African Fig Fly (Diptera: Drosophilidae): Biology, Expansion of Geographic Range, and Its Potential Status as a Soft Fruit Pest

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Abstract

African fig fly, Zaprionus indianus Gupta (Diptera: Drosophilidae), is originally from the Afrotropics but has been expanding its geographical range globally, including the United States. It was first reported in Virginia northward in 2012. The current established range of African species is thought to be limited to the southern states in winter, and populations must disperse northward each season. Adults are normally caught in Virginia in mid-summer and later. African fig fly is a competitive invader and affects the dynamics of native drosophilid communities when it invades a new area. While lacking the hardened, serrated ovipositor seen in spotted-wing drosophila, another invasive frugivore, it may come to outnumber that species in commercial plantings. It can lay eggs and develop in many kinds of fruit that have been otherwise injured. However, the ovipositing fly may take advantage of oviposition sites of spotted-wing drosophila, thereby allowing entry of African fig fly larvae, which may outcompete the original inhabitants. Furthermore, African fig fly may be able to infest certain soft-fruit hosts. Biological control in North America and Europe is limited at this time by immunological responses of host larvae; naturally occurring parasitoids have been unable to achieve significant parasitization.

Key words: invasive species, biogeography, Zaprionus indianus

A Pair of Invasive Drosophilids

In August 2012, we received an e-mail message from a commercial grape grower in the Virginia Piedmont, saying that while investigating suspected spotted-wing drosophila (SWD), Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), in his vineyard, he had happened upon a distinctly different-looking fly. We visited this vineyard and easily found flies with a distinctive appearance—dark reddish brown thorax and head, with marked silver and black longitudinal stripes—easy to see with the naked eye. We were able to confirm the identity of this new fly as African fig fly (AFF), Zaprionus indianus Gupta, thanks to fact sheets and species confirmation by a Florida worker (coauthor KVDL) from the original U.S. infestation (Steck 2005, van der Linde 2010).

African fig fly is another invasive, human-commensal drosophilid that has been on the move globally (Yassin et al. 2008). This species is easily identified because of its unique longitudinal black and white stripes that can be observed with the unaided eye (Fig. 1). The stripes that are characteristic in this genus are apparently used in courtship (Bennet-Clark et al. 1980). During the male's courtship dance, the male appears to display his thoracic stripes to the female. The female then rocks side to side, in a motion of the same amplitude of the stripes. The fine morphology of these stripes in a closely related species, Z. vittiger Coquillett, has been investigated (Walt and Tobler 1978). The white stripes in that species bear bent trichomes containing cavities; these trichomes polarize light. The neighboring dark stripes contain pigment, and trichomes not containing cavities; light is not polarized here. Hence, there may be...
optical differences in the stripes beyond what the human eye can see. After the introduction of AFF into Brazil, it was determined that there can be environmentally induced changes in wing size and shape (Loh and Bitner-Mathé 2005). Studies of populations in a north-south transect in India also showed morphological variation (Karan et al. 2000).

**Global Expansion of Range**

African fig fly has been reported through most of Africa (the original home), Austria, Italy, Spain, the Middle East, and much of India. Yassin and David (2010) considered AFF to be the most polyphagous ("ecologically diverse") drosophilid in the Afrotropical fauna; this polyphagy is likely involved with its increasing geographical spread. The global distribution is given in Fig. 2. It is unclear how many of these areas have established populations, or late season immigrants.

This invasive drosophilid invaded Brazil in 1999 (Vilela 1999) and was found in Florida in 2005 (van der Linde et al. 2006). The Brazilian and Floridian invasions are probably two independent occurrences linked to two different regions in Africa (van der Linde 2010, Yassin and David 2010, Markow et al. 2014). The colonization pattern of the Brazilian invasion suggests that the U.S. west coast colonization is most likely an extension of the Brazilian invasion as this species was found in Mexico in 2002 (Castrezana 2007) and in Panama in 2003 (van der Linde et al. 2006) before the species was first spotted in Florida in 2005. In Brazil, AFF comprises about 64% of total drosophilids collected (Roque et al. 2017). Further international expansion has included Saudi Arabia (Amoudi et al. 1991), Uruguay (Goñi et al. 2001), and France (Kremmer et al. 2017).

