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# Reproductive decisions of pollinator (Agaonidae) and non-pollinator (Torymidae) fig wasps of *Ficus pertusa* (Moraceae)

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## ABSTRACT

*Ficus pertusa* (Moraceae), a common Neotropical fig, is host to one pollinating (Agaonidae) and three non-pollinating (Torymidae) fig wasps. Bronstein (1991) addressed interspecies interactions between these species and suggested they may be partitioning resources within individual fig inflorescences (syconia) due to a forced association and observed morphological differences. I tested whether or not these wasps' partition oviposition sites within a fig based upon distance from the syconium wall. Also, these wasps exhibit different reproductive strategies that vary the degree of local mate competition (LMC) between brothers for mates. LMC and inbreeding have been used to explain female-biased sex ratios (Harre 1985; Frank 1985) and this system provides an excellent opportunity for comparison between different reproductive strategies. I censused 30 syconia to determine distribution of different species within the syconia and the sex ratios of each species. I found that the wasps do not partition florets based upon height (ANOVA,  $F = 0.148$ ,  $p > 0.05$ ,  $df = 3$ ). However, the presence of many (16 out of 30) unpollinated but torymid-infested syconia call into question the assertion that torymids rely on the pollinator wasps, as suggested by Bronstein (1991). In addition, I found that while LMC/inbreeding may impact the sex ratios of two wasps, *Pegoscapus silvestrii* (Agaonidae) and *Idarnes* sp. (Torymidae), another mechanism is needed to explain the high sex ratios, 0.5 and 0.6, found in the torymids *Species 3* and *Aepocerus* respectively. I suggest several potential explanations: a high cost for female production, local resource competition (LRC) among related females or an equilibrium established between natal-fig mating and dispersing males.

## RESUMEN

*Ficus pertusa* (Moraceae), un higo neotropical común, es el anfitrión de una avispa polinizadora (Agaonidae) y tres no polinizadoras (Torymidae). Bronstein (1991) estudió las interacciones interespecíficas entre estas especies y sugirió que pueden estar dividiendo los recursos dentro de las inflorescencias individuales de los higos (siconia) debido a una asociación forzada y a diferencias morfológicas observadas. Probé la idea de que estas avispas dividen los sitios de ovoposición dentro de un higo basado en la distancia de la pared del siconium. Estas avispas también exhiben estrategias reproductoras diferentes que varían según el grado de la competencia local de parejas (LMC) entre hermanos. La LMC y la endogamia se han utilizado para explicar proporciones sexuales que favorecen a las hembras (Harre 1985; Franco 1985); este sistema proporciona una oportunidad excelente para la comparación entre estrategias reproductivas diferentes. Yo examiné 30 siconia para determinar la distribución de las diferentes especies dentro de los siconios y las proporciones sexuales de cada especie. Encontré que las avispas no dividen los flósculos basados en la altura (ANOVA,  $F = 0,148$ ,  $P > 0,05$ ,  $df = 3$ ). Sin embargo, la presencia de muchos (16 de 30) siconios sin polinizar pero infestados de torímidos pone en duda la dependencia de los torímidos en la polinización sugerido por Bronstein (1991). Además encontré que mientras que la LMC y la endogamia pueden controlar las proporciones sexuales de dos avispas, *Pegoscapus silvestrii* (Agaonidae) e *Idarnes* sp. (Torymidae), otro mecanismo es necesario para explicar las altas proporciones sexuales, 0,5 y 0,6, encontradas en la *Especie 3* de los torímidos y en *Aepocerus*, respectivamente. Sugiero varias explicaciones potenciales: un costo alto para la producción de hembras, la competencia local del recurso (LRC) entre hembras relacionadas o un equilibrio establecido entre el apareamiento en el higo natal y la dispersión de los machos.

