NATURAL HISTORY OF *ANIDARNES BICOLOR* (HYMENOPTERA: AGAONIDAE), A GALLER OF THE FLORIDA STRANGLING FIG (*FICUS AUREA)*

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ABSTRACT

The natural history of *Anidarnes bicolor* (Ashmead) Boucek (Hymenoptera: Agaonidae: Sycophaginae), a host-specific galler of the Florida strangling fig (*Ficus aurea*, Moraceae), is described. *A. bicolor* females oviposit through the outside of the globular fig inflorescence; offspring feed on sterile tissue within galls induced on the inner wall of fig. Oviposition coincides with entry of the pollinators (*Pegoscapus mexicanus*; Hymenoptera: Agaonidae: Agaoninae) into the fig, and does not interfere with pollination. Pollinator presence is in fact crucial to *A. bicolor* success, because unpollinated, galled figs are aborted by the tree. However, *A. bicolor* may nevertheless reduce pollinator success: maturation of pollinator offspring appears to be negatively affected by the developing *A. bicolor* galls. Although the composition of the wasp community associated with the native Florida figs is relatively well-known, this is one of the first studies of the natural history of one of the non-pollinator species.

Key Words: gall, wasp, fig, Agaonidae, *Ficus aurea*, *Anidarnes*

RESUMEN

Se describe la historia natural del agallero *Anidarnes bicolor* (Ashmead) Boucek (Hymenoptera: Agaonidae: Sycophaginae), cuyo hospedero específico es el higo estrangulador (*Ficus aurea*, Moraceae), de Florida. Las hembras de *A. bicolor* ovipositan desde afuera dentro de la inflorescencia globular; la progenie se alimenta de tejido estéril dentro de las agallas inducidas en la superficie interna del higo. Esta oviposición coincide con la entrada de los polinizadores (*Pegoscapus mexicanus*; Hymenoptera: Agaonidae: Agaoninae), y no interfiere con la polinización. La presencia de los polinizadores es esencial para el éxito de *A. bicolor* porque higos que no son polinizados son abortados por el árbol. Sin embargo, es posible que *A. bicolor* reduzca el éxito de los polinizadores: aparentemente el desarrollo de la progenie de los polinizadores es afectado negativamente por el desarrollo de las agallas de *A. bicolor*. Aunque la composición de la comunidad de avispas asociadas con los árboles de higo nativos de Florida es relativamente bien conocida, éste es uno de los primeros estudios sobre la historia natural de una de las especies no polinizadoras.

The mutualism between figs (*Ficus* spp., Moraceae) and the agaonid wasps that pollinate them is one of our most spectacular examples of coevolution. Ecological aspects of this interaction are now rather well-known (Janzen 1979, Bronstein 1992, Anstett et al. 1997). Each of the more than 700 fig species can be pollinated by only one (rarely two) fig wasp species. Pollinators gain access to flowers within the globose inflorescences, or figs, via a bract-lined entry pore (the ostiole). Once inside, they pollinate the flowers, then lay eggs within some of them. Pollinator offspring thus consume many of the developing seeds.

Figs are also exploited by a large community of chalcidoid wasps that develop within the figs but do not transfer pollen. Little is known about the natural history of these wasps, their interactions with and impact on the mutualism that they exploit, and their evolutionary origins (Hamilton 1979, Bronstein 1991, Compton and Hawkins 1992, West and Herre 1994, West et al. 1996, Kerdelhué and Rasplus 1996, Machado et al. 1996). These wasps include gallers, inquilines, cleptoparasites, parasitoids of the pollinators, and parasitoids of other non-pollinating wasp species. Up to 32 species have been described in association with a single fig species (J.-Y. Rasplus, *unpublished data*). Multiple species often develop side by side in a single fig; in the New World figs, offspring of non-pollinators can outnumber the pollinator offspring (Bronstein and Hossaert-McKey 1996). Their sporadic appearance in samples, diverse feeding niches, often extreme sexual dimorphism, and small size have impeded detailed study. Some genera and many common species remain undescribed.

