± SD
Foundress number	8	210	2.4 ± 2.4
Fig diameter (mm)	19	660	16.7 ± 2.0
Number of seeds	19	660	197.0 ± 78.3
P. tonduzi brood size	19	660	196.1 ± 84.0
Number of *P. tonduzi* females	19	660	175.0 ± 72.9
Number of *P. tonduzi* males	19	660	21.0 ± 19.0
Number of *Idarnes* (*carme* group)	19	660	14.7 ± 21.3
Number of *Idarnes* sp. 3 (*flavicollis* group)	19	660	8.3 ± 16.7
Number of other species	19	660	2.4 ± 5.6
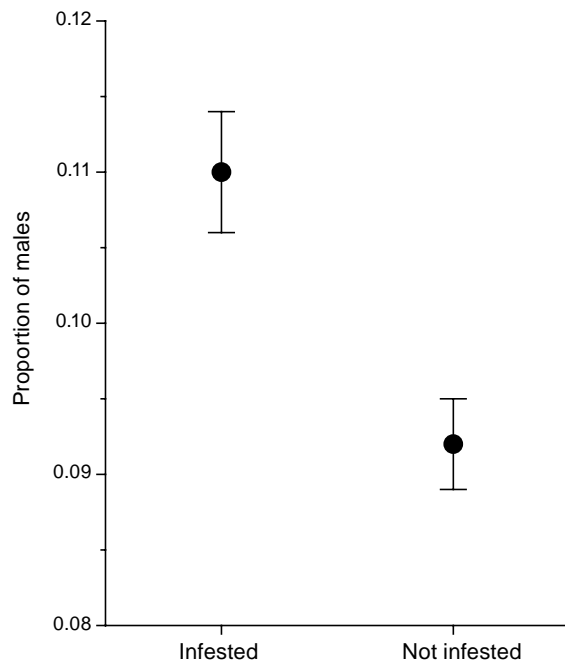
Fig. 1. Sex ratios (proportion of males) of *Pegoscapus tonduzi* broods from figs infested ($\geq$ 10 individuals) and not infested by non-pollinating fig wasps. The bars represent the standard error of the means. Infested: n = 363 figs; not infested: n = 297 figs; t test$_{658}$ = 3.67, prob. = 0.0003.

relationships between non-pollinating wasps and the sex ratio (Table 3b). These findings indicate that non-pollinating species were not significantly related to the sex ratio in the data subset. In addition, the number of foundresses did not appear to be driving the relationship since none of the non-pollinating wasp categories analyzed in the data subset was positively correlated with the number of foundresses (*Idarnes* sp. 3: r = −0.132, t_{208} = −1.91, probability = 0.057; *Idarnes* (*carme* group): r = 0.091, t_{208} = 1.32, probability = 0.188; others: r = −0.042, t_{208} = −0.61, probability = 0.544).

Table 2. Linear model of the arcsine of the square root of the *Pegoscapus tonduzi* brood sex ratio (dependent variable) and groups of wasp species associated with *Ficus citrifolia* (explanatory variables). "Crop" was included as a co-variate and its variation was significant in the model (F_{18} = 15.22; prob. $< 10^{-4}$). *P. tonduzi* brood sizes were used as weights in the analysis. Model statistics: adjusted R^2 = 0.384; $F_{22,637}$ = 19.66; prob. $< 10^{-4}$; n = 660 figs.

Effect	Standardized coefficient	t	Prob.
Constant	0.000	16.381	$< 10^{-4}$
P. tonduzi	0.360	7.836	$< 10^{-4}$
Idarnes (*carme* group)	0.145	2.951	0.0033
Idarnes sp. 3	0.082	1.9457	0.0521
Other species	0.084	1.787	0.0744

Number of females and males vs non-pollinating wasps

The number of female offspring of *P. tonduzi* was negatively related to the number of non-pollinating wasps (Table 4a). Within the data subset, the number of *P. tonduzi* females was negatively related to the number of wasps of the *Idarnes carme* group, whereas the number of foundresses, the number of *Idarnes* sp. 3, and the number of other non-pollinating species were not significantly related (Table 5a). In contrast, the number of male offspring was not significantly related to the number of non-pollinating wasps in the overall dataset (Table 4b) or in the data subset (even when the number of foundresses was included as a covariate-Table 5b).

Discussion

Our analyses showed that the positive relationship between the *P. tonduzi* sex ratio and the number of non-pollinating fig wasps was accompanied by varying correlations between the sex of *P. tonduzi* offspring and the presence of non-pollinating wasps. This finding suggested that non-pollinating fig wasps may distort the secondary pollinating brood sex ratio and could reflect an incorrect assessment of LMC by foundress pollinating fig wasps or sex-dependent parasitism.

An incorrect assessment of the level of LMC would occur if the foundress pollinating wasps were unable to discriminate whether the eggs deposited in the ovary flowers came from conspecific wasps or from non-pollinating females. This could occur when non-pollinating wasps colonize the figs at the same time as pollinators (e.g. *Idarnes* sp. 3). As an implication, the incorrect assessment of LMC could result in a weaker selection for sex ratio adjustment because of its low environmental predictability for pollinators (West and Sheldon 2002), since there is no physical interaction between the non-pollinators and pollinators during oviposition (in the Neotropics, all non-pollinating fig wasps oviposit from outside the fig), and since infestation by non-pollinating wasps may vary with time.