## INTRODUCTION

Natural selection predicts that individuals will make reproductive decisions that maximize their fitness. The unique natural history of fig wasps provides an excellent system to study reproductive decision-making on two levels; the effect of intraspecific competition for mates and resources and inbreeding on sex ratio (Hamilton 1967; Herre 1985; Frank 1985) and the effect of interspecific competition and parasitism on resource partitioning between and within syconia (Bronstein 1991; LaCorte 1994). These factors may be extremely important in determining the population dynamics of these four species; by influencing the decisions made before oviposition, these factors determine the composition of populations and the distribution of populations in relation to each other and their resources.

### Natural History

This study examines the reproductive decisions of four species of wasps that inhabit *Ficus pertusa*, a common monoecious fig. One, *Pegoscapus silvestrii* (Hymenoptera: Chalcidoidea: Agaonidae), is an obligate pollinator mutualist while three, *Idarnes* sp., *Aepocerus* sp. and an unnamed *Species 3* (Chalcidoidea: Torymidae), are exploiters of the agaonid-*Ficus* mutualism (Bronstein 1991). This means that they make use of resources provided by the fig in exchange for pollination yet provide no pollination services. The differences in the natural histories of these wasps are important in understanding their reproductive strategies. *Pegoscapus silvestrii* has a story similar to most other fig pollinators (Bronstein 1991; Janzen 1979). A female pollinator (foundress) enters a syconium (an inverted fig inflorescence) through a tunnel (osteole) that closes soon after, pollinates the female florets and deposits single eggs down the styles into the ovaries of some florets using an elongated ovipositor. The foundress dies in the syconium and the brood feed on the developing seeds. Eventually, wingless males emerge, mate with females still in florets (their sisters if there is only one foundress), and chew an exit hole with their powerful jaws. The females emerge, gather pollen from male flowers within the syconium and leave through the exit hole in search of a new *Ficus* tree (Janzen 1979).

The torymid exploiters have different life histories: they never enter the syconium but instead lay eggs through the syconium wall. For this reason, they have no chance of acting as pollinators. Females vary greatly in their ovipositor lengths. *Idarnes* sp., *Aepocerus* sp., and *Species 3* have ovipositors 3.28 mm, 0.37 mm and 1.11 mm long, respectively. Males of exploiters also differ: *Idarnes* males are wingless and similar in appearance to *P. silvestrii* males; *Aepocerus* has two winged male morphs, one small and clear-winged and one large with dark wing patches; *Species 3* has two male morphs, one winged and one wingless. The *Aepocerus* and *Species 3* morphs represent two reproductive strategies. Wingless *Species 3* and patch-winged *Aepocerus* males mate with females from the natal fig, inside in the case of *Species 3* and immediately outside with much fighting and competition in *Aepocerus*. Both the clear-winged *Aepocerus* and the winged *Species 3* leave the natal syconium and mate elsewhere (Bronstein 1991).

### Interspecific Interactions

Bronstein (1991) observed that torymids seek out pollinated syconia and suggested that these non-pollinators rely on *P. silvestrii* at two stages: 1) torymids must inhabit pollinated syconia because *F. pertusa* drops unpollinated figs following the arrival of agaonids (Bronstein 1988a); 2) Also, male torymids cannot chew exit holes and rely on the agaonid males to do so.

Bronstein (1991) reports that the torymids are gall forming, that is, their larvae feed on induced growth in the florets they occupy rather than feeding on seeds. They do not, like some torymids, kill agaonids and steal their food resources (Bronstein 1991). Their per-syconium populations are not correlated, suggesting that this system may be relatively free of competitive exclusion. However, florets are a resource and available oviposition sites may be limiting, creating competition. Because of their reliance on the pollinator, Bronstein (1991) suggests that species may be partitioning within rather than between syconia, perhaps facilitated by differing ovipositor lengths. Past studies suggest that ovipositor length restricts pollinating agaonids to use only short-styled florets (Bronstein 1988b). Torymids lay eggs from the outside and will reach long-styled florets most easily. Ovipositor length may limit *Aepocerus* to very long-styled florets while *Idarnes* and *Species 3*, with their longer ovipositors, may compete with the pollinator and each other for the short-styled florets. The first question this study will address is whether or not florets are partitioned by distance from the syconium wall, particularly if ovipositor length corresponds to this distance.