The interaction between *Ficus aurea* Nuttall (the Florida strangling fig) and *Pegoscapus mexicanus* (Grandi) Wiebes (Agaonidae: Agaoninae) is one of the best understood fig pollination mutualisms (Frank 1983, 1984, Bronstein and Patel 1992a, 1992b, Bronstein and Hossaert-McKey 1995, 1996, Khadari et al. 1995, Gibernau et al. 1996, Anstett et al. 1996). The non-pollinating wasp communities associated with *F. aurea* and the one other native Florida fig species, a member of the *F. citrifolia* P. Miller complex, are also comparatively well-known. Expanding on older work of Butcher (1964) and Burks (1969), Nadel et al. (1992) identified nine species occupying *F. citrifolia* figs and eight occupying *F. aurea* figs. Five of these wasps were associated with both fig species, while the others were apparently host-specific. Most of these species are described under a reworked classification by Boucek (1993), who places the Florida non-pollinators into the Eurytomidae, Torymidae, and two subfamilies of the Agaonidae (Otitesellinae and Sycophaginae). The natural history and ecology of these wasps are unknown, with the exception of one torymid (*Physothorax bidentulus* Burks) known to parasitize the galls of a cecidomyiid fly in *F. laevigata* figs (Roskam and Nadel 1990).

This paper describes the natural history of *Anidarnes (= Neosycophila) bicolor* (Ashmead) Boucek (Agaonidae: Sycophaginae), a common non-pollinating wasp associated exclusively with *F. aurea* in southern Florida (Nadel et al. 1992). In addition, I examine the possible impact of *A. bicolor* on the fig's interactions with its obligate pollinator.

Materials and Methods

Ficus aurea is a Caribbean Floristic Region species that reaches its northern limit in south central Florida (Condit 1969). The study was conducted in a large, natural *F. aurea* population located on the campus of The University of Miami in Coral Gables, Florida. About 50 individuals, ranging in size from 40 to 250 cm d.b.h., are found at this site growing in hammock remnants along old canals, with the majority in areas removed from human disturbance. Long-term phenological patterns within this population, as well as their implications for interactions with pollinators and other wasps, are described by Bronstein and Patel (1992a, 1992b) and Bronstein and Hossaert-McKey (1995, 1996).

Anidarnes bicolor is one of the largest nonpollinating wasps found in *F. aurea*, reaching about 2.0 mm in length (about 2-3 times larger than the pollinator). Females and males are both winged and resemble each other closely, but can easily be distinguished by the female's ovipositor, about half the length of the gaster. Boucek (1993) gives a description of this species and provides identification keys; his Figure 41 illustrates a female individual.

The distribution and abundance of *A. bicolor* were determined from three sets of figs. The first set consisted of 748 figs sampled during and soon after pollination (i.e., B and early C phase; Galil and Eisikowitch 1968), from trees flowering between January and mid-August 1992. On 15 dates, at about 10-day intervals, 34 trees in the study population were examined to see if they bore newly pollinated figs. When such figs were located, a sample of 10 was removed from the tree. In the laboratory, each fig was split open and examined under the dissecting microscope. *A. bicolor* galls, which are already quite obvious at this stage, were counted. We also recorded the number of dead pollinators within each fig to look for associations between pollination intensity and *A. bicolor* galls. Pollinators typically although not invariably become trapped in the figs they enter, and die within 24 hours (Gibernau et al. 1996, Bronstein and Hossaert-McKey 1996). It was noted if each pollinator had died within the fig cavity or within the ostiole (entry pore), where it might have become trapped either during entry to or exit from the cavity.

The second set of figs was collected when seeds and wasp offspring were mature (D phase). On each census date between February and December 1991, 20 trees in the study population were each examined for the presence of figs in which developing wasps had reached adulthood and were ready to depart. When detected, a haphazard sample (usually 5) was removed. In the laboratory, each fig was split open, placed into a vial, and covered tightly with fine mesh. Each vial was then placed in the dark for 24 hours to allow wasp escape, then filled with a preservative and capped. Seeds and all wasps were later counted, and wasps were identified to species or morphospecies and to sex. Wasps still trapped within galls were removed and identified when possible.

A third set of 313 figs was also collected when seeds and wasps were mature. These figs had been bagged several days prior to receptivity; when receptive, they had pollinators but no other insects deliberately introduced to them (detailed methods are provided by Khadari et al. 1995 and Anstett et al. 1996). These experiments were conducted on 13 trees between 1991 and 1995. Wasps were reared from these figs, preserved, and later identified, using the methods described above.