Sex-dependent parasitism would occur if cleptoparasitic species (e.g. *Idarnes carme* group) laid eggs preferentially in galls containing female larvae of pollinating fig wasps. This preference could be a function of (1) differences in the resource quality of galls containing females and males of pollinating fig wasps, (2) the development of males in an ovary layer less accessible to cleptoparasites, or (3) a dependence on pollinating males to open the exit hole (non-pollinating offspring cannot leave the fig if all pollinating males are killed). The stronger negative relationships (greater slopes) observed between females of *P. tonduzi* and the *I. carme* group

Table 3. Linear model of the arcsine of the square root of the *Pegoscapus tonduzi* brood sex ratio (dependent variable) and groups of wasp species associated with *Ficus citrifolia* (explanatory variables) in the data subset for which foundress number was recorded. "Crop" was included as a co-variate and its variation was significant in the models: (a) $F_7 = 6.46$, prob. $< 10^{-4}$; (b) $F_7 = 16.51$, prob. $< 10^{-4}$. *P. tonduzi* brood sizes were used as weights in the analysis. Model statistics: (a) adjusted $R^2 = 0.545$, $F_{13,196} = 20.28$, prob. $< 10^{-4}$; (b) adjusted $R^2 = 0.442$, $F_{12,197} = 14.8$, prob. $< 10^{-4}$, n = 210 figs.

Effect	(a) Including foundresses			(b) Excluding foundresses		
	Standardized coefficient	t	Prob.	Standardized coefficient	t	Prob.
Constant	0.000	8.518	$< 10^{-4}$	0.000	7.606	$< 10^{-4}$
Foundresses	0.464	6.767	$< 10^{-4}$	–	–	–
Seeds	−0.199	−2.076	0.0392	−0.200	−1.887	0.0607
P. tonduzi	0.168	2.658	0.0085	0.347	5.457	$< 10^{-4}$
Idarnes (*carme* group)	0.062	1.012	0.3126	0.058	0.862	0.3899
Idarnes sp. 3	0.016	0.3032	07620	−0.014	−0.236	0.8141
Other species	−0.015	−0.256	0.7985	−0.009	−0.142	0.8871

compared to other non-pollinators (Table 4a, 5a) support our assumption of sex-dependent parasitism for the cleptoparasitic species. Although distortions of the sex ratio through differential parasitism of the sexes cannot affect the sex ratio allocation because death occurs after investment (Leigh Jr 1970), our results emphasize that secondary sex ratios may not precisely reflect primary sex ratios when there are high infestations by non-pollinating fig wasps.

Our results do not support the alternative interpretation that the density of non-pollinators was positively correlated with a third variable associated with sex ratio allocation, e.g. number of foundresses (Frank 1985, Herre 1985). The number of foundresses was not positively correlated with the number of non-pollinating wasps. Analyses within the data subset showed qualitatively similar results, regardless of whether the number of foundresses was included as a co-variate or not. Therefore, the absence of significant correlations in the data subset could reflect the lower levels of infestation and densities of non-pollinating fig wasps relative to the whole dataset (Fig. 2). Moreover, all categories of non-pollinating species within the whole dataset, and of the *Idarnes carme* group within the data subset, were significantly negatively correlated with the number of *P. tonduzi* females but not significantly correlated with males, indicating a major negative impact on females.

A preliminary inspection of data for other species indicated a sex ratio distortion in samples of *F. citrifolia* from Panama, but not in two other Panamanian species (*F. obtusifolia* and *F. popenoei*) with larger figs and wasps (E. A. Herre, unpubl.). Apparently, the ability of non-pollinating wasps to distort the sex ratio of *Pegoscapus* broods is stronger for species with smaller figs (flowers per fig ($\pm$SD) in Panamanian species-*F. citrifolia* $= 325 \pm 38$, n = 55 figs; *F. obtusifolia* $= 976 \pm 93$, n = 34 figs; *F. popenoei* $= 1124 \pm 181$, n = 78 figs (Herre 1989), and Brazilian *F. citrifolia* $= 461 \pm 89$, n = 25 figs). The lower number of flowers and, consequently, of pollinating wasps relative to the infestation by non-pollinators would make it easy to detect sex ratio distortions in species that use smaller figs. However, this question needs to be investigated further using figs of different sizes and similar methods of collection to those used here (including the same variables and co-variates).

Another interesting finding in the present study was that the sex ratio correlated positively with brood size, in contrast to that observed in *Liporrhopalum tentacularis* (Moore et al. 2002). This relationship probably reflected the positive correlation between foundress number and pollinating brood size, since the relationship was weaker after controlling for foundress number (Table 3).