**African Fig Fly Moves Through North America**

When we investigated the grape grower report of the suspect vinegar fly in the Albemarle County vineyard in 2012, we visited a block of Petit Verdot grapes, where we saw many individuals of this fly flying from between grapes in a cluster when disturbed. A few individuals of SWD were also observed. The clusters looked generally intact, except for portions with shriveling berries typically seen in cases of SWD infestation, with a characteristic odor of sour rot. The striped fly was determined to be *Z. indianus*.

The AFF collected and reared in August 2012 from this and other Virginia vineyards were the northernmost-reported populations of this drosophilid at that time. The species was collected later that year (September and October) in Michigan (Van Timmeren and Isaacs 2014), Pennsylvania (Joshi et al. 2014), Wisconsin (Sigler 2013), and Connecticut (Biddinger et al. 2012, Sigler 2013). Field observations

![Fig. 1. Adult African fig fly, *Zaprionus indianus*, collected in a Petit Verdot winegrape vineyard in Albemarle County.](image1)

![Fig. 2. Global distribution of *Zaprionus indianus*. Source: van der Linde (2012).](image2)
and examinations of specimens previously collected in 2011 indicate that AFF was probably present in Virginia and Pennsylvania at that time. African fig fly has been reported from Florida (2005) (van der Linde et al. 2006), Alabama, Georgia, Mississippi, Arizona and California (San Diego) (first record in 2006), South Carolina and Oklahoma (2007), Texas (2009), North Carolina, Louisiana, and Mississippi (van der Linde 2012, Sigler 2013). The northward annual expansion can reach as far as Minnesota (Anon. 2018), Ontario, and Quebec, Canada (Renkema et al. 2013). Host data in most of these records are not given; many collections are from traps for adults. The U.S. distribution in November 2012 is shown in Fig. 3 from a map posted by van der Linde (2012). After its annual arrival in Virginia, it may be found throughout the state including the most important fruit (including winegrape) counties in Virginia.

The established range of AFF in the United States is limited to the southern states (van der Linde 2010). Being intolerant of cold (Araripe et al. 2004), it likely must overwinter in Florida and disperse northward each season (van der Linde, unpublished data). African fig fly most likely is unable to overwinter in northern states and must reinvade from the southern part of the U.S. range each season. Joshi et al. (2014) believed that AFF can overwinter in Pennsylvania; this should be confirmed. AFF has shown itself to be highly adaptive and may be able to adapt its ecological niche requirements (da Mata et al. 2010).

Other grape growers communicated that they also saw striped flies in Petit Verdot blocks. We collected flies in apple cider vinegar traps for SWD from such blocks in Nelson and Orange Counties. Grapes were retrieved from one of the affected vineyard blocks to the lab in Blacksburg in order to rear adults. Both SWD and AFF were reared from grapes. In one sample, AFF comprised about 90% of the emerging adults. Sweep net sampling in Pennsylvania found AFF to outnumber SWD in some vineyards (Anon. 2012).

African fig fly is probably less able to attack intact fruit because of the less developed ovipositor (Fig. 4). The fact that AFF outnumbered SWD emerging from grapes needed further consideration in order to clarify its potential status as a berry pest. It may be secondary in nature, taking advantage of injury inflicted by SWD or other factors. Secondary in this sense does not mean unimportant, however. African fig fly is known to inoculate host fruits with the yeast, Candida tropicalis, in Brazil (Gomes et al. 2003). Drosophilid-infested grape berries become affected by sour rot, and hence, the quality of the crop may be affected. The grower in the Albemarle County vineyard heavily infested with SWD and AFF removed the most affected clusters, and estimated a 30% reduction in the crop in the vineyard block. Commercial grape growers attributed significant loss of grapes to AFF, often in conjunction with SWD. Whether AFF causes injury, or rather exacerbates injury from SWD, in grapes needs to be clarified.