### **Intraspecific Interactions and Sex Ratios**

Along with possibly deciding where to deposit an egg, a female may decide which type of offspring, male or female, to produce. This is possible because fig wasps are haplodiploid, i.e. male offspring are haploid, the result of an unfertilized egg, and female offspring are diploid, receiving genes from two parents. By choosing how many eggs to fertilize with stored sperm, a female can adjust the sex ratio of her brood to optimize fitness depending on conditions (Charnov 1982).

Within most animal populations, the sex ratio (by convention, the fraction of the population that is male) is usually 0.5 (Fisher 1930). Normally, if one sex is more common, selection will favor individuals who produce more offspring of the less common sex because they will have greater reproductive success. As the sex ratio approaches 0.5, this selection pressure will lessen until equilibrium is reached. Therefore, in outcrossing populations where mating is generally unrestricted, population sex ratios are optimal at 50:50.

However, certain conditions will favor stable sex ratios that break this general rule (Hamilton 1967). One such condition is a high level of local mate competition (LCM), as when brothers compete for mates. Such populations are patchy and dispersal between patches is low so that siblings are likely to remain together. If males have no investment in offspring other than sperm, their reproductive success is limited only by how many times they can mate. If sons competitively exclude one another for a limited number of mates, then some sons inevitably are “wasted”, i.e. they do not pass on the mother’s genes. Investment in these extra sons could be better spent producing more daughters. A female-biased sex ratio, then, minimizes competition and maximizes fitness through additional females. The reproductive behavior of some fig wasps involves the isolation of broods and competition between males and LCM has been used to explain female-biased sex ratios in fig wasps (Hamilton 1967; Frank 1985; Herre 1985; Zadovna *et al* 2005).

In systems with limited dispersal, such as those that facilitate LCM, the combination of haplodiploidy and inbreeding between siblings can further skew the sex ratio toward females (Herre 1985). When inbreeding occurs, the relatedness of sons and mothers does not change since only the mother’s genes are passed to sons. However, when a female mates with a related male, her female offspring receive her direct genetic contribution as well as some of her genes indirectly through those shared with the related father. This increased relatedness between

mothers and daughters favors the production of proportionately more daughters because daughters share proportionately more of the mother's genes. This effect has been used to explain the difference between observed and predicted sex ratios in agaonids seen in Hamilton's (1967) models based on LCM (Frank 1985; Herre 1985).

In figs with few foundresses, the effects of LMC and inbreeding clearly generate female-biased sex ratios (Herre 1985). In Herre's (1985) model, the effects of each have been separated, but in general LMC and inbreeding co-occur and are difficult to distinguish. Since both are the result of related males mating at the natal fig, and both shift the sex ratio toward females, I will address their combined effect on the sex ratios of the four *F. pertusa* wasps. The likelihood for LMC differs between fig wasp species based on their natural histories. *Idarnes* and *P. silvestrii* should have strongly female-biased sex ratios because their males are confined within a syconium and therefore must compete with siblings and are likely to mate with sisters. Alternatively, *Species 3* and *Aepocerus* exhibit varying degrees of extrasyconium male dispersal. Thus they should have a reduced LMC/inbreeding effect, yielding a less strongly female-biased sex ratio.

I investigated within-fig species dispersal and sex ratios of each species to test the theoretical predictions outlined above. Based on Bronstein's (1991) observations, I expected to see flower ovule partitioning between species depending on ovipositor length and whether they oviposit from within the syconium or outside. Based on the natural histories and theoretical LMC and haplodiploid/inbreeding predictions, I expected to see lower sex ratios in *Idarnes* sp. and *P. silvestrii* than in *Species 3* and *Aepocerus* sp.

