From Eradication to Containment: Invasion of French Polynesia by *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) and Releases of Two Natural Enemies: A 17-Year Case Study

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Abstract. Four economic species of *Bactrocera* flies have sequentially invaded French Polynesia: *B. kirki* (Froggatt) in 1928, *B. tryoni* (Froggatt) in 1970, *B. dorsalis* (Hendel), detected on Tahiti in 1996, and *B. xanthodes* (Broun), detected on the Austral Islands in 1998. Following a failed attempt to eradicate *B. dorsalis*, documented in this paper, it became established and the dominant fruit fly, displacing *B. kirki* and *B. tryoni*. Two braconid parasitoids were introduced from Hawaii and established: *Fopius arisanus* (Sonan) (released in 2002) and *Diachasmimorpha longicaudata* (Ashmead) (released in 2007). By 2009 mean parasitism for fruit flies infesting common guava (*Psidium guajava*), Tahitian chestnut (*Inocarpus fagifer*), and tropical almond (*Terminalia catappa*) fruits on Tahiti was 70%, and 95% of the emerged parasitoids were *F. arisanus*. Numbers of *B. dorsalis* trapped from methyl eugenol and bred from guava, Tahitian chestnut and tropical almond have been reduced by 87%, 89%, 88%, and 91–94%, respectively, from the 2002–03 peaks.

Key words: Oriental fruit fly, competitive displacement, biological control, area-wide suppression, *Fopius arisanus*, *Diachasmimorpha longicaudata*.

Introduction

Oriental fruit fly (*Bactrocera dorsalis* (Hendel)) (herein referred to as OFF) is native to and widespread throughout tropical Asia, from India, through southern China, east to Taiwan and south to Vietnam and Thailand (Drew and Hancock 1994). OFF and its close relatives, *B. papayae* Drew and Hancock, *B. carambolae* Drew and Hancock, and *B. invadens* Drew, Tsuruta and White, are extremely polyphagous invasive pests that have readily established and become widespread in every country or island they have invaded. Invasions of OFF and its close relatives were successfully eradicated, through male annihilation combined with protein bait sprays, from the Mariana Islands (Steiner et al. 1970), the Ryukus (Koyoma et al. 1984), Australia (Cantrell et al. 2002), and Nauru (Allwood et al. 2002).

OFF was detected in Hawaii in 1946 (Clausen et al. 1965), and quickly became a prominent pest, resulting in the largest classical biological control program

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against fruit flies, with 32 natural enemies introduced (Bess and Haramoto 1961, Clausen et al. 1965). Two of these became the main parasitoids associated with OFF: *Fopius arisanus* (Sonan) (introduced 1950) and, to a lesser extent, *Diachasmimorpha longicaudata* (Ashmead) (introduced 1948) (Haramoto and Bess 1970). Biological control reduced OFF populations in Hawaii to much lower levels, possibly by as much as 95% (Waterhouse 1993).

OFF was discovered on Tahiti (French Polynesia) in June 1996, most probably introduced from Hawaii (Vargas et al. 2007). Two other economically important *Bactrocera* species had previously invaded Tahiti: *B. kirki* (Froggatt) (in 1928), and *B. tryoni* (in 1970). The failure of an OFF eradication attempt provided a unique opportunity to document subsequent interspecific competition and displacement among these three species, as OFF was becoming established, and attempt to replicate the biological control success achieved in Hawaii 50 years earlier. The impact of *F. arisanus* and *D. longicaudata* releases in Hawaii, Tahiti, and throughout the Pacific region were presented and summarized in Vargas et al. (2007, 2012a, 2012b). In this paper we focus on reviewing the previously unpublished history of the eradication attempts, the spread of *B. dorsalis* and parasitoid introductions to other French Polynesia islands to this date, and the long-term impact of biological control, based on unpublished data from 17 years of methyl eugenol trapping, maintained to this day, and 12 years of intensive host fruit surveys.

Materials and Methods

The impact of eradication measures and biological control were monitored through male lure trapping and host fruit surveys.