**AFF Arrival in the Hawaii Archipelago**

In 2017, AFF was reported on the island of Oahu by Evenhuis et al. (2017). Subsequently, in a test of several baits for drosophilids on the island of Maui, Hawaii, adults of AFF were detected and a new island record was reported (Willbrand et al. 2018). This is worth separate mention, because the nature of the archipelago indicates not just a simple geographic spread, but a separate introduction, and because of the ecologically sensitive nature of this island chain regarding invasive species. No references to AFF in Hawaii were found during previous surveys on the Big Island of Hawai’i and Maui in 2006 (Leblanc et al. 2009), suggesting that the AFF introduction to Maui may be recent. Additional assessments are needed to determine whether AFF is present on other major Hawaiian islands including Moloka’i, Lanai, the Big Island of Hawai’i, Kaua’i, and Ni’ihau. One other species of Zaprionus has been reported in Hawaii; Zaprionus ghesquierei Collart has been reported on the Big Island and Maui (O’Grady et al. 2002, Leblanc et al. 2009). African fig fly is separated from Z. ghesquierei by the lack of a white spot on the scutellum, and the presence of spines on the foretibiae (Fig. 5). Several exotic
drosophilids were recently introduced into another island system, the Madeira Archipelago: AFF, SWD, and Acletoxensus formosus (Loew) (Rego et al. 2017). So far, these species appear restricted to human-disturbed environments.

**Host Range and Impacts**

African fig fly feeds on more than 80 host plant species (Lachaise and Tsacas 1983, van der Linde et al. 2006); this relative polyphagy among the Drosophilidae has contributed to its noted ability to invade new areas (Commar et al. 2012). While it has been noted to be able to attack unripe fruit (Commar et al. 2012), most hosts are fruits that have been injured or have fallen. However, in the Valinhos region of Brazil AFF became a pest in eyed figs, *Ficus carica* L., since females could oviposit into the ostiole of fruits. Since its introduction, AFF has become the most important pest of figs (Gomes et al. 2003). Entire lots of figs were rejected, with an estimated overall loss of 50% (Tidon et al. 2003). In the Brazilian

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**Fig. 4.** (a) African fig fly, *Zaprionus indianus*, above, spotted-wing drosophila, *Drosophila suzukii*, female below, (b) ovipositor of African fig fly, and (c) ovipositor of spotted-wing drosophila.

**Fig. 5.** The lack of a white spot on the scutellum (a) and the presence of spines on the foretibiae (b) separates *Zaprionus indianus* from *Z. ghesquierei*. 
Cerrado, AFF adapted to another plant, *Solanum lycocarpum* St. Hil., attacking fruits throughout the fruit development period (Leão and Tidon 2004). This plant is known locally as fruta do lobo, lobeira, or jurubebao, with edible berries, and is the most abundant native fleshy-fruited plant in the region. Leão and Tidon (2004) found that AFF predominated in fresh fruit of that host, but declined markedly in damaged fruit, rising again in severely overripe fruit. African fig fly is generally regarded as unable to attack intact fruit (Renkema et al. 2018). However, in ripe strawberries, AFF will lay eggs near the achenes, and the larvae are able to enter and develop in the berries; AFF attack is more successful, however, if the berries are injured by SWD or by mechanical means (Bernardi et al. 2017). African fig fly could become an economic pest in smooth-skinned fruit that are harvested close to ripeness, such as nectarines and winegrapes (Joshi et al. 2014).

**Temperature Requirements**

African fig fly may be adapting to cooler temperatures (Castro and Valente 2001). It is often associated with human activities; such areas may provide warm areas enabling it to survive in otherwise cold areas (Commar et al. 2012). African fig fly has great adaptive flexibility and can develop tolerance to a wide range of environmental conditions (da Mata et al. 2010). It has shown the ability to establish in different ecological niches in new areas of invasion, with different temperature regimes (da Mata et al. 2010); AFF has become established from southern to northern parts of India. In India, several morphological traits have shown variation with latitude and elevation, indicating genetic adaptation to different environmental conditions (Karan et al. 2000).

Development of AFF was studied by Nava et al. (2007). African fig fly was reared at several constant temperatures. At 20°C, the egg stage lasts 1 d, larval development takes 13 d, and the pupal period 6.9 d, resulting in a total of 20.9 d. Development at 18°C took 28.8 d, 20°C took 20.9 d, 22°C took 17.6 d, 25°C took 15.4 d, 28°C took 12.7 d, 30°C took 13.3 d, and at 32°C took 13.0 d. It was projected that AFF may develop 13–17 generations in different parts of Brazil. By contrast, developmental time for SWD began to increase at 30°C (Tochen et al. 2014), indicating a lower adaptation to warm temperatures; the duration from egg to adult at 28°C for SWD was 10.8 d. Development for the two species at three developmental temperatures in common between two laboratory studies is presented in Table 1. African fig fly generally takes longer to develop at each temperature. It must be noted that the two studies used separate rearing media; Nava et al. (2007) used an artificial diet, while Tochen et al. (2014) used blueberries and cherries. This could have had an effect on developmental time.