## **METHODS**

Approximately 200 *Ficus pertusa* syconia were collected from a single tree in Monteverde, Costa Rica, on May 1st, 2006 in the late dry season. Many figs on the tree had already lost their wasps, so several branches containing relatively young figs lacking visible exit holes were collected. Figs without wasp exit holes were removed and placed individually into small plastic vials. The first 30 syconia to have wasps emerge were examined. All emerged wasps were killed with acetone. These wasps were identified to species, sex and morph. Each fig was cut into quarters and examined under a dissecting scope. A needle was used to extract all unemerged wasps from florets. Each extracted wasp was classified as occupying one of three height classes: "low" florets were those touching the wall of the syconium, "high" were those that emerged above the tops of most florets and "medium" were the remaining florets. Seeds, if present, were classified in the same manner.

Because the ratio between the total number of florets in the three height classes was not known, low, medium and high classes were ranked one, two and three respectively and average rank of each species was compared with an ANOVA to determine relative oviposition distributions.

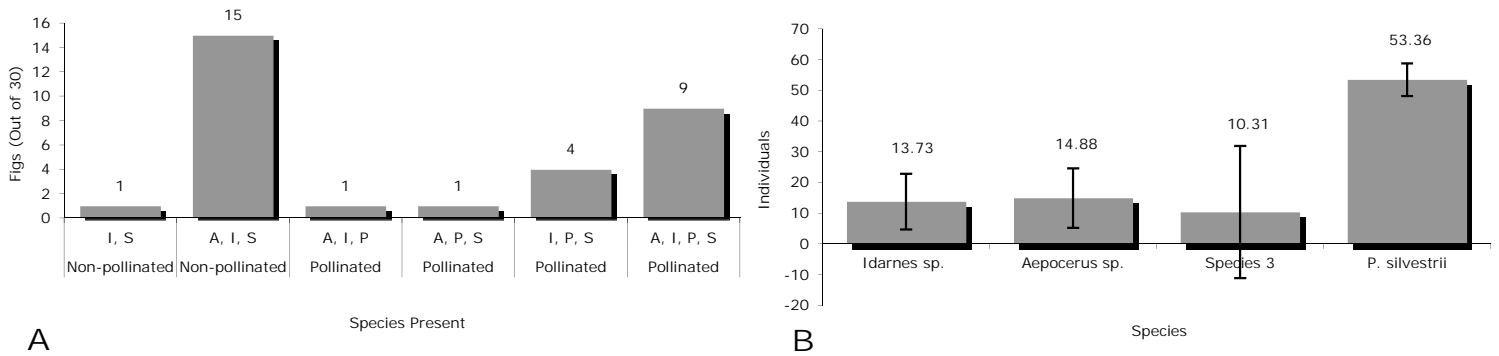
## **RESULTS**

### **Distribution of Offspring**

Species showed no detectable differences in the florets used. The average distributions of the unemerged offspring of all four wasp species, based on the categories of distance from the syconium wall, were nearly identical and very close to two, the rank of the medium-height

category (ANOVA,  $F = 0.148$ ,  $p > 0.05$ ,  $df = 3$ ). These means ( $\pm$  SD) were  $1.932 \pm 0.751$  ( $N = 73$ ),  $1.865 \pm 0.822$  ( $N = 37$ ),  $1.857 \pm 0.695$  ( $N = 140$ ),  $1.877 \pm 0.659$  ( $N = 130$ ) for *Aepocerus* sp., *Idarnes* sp., *P. silvestrii* and *Species 3* respectively. The same test considering only the low and high categories (re-ranked as 1 and 2, respectively) yielded similar results.

Only 53% of the figs contained pollinating *P. silvestrii*, the least common species, while all contained non-pollinating *Idarnes* sp. (Figure 1A). For figs with *P. silvestrii*, average brood size of *P. silvestrii* ( $53.36 \pm 21.50$ ) was significantly greater than brood sizes of the Torymids, and variance of *P. silvestrii* brood size was significantly less (Figure 1B, see Table 1 for stats). Brood sizes of all species within shared figs were independent of each other in pairwise comparisons between species (Simple Linear Regression,  $p > 0.05$ ).