The trapping system in French Polynesia for population monitoring and detection of new invasions is a modified version of the Steiner trap (Steiner 1957), baited with liquid male lure (methyl eugenol or cue-lure) and malathion. The trap consists of a plastic 1-liter container (7.0 cm radius and 12.5 cm in height) (Platiserd, Papeete, Tahiti FP) with four 1.5-cm diameter holes, suspended by a tie wire in a horizontal position. The lure mixture in OFF detection traps is 4 ml of methyl eugenol solution (Farma Tech, North Bend, WA), including 1 ml of Malathion 50% EC (Venture Export Ltd, Auckland, NZ), applied with a dropper to two cotton dental wicks (Henry Schein Inc., Melville, NY) suspended inside the trap. The number of trapping sites varied greatly over the years, with traps around the entire island of Tahiti between 1996 and 2004, as follows: 44 sites (Jul96–Mar98), 34 sites (Mar–Dec98), 493 sites (1999), 262 sites (2000), 240 sites (Jan–Oct01), 424 sites (Oct01–Mar02), 387 sites (Apr–Jun02), 350 sites (Jun–Aug02), 143 sites (Sep02–Apr03), and 135 sites (Jan–Jun04). Trapping was interrupted between May and Dec 2003, and again between Jul 2004 and Jan 2006. When trapping resumed in 2006, the number of sites was reduced to 13, located along the most densely inhabited northwest coast of Tahiti, from Punaauia to Mahina communes, and these have remained continuously in service to this date. On nearby Moorea, traps were maintained continuously, between 1996 and 2002, as follows: 15 sites (Jul–Aug96), 19 to 25 sites (Sep96–Mar99), 34 to 38 sites (Apr99–Jul02), and 20 sites (Sep–Dec02). At all sites, each trap was emptied weekly and the wicks replaced with fresh lure solution every 6–8 weeks. Trapping results are presented as monthly mean number of flies per trap per day (herein referred to as FTD) for methyl eugenol traps. Data from cue-lure trapping was limited and fragmented by long interruptions, therefore not presented here.

Samples of potential host fruits were regularly collected along major roadways

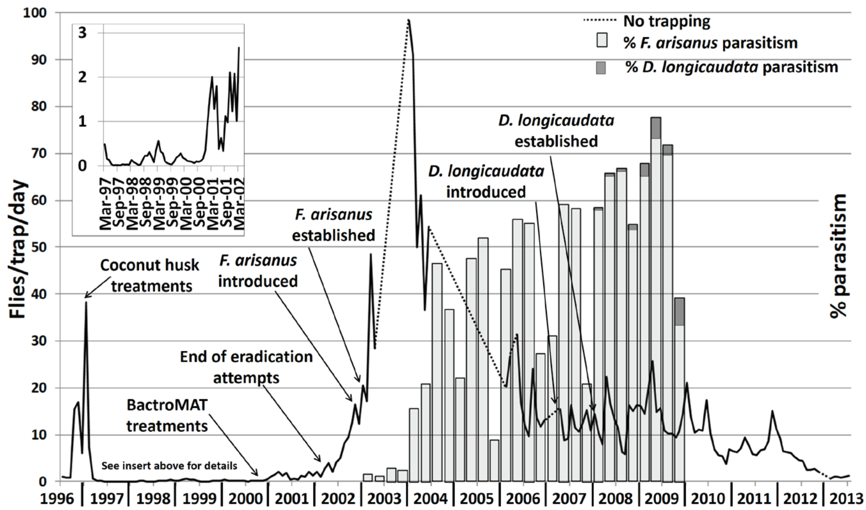

Figure 1. Monthly captures of *B. dorsalis* in methyl eugenol traps and quarterly percent parasitism on guava, Tahitian chestnut and tropical almond on Tahiti.

and in farms, mainly on Tahiti, and held in laboratory for fly and parasitoid emergence. Fruits were counted, weighed and placed in batches on wire metal screen (43x28x6 cm) inside plastic holding boxes (50x32x15 cm) that contained 1.5 cm of fine moist sawdust as pupation medium, and were held for 3 weeks until completion of larval development. Sawdust was sifted weekly to extract the pupae, which were transferred to smaller plastic containers and held in sawdust until emergence of flies or parasitoids. Fruits and pupae were kept in a room maintained at 22 ± 5°C, ambient (40–90%) RH, and a 12:12 (L:D) h photoperiod. Individual fruits were also frequently incubated in separate, smaller containers, to obtain additional information on variation of infestations within fruits and the percentage of fruits infested. Whether fruits were incubated in bulk or individually, a sample in this paper is defined as all fruits collected from one host species (or variety within a species) at one location during one day. For all samples and individually incubated fruits, fruit flies and parasitoids that emerged were counted and identified. We present here detailed data on the four most commonly sampled hosts during the study: *Psidium guajava* L. (guava), *Terminalia catappa* L. (tropical almond), *Inocarpus fagifer* (Parkinson) Fosberg (Tahitian chestnut), and *Mangifera indica* L. (mango). Results are presented as annual percentage of individual fruits infested, quarterly numbers of flies or parasitoids emerged per fruit and per kg fruit, and quarterly percent parasitism, calculated as [number of parasitoids x 100] / [number of flies (*B. dorsalis*, *B. tryoni*, *B. kirki*) + parasitoids (*F. arisanus*, *D. longicaudata*)]. It may not reflect the actual percentage mortality due to parasitoids, since unemerged pupae were not dissected to verify the cause of death.