RESULTS AND DISCUSSION

General Natural History

Ovipositing *A. bicolor* were never found within the fig cavity, and presumably never enter it. Rather, oviposition occurs through the fig wall, as in the other non-pollinating wasps associated with *F. aurea* (unpublished data). Each offspring matures inside a large, thick-walled gall. When these galls are numerous, they can occupy nearly the entire volume of the fig. Superficially, these galls appear to be greatly swollen female florets similar to, but much larger than, those occupied by offspring of the pollinators and other non-pollinator species. However, closer inspection reveals them to be rotund invaginations of the inner wall of the fig. Hence, *A. bicolor* is apparently a galler that is dietarily independent of the seeds or wasps developing simultaneously in the fig. This type of gall appears to be generally rare among fig wasps, and has not previously been reported in the New World. It has been observed most commonly in species of Epichrysomallinae (Agaonidae) associated with African figs (Compton and van Noort 1992; J.-Y. Rasplus and C. Kerdelhué, unpublished data). The eurytomid genus *Sycophila* has also been reared from such galls in Africa, but is apparently a parasite of the epichrysomallines (J.-Y. Rasplus, unpublished data).

When mature, *A. bicolor* individuals chew out of their galls and enter the fig cavity. They depart the fig through the exit tunnel constructed by the males of the pollinator species. It is not known if or how *A. bicolor* is able to escape from figs in which all *P. mexicanus* males have died prior to maturity (17% of all figs; unpublished data). It is very likely that *A. bicolor* matings occur outside of the fig, as is usual for the subset of fig nonpollinators in which both males and females are winged (Hamilton 1979).

Phenology of *A. bicolor*

Of 748 figs sampled within a week of pollinator arrival, 225 (30.1%) already contained the characteristic galls of *A. bicolor.* Three lines of evidence suggest that *A. bicolor* attack can precede pollination. First, 17.8% of the galled, immature figs sampled (n = 225) did not contain trapped pollinators. Second, many *A. bicolor* galls were already quite large at the time of sampling, suggesting that they had been developing for some days. Third, 12.7% of the figs bagged as much as a week prior to pollinator introduction experiments (n = 313) contained *A. bicolor* individuals when mature. This species made up over 80% of the non-pollinator individuals reared in these experiments. It is unlikely that *A. bicolor* would have regularly penetrated the bagging material while two significantly smaller and more common species, *Idarnes carme* Walker and *Heterandrium* sp., almost never did. Instead, these observations suggest that *A. bicolor* had attacked these figs prior to bagging, i.e., in A phase, well before the figs were receptive to pollinators. A number of other fig gallers (Kerdelhué and Rasplus 1996), including one epichrysomalline that galls the fig wall (S. G. Compton, unpublished data), are known similarly to oviposit prior to pollination.

Although *A. bicolor* offspring begin development earlier than the pollinator offspring, they take as long or somewhat longer to mature. Figs cut open 1-2 days before *P. mexicanus* have completed maturation never contain mature *A. bicolor* individuals ready to depart (unpublished data). In fact, in the galled figs examined when *P. mexicanus* were departing, 23% of *A. bicolor* individuals had not yet left their galls. Males emerged earlier than females: 27% of *A. bicolor* females (n = 133) were still within the galls when pollinator offspring were mature, compared to only 16.5% of the males (n = 89).

Over 99% of mature galled figs contained seeds and pollinator offspring, implying that *A. bicolor* only matures in pollinated figs. While immature figs sometimes contained galls but no trapped pollinators (see above), it is probable that at the time of sampling, pollinators had either not yet entered these figs or else had entered them and then departed. Hence, although certain non-pollinator species can induce the tree to retain rather than abscise unpollinated figs (Bronstein 1991), this does not appear to be the case for *A. bicolor.*

Frequency of Attack

Figs attacked by *A. bicolor* during 1992 (30.1% of sampled figs) contained 5.4 ± 4.4 galls (mean ± 1 SD, range 1-23, n = 225 figs). Attack was strongly skewed towards few galls per fig (Fig. 1). The number of galls per fig varied significantly with both tree and with month of sampling, as well as with the interaction between month and tree (Table 1). There were no obvious seasonal patterns of attack in 1992 (Fig. 2), at least up to mid-August, when winds from Hurricane Andrew blew all figs off all study trees. *Anidarnes bicolor* was found once again occupying figs by the second week of January 1993, at which point local pollinator populations had successfully reestablished (Bronstein and Hossaert-McKey 1995).