**FIGURE 1. A.** Frequencies of species combinations found in dissected figs with emerged wasps ( $N=30$ ). Over half (16 out of 30) of the figs containing Torymids were not pollinated, much more than the 6% reported by Bronstein (1991). **B.** Average number of individuals present in syconia containing at least one individual of that species ( $\pm$  1SD). While *P. silvestrii* has significantly higher average brood size than the Torymids, it also has significantly lower variance in brood size (Table 1).

**TABLE 1. Pairwise comparisons of per syconia brood size means and variances between four species of fig wasps in *Ficus pertusa* ( $N=30$ )**

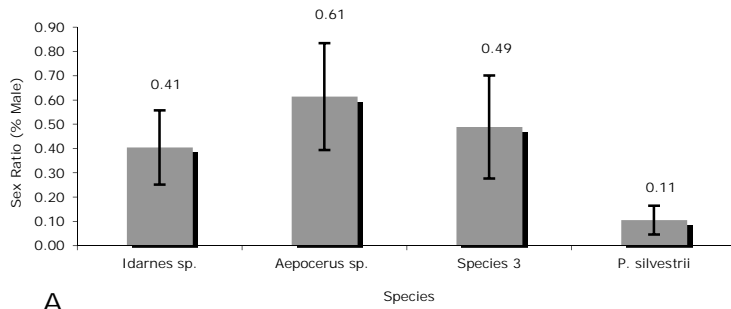
	Fisher's PLSD			F Test			
	Mean Diff.	Crit. Diff.	p	Num. DF	Den. DF	F-value	p
<i>Aepocerus</i> vs <i>Idarnes</i>	1.307	5.938	0.663	24	29	0.852	0.6851
<i>Aepocerus</i> vs <i>P. silvestrii</i>	-38.327	7.319	<0.0001	24	13	0.173	0.0011
<i>Aepocerus</i> vs <i>Species 3</i>	4.397	6.033	0.1512	24	27	3.106	0.0058
<i>Idarnes</i> vs <i>P. silvestrii</i>	-39.624	7.097	<0.0001	29	13	0.203	0.0022
<i>Idarnes</i> vs <i>Species 3</i>	3.09	5.762	0.2896	29	27	3.644	0.001
<i>P. silvestrii</i> vs <i>Species 3</i>	42.714	7.177	<0.0001	13	27	17.973	<0.0001

### Sex and Morph Ratios

Sex ratios were highest in *Aepocerus* sp. ( $0.61 \pm 0.22$ ) and lowest in *P. silvestrii* ( $0.11 \pm 0.06$ ; Figure 2A), and all means differed significantly except for *Species 3* and *Idarnes* sp. (Table 2). As with average brood size, *P. silvestrii* had a significantly lower variance in sex ratio than the Torymids (Table 2).

More *Aepocerus* males were clear-winged (dispersers) than patched (natal-syconium maters) and more *Species 3* males were wingless (natal-syconium maters) than winged

(dispersers) (Paired t-tests:  $t_A = 4.5$ ,  $p_A = 0.0001$ ;  $t_S = 2.45$ ,  $p_S = 0.021$ ) (Figure 2B). *Aepocerus* patch-winged males were present in 61% of figs containing *Aepocerus*, clear-winged males occurred in 96%. Of figs that contained *Species 3*, 93% had wingless males and 82% had winged males. When present, the average ratio of patch-winged males to females and patch-winged males in *Aepocerus* was  $0.43 \pm 0.52$  and the average ratio of wingless males to females and wingless males in *Species 3* was  $0.42 \pm 0.19$ . Neither sex ratios nor morph ratios correlated with brood size in any species (Simple Linear Regression,  $p > 0.05$ ).