Results and Discussion

Eradication attempt. At the time of its detection, in June 1996, OFF was confined to the southeast portion of Tahiti (Tahiti Iti or Tai'arapū), but it rapidly spread to the entire island and was detected on nearby Moorea in July. By the time the eradication program was initiated, in January 1997,

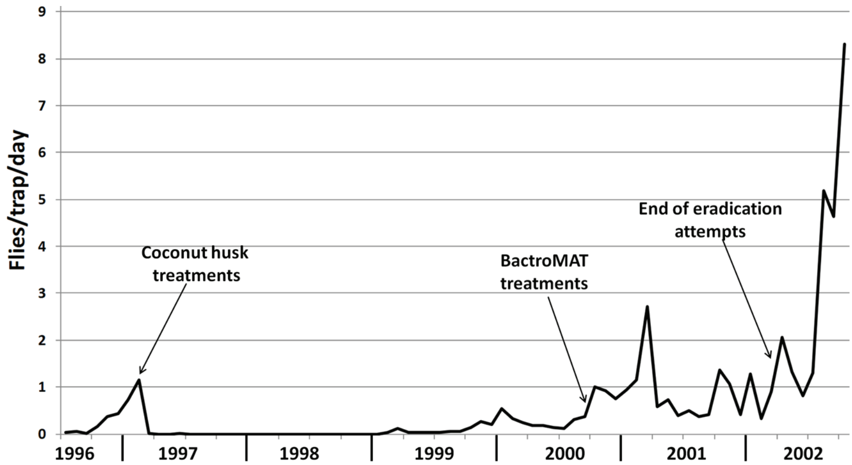

Figure 2. Monthly captures of *B. dorsalis* in methyl eugenol traps on Moorea.

captures were high on Tahiti (38 FTD) (Fig. 1), but still low on Moorea (0.7 FTD) (Fig. 2). Six eradication campaigns were applied, every 8 weeks, from Jan 27 to Dec 11, 1997. Male annihilation bait stations were prepared by soaking, for 2 hours, blocks cut from coconut husk (Fig. 3a) in a 3:1 methyl eugenol–malathion solution, resulting in 16–20-ml liquid per block on average. At each campaign, blocks were nailed to trees in all areas accessible by ground, at a density of 50x50m (400/km^2, or about 50–60 ml methyl eugenol per ha), along the narrow strip of inhabited regions along the coast line, with a mean number per campaign of 62,000 blocks on Tahiti and 23,500 on Moorea. Blocks were also dropped by helicopter along a 2-km wide belt inland of the ground treatment zone, in areas inaccessible by land, including the inland valleys. A mean of 2,400 kg of blocks were dropped by helicopter over Tahiti and Moorea each campaign. Additionally, limited protein bait spraying was applied on roadside vegetation in hot spot areas of high trap captures. Within two campaigns, trap captures quickly dropped to 0.49 FTD on Tahiti and 0.017 FTD on Moorea in March, 0.15 FTD on Tahiti and 0.002 on Moorea in April, and 0.01 FTD on Tahiti and zero on Moorea in July, and numbers subsequently remained very low (Figs. 1–2).

The program was however interrupted after six campaigns, leaving small residual hot spots of OFF breeding populations at five locations. Trap captures remained low (at most 0.3 FTD on Tahiti and only two flies trapped on Moorea) throughout 1998.

Eradication campaigns were resumed in April 1999, with 9 campaigns between April 1999 and September 2000, with mean ground applications of 61,000 blocks on Tahiti and 25,600 on Moorea, and aerial applications of 3,000 kg of blocks per campaign. Throughout that period, monthly FTD remained low on both islands, at most 0.56 but never below 0.03 (Figs. 1–2).