Anidarnes bicolor was the third most common non-pollinating wasp in mature *F. aurea* figs sampled during 1991, after *Idarnes carme* (found in 77.8% of the figs) and a *Heterandrium* species (39.5% of figs). An average of 4.30 ± 3.38 individuals matured

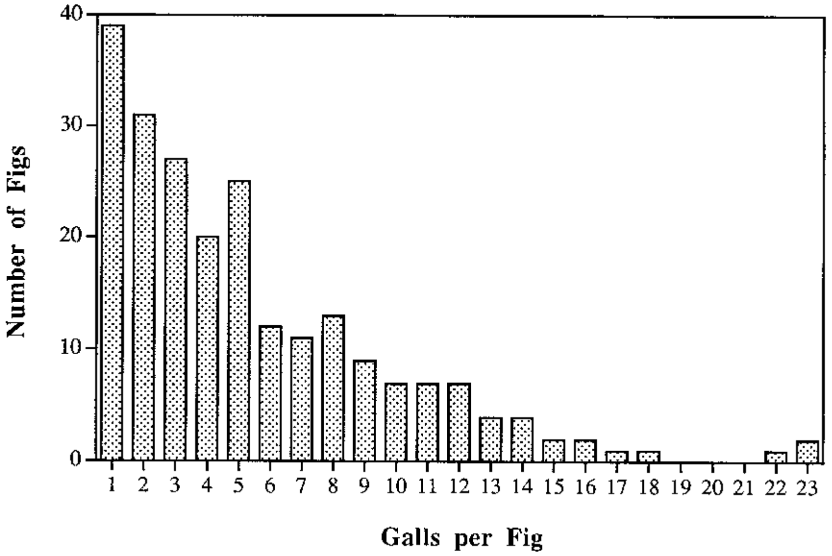

Fig. 1. Frequency distribution of Anidarnes bicolor galls in 225 immature, newly galled figs sampled from January to August 1992.

in the 27.1% of sampled figs (n = 52) that contained *A. bicolor*. The range was large (1-19 individuals) and skewed towards low numbers, as in the 1991 sample of immature figs. The number of *A. bicolor* (which do not mature inside fig florets) was not correlated with the number of florets per fig (Spearman rank correlation, r_s = -0.205, P = 0.116, n = 52), unlike the numbers of seeds, pollinator offspring, and other non-pollinator wasps (Bronstein and Hossaert-McKey 1996, Anstett et al. 1996).

Fifty percent of the mature *A. bicolor*-infested figs contained either exclusively males or exclusively females; it was not uncommon to find four or more individuals of one sex and none of the other. The sex ratio was female-biased, with males making up 40% of all mature individuals (n = 222 wasps).

Impact on the Pollination Mutualism

The presence of the large *A. bicolor* galls crowding the cavity apparently did not restrict pollinator entry into figs. Galled figs contained no fewer trapped pollinators than did ungalled ones, although there was a trend in this direction (Mann-Whitney test, U = 54305, P = 0.082, df = 746). However, the number of pollinator offspring maturing in galled figs decreased as the number of galls increased (Spearman rank correlation, r_s = -0.353, P = 0.039, n = 32).

There are four possible mechanisms for this negative effect of *A. bicolor* on pollinator offspring numbers. First, once pollinators manage to enter the fig, the galls may impede their access to the flowers. This is unlikely. Pollinators found trapped within figs were equally likely to have successfully reached the fig cavity in galled as compared to ungalled figs (U = 41712, P = 0.732, df = 746). Furthermore, seed set in galled figs was not reduced compared to ungalled figs (r_s = -0.119, P = 0.396, n = 52), implying that pollinators conducted their usual pollination behaviors once there. Second,

TABLE 1. RESULTS OF A TWO-WAY ANALYSIS OF VARIANCE QUANTIFYING TEMPORAL AND SPATIAL EFFECTS ON THE NUMBER OF ANIDARNES BICOLOR GALLS INFESTING FICUS AUREA FIGS. "MONTH" IS THE MONTH OF 1992 IN WHICH THE FIGS WERE INFESTED; "TREE" IS THE F. AUREA TREE ATTACKED.

Source	df	Sum of squares	Mean square	F-Value	P-Value
Tree	28	1485.237	53.044	7.494	0.0001
Month	7	310.098	44.300	6.259	0.0001
Tree* month	35	2009.997	57.428	8.113	0.0001
Residual	677	4791.975	7.078		

P. mexicanus might pollinate normally in galled figs, but lay fewer eggs there. Third, they might both pollinate and oviposit normally in galled figs, but the expanding *A. bicolor* galls might then crush some of the delicate larvae as they develop. Many fig ovaries were in fact obviously flattened by the expansion of these large galls. However, maturation of other non-pollinator species was not similarly depressed by galling (r_s = 0.106, P = 0.600, n = 32), weakening this hypothesis. Finally, it is possible that developing *A. bicolor* draw away fig resources that might otherwise be put into *P. mexicanus* development. Further studies are needed to evaluate these hypotheses thoroughly.