**Table 1. Egg-adult durations determined at varying temperatures for African fig fly in artificial diet, and spotted-wing drosophila in two host fruits**

| °C | African fig fly | Spotted-wing drosophila |
|----|----------------|------------------------|
|    | Female         | Male                   |
|    | Blueberry      | Cherry                 | Blueberry | Cherry |
| 18 | 28.8           | 20.1                   | 18.2      | 19.5    | 18.9 |
| 22 | 17.6           | 14.0                   | 14.0      | 14.1    | 14.0 |
| 28 | 12.7           | 10.1                   | 9.9       | 10.1    | 10.0 |

Nava et al. (2007).
Tochen et al. (2014).

**Interspecific Interactions**

Once established in a new area, AFF upset the dominance in the drosophilid community of *Drosophila simulans* and *D. willistoni* (Castro and Valente 2001, da Silva et al. 2005b, da Silva et al. 2005a) and can come to dominate the drosophilid community (Emerich et al. 2012). Effects on other drosophilid species were studied by Tidon et al. (2003). At the beginning of the wet season, endemic species predominated in their samples; however, by the end of the season, AFF predominated. African fig fly is able to coexist in figs with other drosophilids by differences in colonization sequence; while AFF attacks ripe figs, *D. simulans* infests decaying fruit (Matavelli et al. 2015).

Gilpin et al. (1986) compared all paired combinations of 28 drosophilid species—all *Drosophila* except for *Z. vittiger*, a species closely related to AFF, and often confused (Yassin and David 2010). Thick and thin food environments were compared, as well as two temperatures—19°C and 25°C. In the design used by Gilpin et al. “thick food” referred to a 40 ml plug (ca. 1 cm deep) of a standard mixture of corn starch and molasses, amended with prorionic acid and tegosept, while “thin food” referred to a layer of only 3 ml of standard medium on top of a 10 ml plug of agar. The food layer was only ca. 1 mm deep and was usually totally consumed. The differences in food supply are expected to result in differing levels of interspecific competition. Some species did better in one medium or the other, some at one temperature or the other. *Zaprionus* was a medium competitor in most of the comparisons, which were carried out in thick food at 25°C. However, one of the comparisons showed that *Zaprionus* was one of the best competitors in thin diets. In thick food, carried out at 19°C, *Zaprionus* was ranked 12 out of 28 in competitiveness; in thick medium at 25°C, it was ranked 8. But in thin food, it was ranked 5 at 25°C and ranked 3 at 19°C. The authors noted evidence for generalized interference under some experimental conditions. The larvae in those cases crowd the entire food surface, leaving insufficient room for other larvae. After a week, the food liquified, and many larvae and eggs drowned and were eaten by other larvae. In that study, *D. viridis* and *Z. vittiger* eliminated habitat for other larvae. The medium became soupy and subsequently turned into a hard, impenetrable surface. Larval competition was concluded to be important to the experimental outcome (Gilpin et al. 1986).

Because AFF outnumbered SWD when rearing drosophilids from field-collected fruit, while lacking the serrated ovipositor that facilitates entry by SWD, we conducted studies on entry into grape berries and development of the two species when present together (Shrader 2017). Berries that had been attacked by SWD were exposed to mated pairs of AFF. *Zaprionus* eggs differ from most drosophilid eggs in possessing four respiratory filaments rather than two (Fig. 6a). Eggs of AFF were sometimes laid singly at or in SWD oviposition sites, but large masses of eggs were also sometimes seen at such sites. The later-arriving AFF eggs were observed sharing the same ovipositional punctures in red grapes with SWD eggs. These eggs were seen with the respiratory horns projecting from the fruit surface (Fig. 6b). When the eggs were dissected from the ovipositional wound, two eggs were observed, one from each of SWD and AFF. Upon rearing the larvae to adults, AFF adults outnumbered those of SWD.

In larval competition studies, SWD developed but survival was hindered by the presence of AFF. Hence, AFF may compensate for a later arrival by its superior competitive characteristics.

**Sampling For African Fig Fly**

Trapping technology for AFF has received less attention than trapping systems for SWD. In India, fermenting fruit traps and sweep netting
were used to sample AFF (Karan et al. 2000). Populations were sampled by collecting fallen fruit by Castro and Valente (2001). Fermenting banana fruit were used as bait for sampling by Tidon et al. (2003). The species was sampled from fallen S. lycocarpum fruit by Leão and Tidon (2004). A 50:50 blend of fig juice (Ficus carica L.) in water was found to be the most attractive blend compared with juice of guava (Psidium guajava L.) and jelly palm (Butia capitata (Mart.) Becc.), and fig juice supplemented with glucose (Pasini et al. 2011).