In October 2000, the coconut husk blocks were replaced with an early version of the fipronil-based BactroMAT-ME (= Amulet-ME) (Aventis CropScience Australia PTY), made of molded paper and each containing 2 ml of methyl eugenol and 0.008 ml of fipronil 25% (Fig. 3b) (8 ml methyl eugenol per ha). These were applied for an additional 9 campaigns,

Figure 3a, b. Coconut husk block (a) and BactroMAT-ME (b) bait stations used for eradication of *B. dorsalis*. (Photos: L. Leblanc).

with ground applications of 72,500 units per campaign on Tahiti and 34,400 on Moorea, plus 34,000 units dropped by helicopter on both islands during each of the first 7 campaigns. The campaigns were not effective, and trap captures gradually increased to 3.98 FTD during the last campaign in April 2002, 4 months after the last airdrop (Fig. 1).

While eradication would have likely been achieved with a few additional campaigns in early 1998, the subsequent failure to eradicate OFF can probably not be attributed to a single factor. However, reduced commitment as the program dragged on without rewarding results may have translated into less effective bait station distribution and protein bait application. Additionally, unlike the durable BactroMAT-CL, it was demonstrated and subsequently confirmed that the BactroMAT-ME bait stations quickly lost their methyl eugenol and were no longer attractive within a month of their application (R.P., unpublished; Vargas et al. 2005, 2010; Leblanc et al. 2011).

OFF becomes the dominant fruit fly. Following the abandonment of the eradication program, OFF trap captures on Tahiti quickly increased to reach a peak of 48.5 FTD in March 2003, and 98.4 FTD when trapping resumed in January 2004 (Fig. 1), and OFF started to spread to other islands. The situation worsened, with the evidence of establishment in the densely forested interior and breeding on strawberry guava, comparable to Hawaii, where strawberry and common guava can sustain as much as 95% of the OFF population (Newell and Haramoto 1968).

OFF eventually displaced *B. tryoni* and *B. kirki* and became the dominant species in many host fruits (Vargas et al. 2007, 2012). The proportion of OFF among flies emerged from fruit samples increased (1998 to 2009) from 0.2 to 85.2% in guava, 0 to 34.0% in tropical almond, 0.7 to 91.4% in Tahitian chestnut, and 0 to 98.5% in mango (Fig. 4). *Bactrocera kirki* was especially affected, reduced by 2009 to 0.3% in guava, 3.4% in tropical almond, 0.05% in Tahitian chestnut, and 0.8% in mango. Similar displacements were also documented by OFF over *Ceratitis capitata* (Wiedemann) in Hawaii (Bess and Haramoto 1961), *B. invadens* over *C. cosyra* (Walker) in Kenya (Ekesi et al. 2009), and *B. zonata* (Saunders) over *C. rosa* Karsch and *C. catoirii* Guérin-Méneville in Réunion (Duyck et al. 2004, 2006). It is also likely that *B. tryoni* displaced and suppressed *B. kirki* after its introduction in 1970, because even before OFF introduction, *B. kirki* was already in minority in French Polynesia, yet a prominent pest in Samoa and Tonga, where *B. tryoni* does not occur (Leblanc et al. 2012).

Although the exact mechanism of

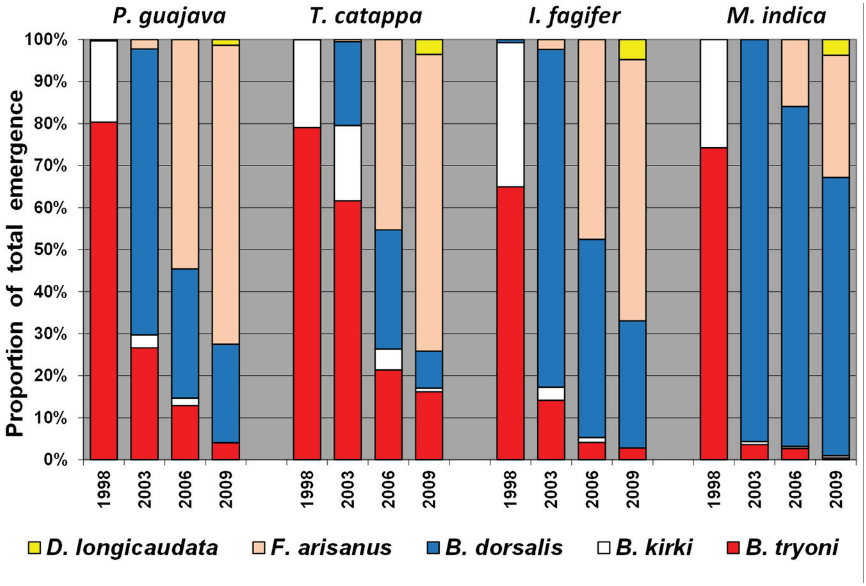

Figure 4. Annual proportion of fruit fly (*B. dorsalis*, *B. tryoni*, *B. kirki*) and parasitoid (*F. arisanus*, *D. longicaudata*) emergences in guava, tropical almond, Tahitian chestnut, and mango fruits for selected years.