Table 4. Linear model of the number of (a) females and (b) males of *Pegoscapus tonduzi* (dependent variables) and groups of wasp species associated with *Ficus citrifolia* (explanatory variables). "Crop" was included as a co-variate and its variation was significant in the models: (a) $F_{18} = 22.29$, prob. $< 10^{-4}$; (b) $F_{18} = 16.21$, prob. $< 10^{-4}$. Dependent variables were square root transformed. Model statistics: (a) adjusted $R^2 = 0.688$, $F_{23,636} = 64.3$, prob. $< 10^{-4}$; (b) adjusted $R^2 = 0.559$, $F_{23,636} = 37.34$, prob. $< 10^{-4}$, n = 660 figs.

Effect	(a) Dependent variable: females			(b) Dependent variable: males		
	Standardized coefficient	t	Prob.	Standardized coefficient	t	Prob.
Constant	0.0000	35.798	$< 10^{-4}$	0.0000	7.252	$< 10^{-4}$
Volume	0.142	3.683	0.0003	0.018	0.391	0.6958
P. tonduzi of the other sex	0.264	9.160	$< 10^{-4}$	0.532	12.819	$< 10^{-4}$
Idarnes (*carme* group)	−0.220	−7.842	$< 10^{-4}$	0.022	0.641	0.5218
Idarnes sp. 3	−0.131	−4.720	$< 10^{-4}$	0.021	0.624	0.5327
Other species	−0.061	−2.194	0.0286	0.031	0.954	0.3404

Table 5. Linear model of the number of (a) females and (b) males of *Pegoscapus tonduzi* (dependent variables) and groups of wasp species associated with *Ficus citrifolia* (explanatory variables) for the data subset in which foundress number was quantified. "Crop" was included as a co-variate and its variation was significant in the models: (a) $F_7 = 6.31$, prob. $< 10^{-4}$; (b) $F_7 = 5.35$, prob. $< 10^{-4}$. Dependent variables were square root transformed. Model statistics: (a) adjusted $R^2 = 0.437$, $F_{13,196} = 13.5$, prob. $< 10^{-4}$; (b) adjusted $R^2 = 0.649$, $F_{13,196} = 30.67$, prob. $< 10^{-4}$, n = 210 figs.

Effect	(a) Dependent variable: females			(b) Dependent variable: males		
	Standardized coefficient	t	Prob.	Standardized coefficient	t	Prob.
Constant	0.0000	16.432	$< 10^{-4}$	0.0000	3.001	0.0030
Foundresses	0.022	0.268	0.7893	0.498	8.709	$< 10^{-4}$
Volume	0.225	2.471	0.0143	0.062	0.861	0.390
P. tonduzi of the other sex	0.370	4.804	$< 10^{-4}$	0.383	7.158	$< 10^{-4}$
Idarnes (*carme* group)	−0.212	−3.539	0.0005	0.001	0.031	0.976
Idarnes sp. 3	−0.007	−0.115	0.909	0.015	0.335	0.738
Other species	−0.030	0.516	0.607	−0.012	−0.249	0.804

This study is the first to show that non-pollinating wasps can distort the sex ratio of pollinating fig wasps. In addition, the fig crop had a large effect on the sex ratio and could contribute to the marked temporal variation seen in these ecological interactions. The complexity of the interactions between fig trees and fig wasps indicates that caution is required when using the fig–fig wasp system as a model to study LMC.

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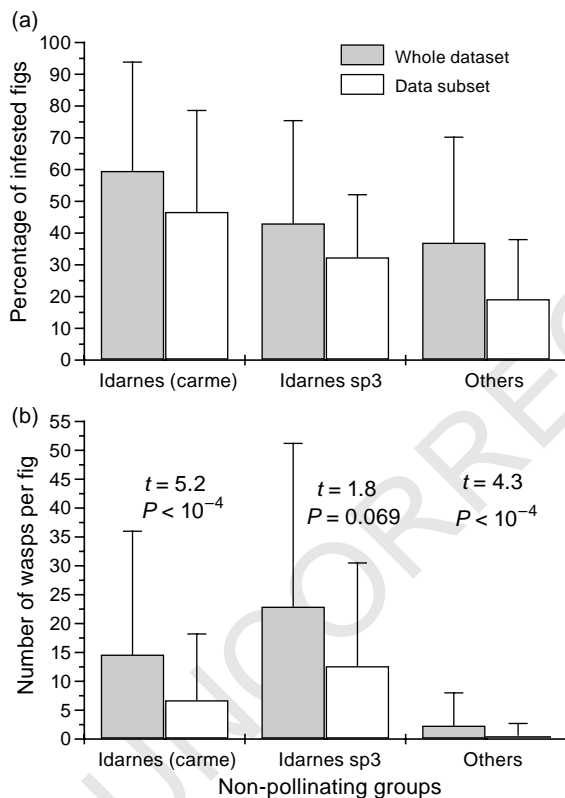

Fig. 2. (a) Percentage of infested figs per crop and (b) average density of non-pollinating fig wasp species per fig in the whole dataset and in the data subset. The bars represent the standard error of the means. Values close to the grey columns are the t test results for comparisons of the means of the whole dataset and the data subset.

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