African fig fly is often caught incidentally in SWD traps. In a comparison of blends for SWD, Iglesias et al. (2014) collected more AFF using a yeast + flour mix than in all other blends (apple cider vinegar, yeast + sugar, wine + vinegar, ACV + wine + sugar). In another SWD trapping study (Cha et al. 2014), AFF were collected in a blend of wine + vinegar. In a subsequent study, Cha et al. (2015) collected low numbers of AFF in traps in a raspberry planting in New York. There was no significant difference between wine + vinegar and a 4-component blend (acetic acid, ethanol, acetoin, and methionol). A combination of red wine and vinegar was more attractive to AFF than either wine or vinegar alone (Epsky et al. 2014). Actively fermenting grape juice was more attractive than unfermented juice, or juice that was older (Epsky et al. 2015). In Florida, a blend of ACV and beer was found to be the most attractive blend for AFF (Renkema et al. 2018). In that study, proximity of nightshade elevated captures of AFF.

Captures of AFF in using several attractant blends were compared in a cherimoya planting on the island of Maui by Willbrand and Pfeiffer (2019). Blends tested were apple cider vinegar, brown rice vinegar, and red wine tested separately, and each vinegar combined with wine. Adult AFF specimens were captured at all four localities surveyed. Both apple cider vinegar and brown rice vinegar when combined with red wine were effective at capturing AFF; however, there were no significant differences among blends (this differed from SWD results).

Pasini and Link (2011) evaluated several trap designs, including different colored plastic bottles and a McPhail trap, for sampling AFF. The clear plastic bottle performed the best; the McPhail trap was not effective.

**Control of African Fig Fly**

**Chemical Control**

African fig fly responds in a similar manner to many insecticides as SWD, but with some notable differences (Andreazza et al. 2017). The organophosphates dimethoate, malathion, the spinosyns spinosad, spinetoram, the pyrethroid lambda-cyhalothrin, and the diamide cyantraniliprole were found to be highly toxic to both larvae and adults of SWD as well as AFF. However, adding a feeding attractant increased mortality of SWD, but not AFF. The neonicotinoids caused moderate mortality for SWD, but only low mortality for AFF. Galego and Carareto (2010) suggested that genetic variation at the Est3 locus may predispose AFF toward resistance to organophosphorus insecticides.

**Biological Control**

Biological control for AFF has received less attention than for SWD. Various hymenopteran parasitoids have already been documented.

![Fig. 6](https://example.com/figure6.png)

**Fig. 6.** (a) Pair of respiratory filaments from Drosophila suzukii eggs protruding from oviposition punctures in a Viognier grape. (b) Four respiratory filaments typical of a Zaprionus egg. (c) Four respiratory filaments from a Zaprionus indianus egg protruding from an oviposition puncture in a Red Flame grape.
parasitizing AFF in Brazil, including *Leptopilina boulardi* (Barbotin, Carton and Kelner-Pillault), *Pachycrepoideus vindemiae* (Rondani), and *Spalangia endius* Walker (Pteromalidae) (Marchiori et al. 2003, Marchiori and Silva 2003, Silva et al. 2004). Low levels of parasitization in those studies (2–4%) were noted. *Leptopilina boulardi* is commonly reported from other drosophilids and is the most common parasitoid collected in northern Italy and Virginia sentinel traps, commonly reported from other drosophilids and is the most common parasitoid of *Drosophila suzukii* (Rossi Stacconi et al. 2013, Mazzetto et al. 2016). Wahls (2017) compared field parasitism between SWD and AFF by native parasitoids in the field in Virginia. Although SWD is notoriously a poor host for native parasitoids, even fewer attempts at parasitization were made on AFF eggs and neonate larvae.

**Summary**

Small fruit growers are still learning to deal with a disastrous new invasive, SWD. It appears that another new drosophilid, AFF, will require attention as we attempt to clarify its ability to survive winters in the eastern United States (including the latitudes where winter survival becomes problematic), phenological development relative to fruit maturation, ability to attack fruit, and ecological relationships with SWD. In situations where control of AFF may be needed, the use of biological control may be at least as problematic as for SWD.

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