competitive displacement by *B. dorsalis* is unknown in French Polynesia, probable contributing factors, based on previous studies in Hawaii and current fruit infestation records, were a high reproductive rate and increased longevity under mild tropical temperatures (Vargas et al. 1997), an aggressive behavior in adult flies and larval competition (Ekesi et al. 2009), a developmental advantage in preferred hosts such as *P. guajava* (Bess and Haramoto 1961, Vargas et al. 1995, 2012a) and a very broad host range. OFF is a polyphagous pest in Southeast Asia, where it was bred from 39 families, 76 genera and 116 species of hosts (Allwood et al. 1999). It is equally polyphagous in French Polynesia, where it was bred from 19 families, 29 genera and 37 species, based on 4306 fruit samples collected in 11 years (Leblanc et al. 2012).

OFF emergences from the main hosts reached peaks at levels of 20.0 per fruit and 246.6 per kg fruit for guava in late 2003 (Figs. 5a, 6a), 13.5 per fruit and 63.7 per kg fruit for mango in late 2003 (Figs. 5d, 6d), 19.8 per fruit and 130.8 per kg for Tahitian chestnut in late 2004 (Figs. 5b, 6b), and two peaks, 6.6 per fruit and 259.1 per kg in late 2002 and 4.1 per fruit and 133.8 per kg in early 2004, for tropical almond (Figs. 5c, 6c).

Parasitoid introductions and their impact. Two species of parasitoids were introduced into French Polynesia from Hawaii, where they had been kept in continuous mass production in laboratory for over 20 years (Bautista et al. 1999, Manoukis et al. 2011). Ten shipments of *F. arisanus* (50,000 wasps each) were sent from Hawaii, between December 2002 and October 2004, and released in 9 communes of Tahiti (Vargas et al. 2007). Establishment was confirmed through host surveys within 3 months, and *F. arisanus* spread to all 21 communes within

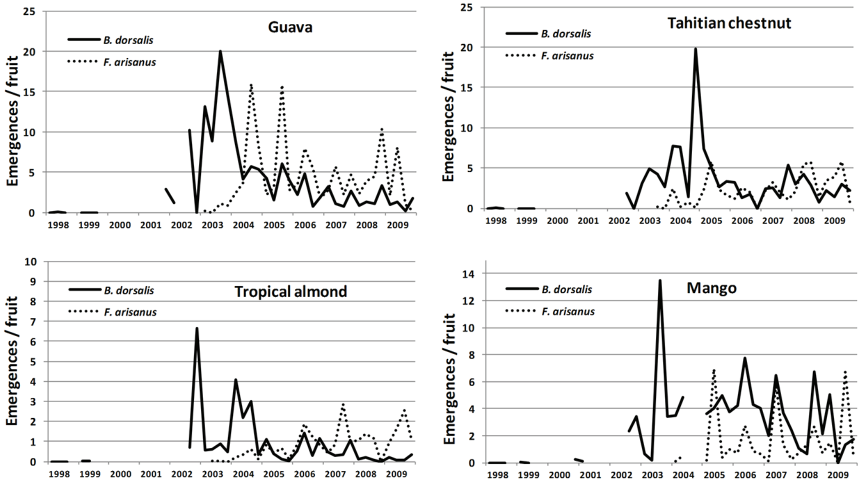

Figure 5a–d. Quarterly emergences on Tahiti of *B. dorsalis* and *F. arisanus* per fruit for guava (a), Tahitian chestnut (b), tropical almond (c), and mango (d). Numbers of fruits used for each host and each year (for guava, Tahitian chestnut, tropical almond and mango, respectively) were: 1998: 1634, 16238, 5314, 67; 1999: 264, 304, 993, 404; 2000: 37, 40, 154, 64; 2001: 52, 0, 20, 74; 2002: 492, 1204, 474, 268; 2003: 1531, 1539, 2685, 977; 2004: 2252, 1324, 810, 291; 2005: 1071, 904, 4373, 436; 2006: 1927, 3343, 3140, 1044; 2007: 1537, 1525, 4200, 1814; 2008: 3255, 2648, 5045, 2052; 2009: 1515, 1972, 5475, 549.