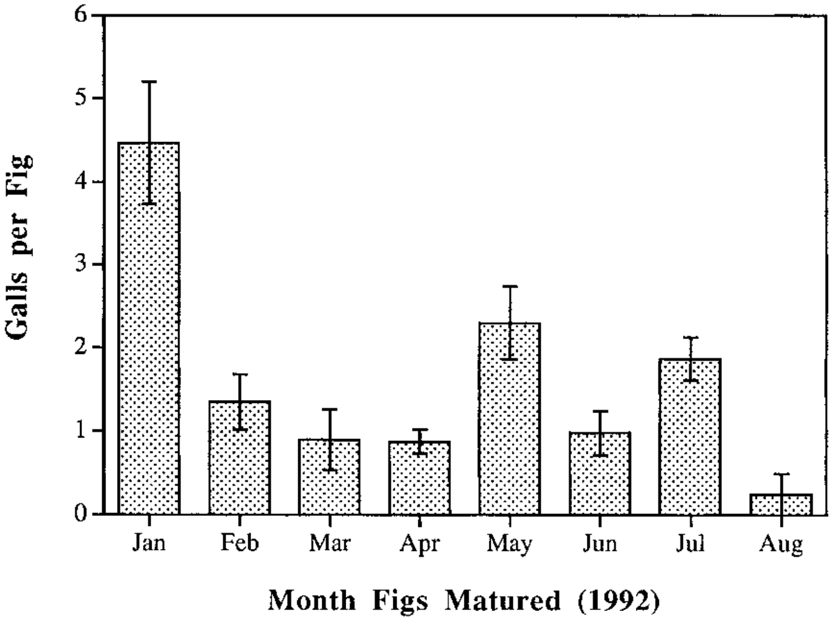

Fig. 2. Attack of Anidarnes bicolor by month, from 748 figs sampled during 1992 (means + 1 SD shown). Although differences among months were highly significant (see Table 1), there was no clear seasonality of attack.

Hence, despite the fact that *A. bicolor* depends on *P. mexicanus* both to assure fig retention to maturity and to create a passage out of the fig, it has a distinctly negative effect on this species. This would appear to be an unusually clear case of a fig inhabitant that imposes a cost to the pollination mutualism, despite feeding on sterile tissue rather than on one of the mutualists (West and Herre 1994, Kerdelhué and Rasplus 1996). Yet, *F. aurea* has no apparent adaptations to prevent *A. bicolor* attack. Bronstein (1991) proposed three alternative hypotheses to explain a similar tolerance of non-pollinators in a Costa Rican fig species. The Commensalism Hypothesis, which states that non-pollinators are tolerated by the fig because they inflict no costs, may be relevant in the present case. Although *A. bicolor* attack does reduce reproductive success of *P. mexicanus*, the only possible pollen vector of *F. aurea*, the cost to *F. aurea* itself might still be negligible. At least in this population, almost every *F. aurea* fig is entered by one or more pollinators. Seed set is highest when a single pollinator enters (unpublished data), but in nature, up to 24 can be found crowding into a single fig (Bronstein and Hossaert-McKey 1996). Hence, if somewhat fewer *P. mexicanus* departed a tree, that tree's success as a pollen donor would not necessarily be depressed. The Coevolutionary Race Hypothesis (Bronstein 1991), which states that non-pollinators evolve adaptations to exploit figs faster than figs evolve counteradaptations to them, may also be relevant, however. *F. aurea* shows no obvious adaptations to avoid attack from any member of its large community of non-pollinators, some of which are likely to impose even higher fitness costs on it than does *A. bicolor.* Understanding *F. aurea*'s tolerance of *A. bicolor* may well require studies of the broader community of these enigmatic wasps.

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REFERENCES CITED

ANSTETT, M.-C., J. L. BRONSTEIN, AND M. HOSSAERT-MCKEY. 1996. Resource allocation: a conflict in the fig/fig wasp mutualism? J. Evol. Biol. 9: 417-426.

ANSTETT, M.-C., M. HOSSAERT-MCKEY, AND F. KJELLBERG. 1997. Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism. Trends Ecol. Evol. 12: 94-99.