**FIGURE 2. A.** *Aepocerus* sp. exhibits a male biased sex ratio while *Idarnes* sp. and especially *P. silvestrii* are female biased. *Species 3* is 50:50 on average though this is not significantly different from the average of *Idarnes* sp. (Table 2). Error bars are 1SD. **B.** The average number of each male morph within species. The dispersers are clear-winged *Aepocerus* and winged *Species 3*; the non-dispersers, or natal-fig maters, are patch-winged *Aepocerus* and wingless *Species 3*. Generally, it is only non-dispersers that should exhibit LMC (see above).

**TABLE 2.** Analysis of differences in means and variances of sex ratios

	Fisher's PLSD			F Test			
	Mean Diff.	Crit. Diff.	p	Num. DF	Den. DF	F-value	p
<i>Aepocerus</i> vs <i>Idarnes</i>	.209	0.098	<0.0001	24	29	0.484	0.0650
<i>Aepocerus</i> vs <i>P. silvestrii</i>	0.508	0.128	<0.0001	24	13	13.608	<0.0001
<i>Aepocerus</i> vs <i>Species 3</i>	0.126	0.099	0.0137	24	27	1.080	0.8438
<i>Idarnes</i> vs <i>P. silvestrii</i>	0.300	0.126	<0.0001	29	13	6.580	<0.0011
<i>Idarnes</i> vs <i>Species 3</i>	-0.083	0.096	0.0885	29	27	0.522	0.0886
<i>P. silvestrii</i> vs <i>Species 3</i>	-0.383	0.126	<0.0001	13	27	0.079	<0.0001

## DISCUSSION

This study was conducted to answer two questions: first, to determine if competition between species for available oviposition sites has led to partitioning of florets between species within syconia; second, to determine if varying degrees of inbreeding and local mate competition inherent in the life histories of the four fig wasps would result in differing sex ratios. The data also address competitive exclusion and the relationships between species.

The results suggest that resource partitioning is not taking place since the distributions of offspring within the syconia are nearly identical for all species. This result is somewhat

surprising given the great difference in ovipositor length and that agaonids oviposit from within the syconium. Although ovipositors must clearly be long enough to reach some florets, the differences in length seen between the species appear not to be currently adaptive and may instead be the product of past competition. This result suggests that oviposition sites are not limiting and that pollinators and non-pollinators are not under strong to partition florets. The high number of seeds and empty florets I saw during data collection supports this conclusion. In addition, my observations of no correlations between species for the number of wasps produced per syconium. This agrees with previous observations (Bronstein 1991), and lends support to idea that non-pollinating wasps likely have little effect on the pollinator.

Furthermore, several results contradict the proposed non-pollinator dependency on pollinators discussed earlier, suggesting a weak relationship between the species. First, over half of the dissected figs contained torymids but neither pollinators nor seeds (Figure 1A). This suggests that *F. pertusa* may not drop all of the unpollinated syconia and thus torymids may not be as reliant on agaonids as previously thought (Bronstein 1991). In addition, the 16 unpollinated, torymid-infested syconia all produced exit holes, obviously chewed by males of the non-pollinators. It is likely the *Idarnes* males that perform this task since their jaws appear more suited for chewing than those of the wingless *Species 3* males or any of the winged types. Thus, while *Idarnes* is not dependent on pollinating *P. silvestrii*, the other torymids may still rely on either one of these species to chew the exit holes.

The results of sex ratio calculations partially agreed with and partially contradicted the predictions based on LMC and inbreeding. As predicted, *Idarnes* sp. and *P. silvestrii* ratios were female biased, and more strongly in the case of *P. silvestrii*. In addition, *P. silvestrii* had a significantly lower variance in sex ratio per syconium. A similar pattern was seen for brood size, with a much more constant number for the pollinators than the torymids (Table 1). This may indicate a variable number of foundresses between. As foundress number increases, LMC and inbreeding both decrease due to the presence on non-relatives within the natal syconia. A subsequent foundress is likely to lay a more male-biased brood so that the sex ratio approaches 0.5 as foundress number increases (Harre 1985). An increase in foundress number would thus lead to a less female-biased sex ratio. Variation in foundress number would also likely lead to variation in per syconium population size since florets do not appear to be limiting.