3 years (Vargas et al 2007). Similarly, five shipments of *D. longicaudata* (5000 wasps in total) were released on Tahiti between May 2007 and August 2008, and establishment was confirmed in March 2008 (Vargas et al. 2012b). By late 2009, it was already widespread over 10 of the 21 communes. On Moorea, *F. arisanus* was released once, in February 2003, and its establishment was confirmed after 6 months.

The impact of *F. arisanus* documented in Hawaii, with 65–70% parasitism (Haramoto and Bess 1970) and a subsequent reduction of *B. dorsalis* populations, possibly by as much as 95% compared to 1947–1949 peak (Waterhouse 1993), was observed and documented in French Polynesia as well. Quarterly percent parasitism on Tahiti, collectively on guava, tropical almond and Tahitian chestnut, was initially low (<3%), as *F. arisanus* was becoming established, but increased to as high as 47% and 52% in 2004 and 2005, respectively, and reached an annual mean of 70% in 2009 (Fig. 4). Quarterly emergences of *B. dorsalis* per fruit from these three fruits were decreased, compared to the 2002–2004 peaks, by an average (from the third quarter of 2005 to late 2009) of 88% for *I. fagifer*, 89% for *P. guajava*, and 91–94% for *T. catappa* (Figs. 5a, b, c), comparable to decreases in emergences per kg fruit (Figs. 6a, b, c) reported previously by Vargas et al. (2012b). Of notable interest, for yet unknown reasons, was the decrease in percent parasitism, and frequently in emergence per fruit as well, during the last quarter of each year for these three fruits (Figs. 5, 6). Also, the

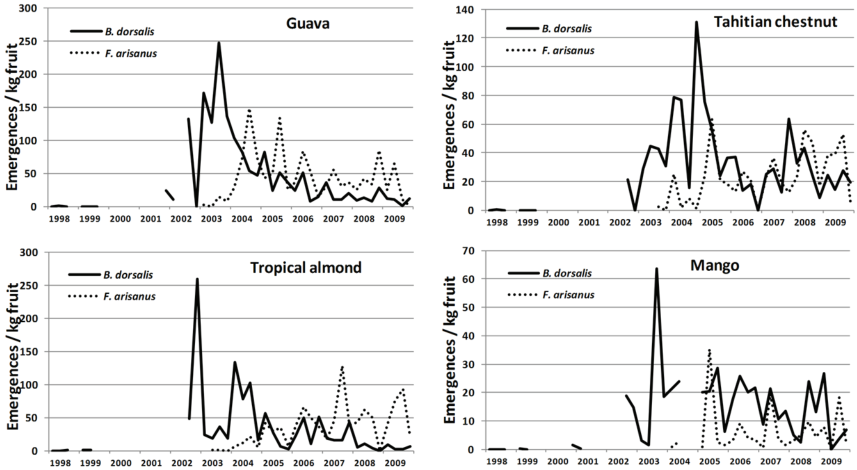

Figure 6a–d. Quarterly emergences on Tahiti of *B. dorsalis* and *F. arisanus* per kg fruit for guava (a), Tahitian chestnut (b), tropical almond (c), and mango (d). See under Figure 5 for number of fruits sampled each year.

impact of *F. arisanus* was not nearly as pronounced for mango, with 24.9% parasitism in 2009 (Vargas et al. 2012b). Nonetheless a 74.4% reduction of infestations per fruit was recorded (Figs. 5d, 6d).

A similar long-term reduction was also observed in OFF captures in methyl eugenol traps. When trapping resumed in 2006, monthly trap captures were never above 30 FTD and were maintained at a mean of 12.5 FTD until late 2011, a 87% decrease compared to the late 2003 all time high (Fig. 4). Trapping data have dropped even further since early 2012 (Fig. 1), but it may be too early to determine whether this is the start of a long-term trend.

Contrary to *F. arisanus*, *D. longicaudata* parasitism has remained generally less than 5% (Vargas et al. 2012b) (Fig. 1), similar to Hawaii and the South Pacific (Vargas et al. 2012a). Nonetheless, this species contributes to overall parasitism by foraging on the ground, seeking mature larvae in fallen fruits (Purcell et al. 1994), and likely infesting a proportion of larvae previously missed by *F. arisanus*.

Biological control has decreased the number of emergences per kg fruit and per fruit, as well as the overall population, but did not decrease the percentage of individual fruits infested as drastically. On guava, infestations were reduced from 88.8% in 2003 to 33.3% in 2009 (Fig. 7), comparable to the 100% to 60.5% reduction on guava in Hawaii between 1947 and 1955 (Clausen et al. 1965). Biological control helps decrease the overall population to a lower level, but only integrated control, combining crop sanitation, male annihilation and protein bait sprays, as was successfully implemented in Hawaii (Vargas et al. 2008), will reduce substantially percent fruits infested, the true indicator of economic losses in commercial fruit production.