BOUCEK, Z. 1993. The genera of chalcidoid wasps from *Ficus* fruit in the New World. J. Nat. Hist. 27: 173-217.

BRONSTEIN, J. L. 1991. The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? Oikos 61: 175-186.

BRONSTEIN, J. L. 1992. Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. *In* Insect-Plant Interactions. Volume IV, edited by E. Bernays. Boca Raton: CRC Press.

BRONSTEIN, J. L., AND A. PATEL. 1992a. Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). Am. J. Bot. 79: 41-48.

BRONSTEIN, J. L., AND A. PATEL. 1992b. Temperature-sensitive development: consequences for local persistence of two subtropical fig wasp species. Am. Midl. Nat. 128: 397-403.

BRONSTEIN, J. L., AND M. HOSSAERT-MCKEY. 1995. Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate mutualism. Biotropica 27: 373-381.

BRONSTEIN, J. L., AND M. HOSSAERT-MCKEY. 1996. Variation in reproductive success within a subtropical fig/pollinator mutualism. J. Biogeogr. 23: 433-446.

BURKS, B. D. 1969. Redefinition of two genera of chalcidoids from figs, with new Florida species (Hymenoptera). Florida Ent. 52: 115-122.

BUTCHER, F. G. 1964. The Florida fig wasp, *Secundeisenia mexicana* (Ashm.), and some of its hymenopterous symbionts. Florida Ent. 47: 235-238.

COMPTON, S. G., AND S. VAN NOORT. 1992. Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilization and host relationships. Proc. K. Ned. Akad. Wet. C 95: 423-435.

COMPTON, S. G., AND B. A. HAWKINS. 1992. Determinants of species richness in southern African fig wasp assemblages. Oecologia 91: 68-74.

CONDIT, I. J. 1969. *Ficus*, The Exotic Species. Berkeley: California Division of Agricultural Sciences.

FRANK, S. A. 1983. Theoretical and empirical studies of sex ratios, mainly in fig wasps. M.S. thesis, University of Florida, Gainesville.

FRANK, S. A. 1984. The behavior and morphology of the fig wasps *Pegoscapus assuetus* and *P. jimenezi*: descriptions and suggested behavioral characters for phylogenetic studies. Psyche 91: 289-308.

GALIL, J., AND D. EISIKOWITCH. 1968. On the pollination ecology of *Ficus sycomorus* in East Africa. Ecology 49:259-269.

GIBERNAU, M., M.-C. ANSTETT, M. HOSSAERT-MCKEY, AND F. KJELLBERG. 1996. Consequences of protecting flowers in a fig: a one-way trip for pollinators? J. Biogeogr. 23: 425-432.

HAMILTON, W. D. 1979. Wingless and fighting males in fig wasps and other insects. *In* Sexual Selection and Reproductive Competition in Insects, edited by M. S. Blum and N. A. Blum. London: Academic Press.

JANZEN, D. H. 1979. How to be a fig. Ann. Rev. Ecol. Syst. 10: 13-51.

KERDELHUÉ, C., AND J.-Y. RASPLUS. 1996. Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. Oikos 75: 3-14.

KHADARI, B., M. GIBERNAU, M.-C. ANSTETT, F. KJELLBERG, AND M. HOSSAERT-MCKEY. 1995. When figs wait for pollinators: the length of fig receptivity. Am. J. Bot. 82: 992-999.

MACHADO, C. A., E. A. HERRE, S. MCCAFFERTY, AND E. BERMINGHAM. 1996. Molecular phylogenies of fig pollinating and non-pollinating wasps and the implications for the origin and evolution of the fig-fig wasp mutualism. J. Biogeogr. 23: 521-530.

NADEL, H., J. H. FRANK, AND JR. R. J. KNIGHT. 1992. Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. Florida Ent. 75: 29-38.

ROSKAM, J. C., AND H. NADEL. 1990. Redescription and immature stages of *Ficiomyia perarticulata* (Diptera: Cecidomyiidae), a gall midge inhabiting syconia of *Ficus citrifolia*. Proc. Ent. Soc. Washington 92: 778-792.

WEST, S. A., AND E. A. HERRE. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. Proc. Roy. Soc. Lond. Ser. B 258: 67-72.

WEST, S. A., E. A. HERRE, D. M. WINDSOR, AND P. R. S. GREEN. 1996. The ecology and evolution of the New World non-pollinating fig wasp communities. J. Biogeogr. 23: 447-458.