No previous studies have published numbers of foundresses for these species. I suggest that the variation in foundress number is low for the pollinator, that most syconia receive only one foundress. This would explain the very low sex ratio and the relatively constant sex ratio and syconia population size. For the torymids, multiple foundresses per syconia may be more frequent though still variable, driving the sex ratio upward while creating a higher variance in syconium population size (sometimes multiple broods) and variance in sex ratio. Also, because the osteole closes soon after the first pollinator enters, likely to prevent more foundresses from entering (Janzen 1979), pollinators have a restriction on the number of foundresses not felt by the externally ovipositing torymids.

However, if this scenario were the case, a positive correlation brood number per syconium and sex ratio is expected but was not observed for any of the species. An alternative explanation for the difference in sex ratio (but not syconium population size) variance between *P. silvestrii* and the non-pollinators is that a small change in syconium brood size, while relatively unimportant to the sex ratios in the large syconium populations of the pollinator, may generate extreme sex ratio swings in per-fig populations of torymids with only a few individuals. A study controlling foundress number in each of the species would resolve this question.



While LMC and inbreeding, perhaps combined with varying foundress numbers between species, are sufficient to explain female biased sex ratios *P. sylvestrii* and *Idarnes* sp., the sex ratios of *Species 3* and especially *Aepocerus* are greater than predicted, including a male bias in *Aepocerus*. At least three possible explanations exist. First, it may be that the cost of producing females is much greater than that of males. Allotment of energy between the two sexes, not necessarily the actual number of offspring of each sex, is what determines fitness (Charnov 1982). If females cost more, fewer of them would be produced than if their cost were equal to that of males. This would work against other effects, such as LMC and inbreeding that reduce the sex ratio and, if the cost differentials were sufficiently great, could produce male-biased sex ratios like those observed in *Aepocerus* in spite of LMC/inbreeding. However, this explanation seems somewhat unlikely considering the size ratio between females and the average of the male morphs is 0.9, very similar to the same ratio in *P. sylvestrii* and *Idarnes* sp. (0.86 and 0.96 respectively) (Bronstein 1991).

A second explanation is that local resource competition (LRC) among females for a resource that limits reproduction acts in the same way that LMC does for males, only in this case biasing the sex ratio toward the production of males (Charnov 1982). This too seems unlikely, considering an apparent lack of resource competition within syconia and because this would probably affect all fig wasps competing for the same resource equally, not just *Aepocerus* or *Species 3*.

A final explanation is that while LMC and inbreeding effects are taking place, the “stay-at-home sex ratio” (the ratio of natal-fig mating males to females and natal-fig mating males) matches these predictions. Instead of producing more females, *Aepocerus* and *Species 3* seem to invest in dispersing males that increase fitness by outcrossing, thus reducing local mate competition as well as average level of inbreeding. Low levels of LMC and inbreeding effects would keep the “stay-at-home ratio” below 0.5 but maintain an overall sex ratio of over 0.5. The observed “stay-at-home” ratios are 0.42 and 0.43, fitting this prediction.

From these results, it is clear that while local mate competition and haplodiploidy/inbreeding effects are important in determining sex ratios of fig wasps; this is not the whole story. Further tests between the three suggested explanations for the high observed sex ratios in *Aepocerus* and *Species 3* are needed. This would be best done by observing the number of foundresses, measuring the degree of LMC/inbreeding, and generating a mathematical model. While the results of this study reinforce the largely neutral relationship between non-pollinators and pollinators, conflicting observations of the frequency of torymid-filled syconia without pollinators means this relationship also needs further clarification.

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