OFF also became established on a number of other islands in French Polynesia, and *F. arisanus*, recovered from infested fruits collected on Tahiti, was subsequently introduced on many of these

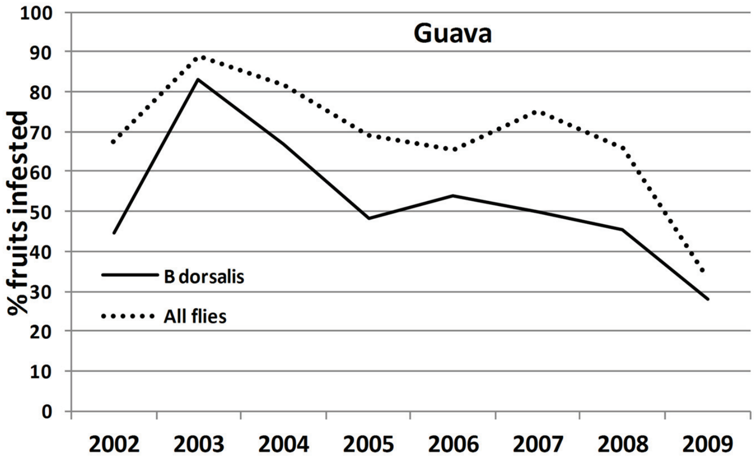

Figure 7. Annual percentage of individual guavas infested with fruit flies on Tahiti. Number of fruits incubated individually each year were: 172 in 2002, 348 in 2003, 539 in 2004, 607 in 2005, 98 in 2006, 4 in 2007, 237 in 2008, and 807 in 2009.

islands (Fig. 8). On the other Society Islands, OFF was detected on Huahine, Raiatea, Tahaa, Bora Bora, and Maupiti in 2002. *Fopius arisanus* was released on Huahine, Raiatea, and Tahaa in 2003, and was recovered from all three islands during host fruit surveys in 2006 (Vargas et al. 2007). In the Austral Islands, OFF was detected on Rimatara in 2002, and later on Rurutu. *Fopius arisanus* was released on Rurutu and Tubuai (to control *B. tryoni*) in 2006, Rimatara in 2009, and Raivavae in 2012 (to control *B. tryoni*). Its establishment was confirmed on Rimatara. *Bactrocera xanthodes* (Broun) also invaded the Austral Islands, from Western Polynesia, initially detected on Raivavae (1998), and subsequently on Rurutu (2000) and Rimatara (2002). It was eradicated from Raivavae by male annihilation. The Marquesas were invaded by *B. tryoni* in 1999, which was widespread over the entire group by 2003, and by OFF, initially detected on Nuku Hiva in 2002, and widespread over most islands by 2009. *F. arisanus* was released on most of the Marquesas islands between 2008 and 2010. On Fatu Hiva, it was released in February 2008, recovered from fruit two months later, and a considerable reduction in OFF trap captures was noted by September, possibly due to *F. arisanus* releases (R.P., unpublished). In the Toamotu-Gambier group, OFF was detected and promptly eradicated from Hao in February 2000. It was detected on Rangiroa and Takaroa in 2002, and successively on Tikehau, Makatea, and Kaukura, between 2008 and 2010. *Fopius arisanus* was released on Fakarava (2010) and Mangareva (2011) to control *B. tryoni*.

In addition to French Polynesia, *F. arisanus* was established to control various species of *Bactrocera* in Australia and 6 Pacific Island countries (Vargas et al. 2012a). Although parasitism has been at times relatively high, it is considerably lower on species of *Bactrocera* other than OFF. However, *B. tryoni* was shown to be a suitable host for *F. arisanus* in laboratory in French Polynesia (R.P., unpublished) and in both lab and field conditions in

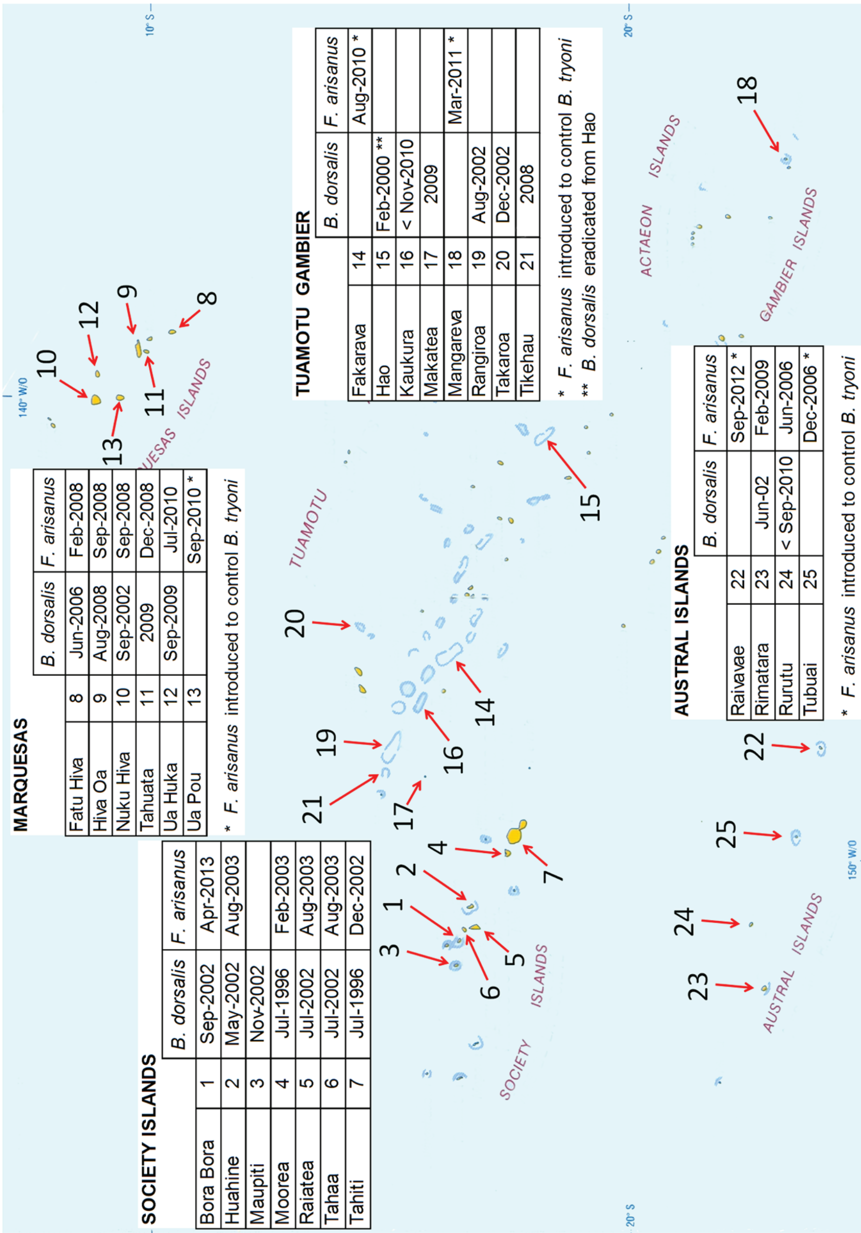

Figure 8. Dates of detection of *B. dorsalis* and introduction of *F. arisanus* on the various islands of French Polynesia.

Australia (Quimio and Walter 2001, Snowball and Lukins 1966). *Bactrocera kirki* is also a suitable host in French Polynesia, since *F. arisanus* breeds on this species in Samoa and Tonga (Vargas et al. 2012a).

Conclusions

The French Polynesia experience has taught important lessons to help conduct fruit fly eradication and is a good example of a well documented classical biological control program, with extensive pre- and long-term post-release monitoring. Words of caution for future eradication endeavors include: to maintain a surveillance trap network for early detection of invasions, and a well defined emergency response plan, including a stockpile of traps and lures, to initiate a prompt response and eradication; to be fully committed to the completion of eradication, avoiding shortcuts, partial treatments or early termination of the program; to correctly apply protein bait spraying, uniformly as spot sprays rather than as a jet along roadsides, in hot spot areas of breeding flies; and to be cautious with adopting a new technology if it was not previously demonstrated to work effectively.

The French Polynesia program is the most successful OFF biological control attempt outside of Hawaii so far. *Fopius arisanus* may perhaps be best adapted to parasitize OFF and its close relatives, such as *B. invadens* in Africa, where *F. arisanus* was recently released and established in such distant countries as Kenya, Sénégal, and Bénin. Plans are also underway to introduce it to northern Brazil, where invasive *B. carambolae* was not successfully eradicated. Since it is not known how this parasitoid will fare on large continents, compared to islands, the progression of its establishment and impact in Africa and South America, before and after releases, should be closely monitored and documented, as was done in French Polynesia.

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