Host use of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), in South Africa

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Abstract

The highly invasive oriental fruit fly, *Bactrocera dorsalis* (Hendel), has been declared present in the northern parts of South Africa since 2013. A study was thus initiated in July 2014 to determine the host range and field population of the pest species in the region. Fruit were collected from commercial fruit production, interface (smaller commercial blocks surrounded by natural savannah vegetation) and natural areas (savannah vegetation) throughout Limpopo and Mpumalanga provinces, South Africa. Field sites consisted of five commercial fruit production sites, two interface sites and two natural areas. Fruit samples from the tree and the ground were collected and incubated separately to determine infesting fruit fly species and the degree of infestation. Adult *B. dorsalis* populations were monitored at each field site using three methyl eugenol-baited bucket traps to estimate population pressure and to determine with the use of time series analysis if monthly trap captures were correlated with fruit infestation. *Bactrocera dorsalis* was reared from seven plant species: two from commercial orchards (*Mangifera indica* cv. [Tommy Atkins, Sensation], *Citrus sinensis* cv. [Valencia]), and five from other plant species (*Psidium guajava*, *Anacardium occidentale*, *Solanum mauritianum*, *Xylotheca kraussiana*, *Vangueria infausta*). Fruit utilized by *B. dorsalis* were also infested or damaged by other species, which may indicate opportunism by the pest, and the potential for competitive interactions. Time series analyses show adult population increased two months after an increase in mean temperature in all sites, four months after rainfall in natural and interface sites, and one month and three months after fruit infestation in commercial and natural and interface sites, respectively. This study

shows *B. dorsalis* utilizing a limited range of hosts in South Africa. However, the host range of *B. dorsalis* may expand as it may not yet have encountered all potential hosts.

Keywords

Mangifera indica, cultivated fruit, *Citrus*, fruit infestation

Introduction

International trade of fresh produce has led to the introduction of new pests into areas where they were previously absent (Kirk and Terry 2003; Levine and D'Antonio 2003). In many cases, these introductions go undetected because the pest fails to become established in the new environment (Williamson and Fitter 1996; Simberloff and Gibbons 2004). However, when biotic and abiotic factors are favourable (e.g., climate, host availability, predators, competition, propagule pressure, etc.), a new pest may become successfully established.

The establishment and then potential invasion of a new pest is a gradual process, whereby the initial area of introduction is first colonised before the pest dominates a niche and spreads further afield (Dobson and May 1986; Liebhold et al. 1995). Biological invasions by fruit flies (Diptera: Tephritidae) have been well documented and have sometimes been correlated with competitive displacement of indigenous or established fruit fly species by the novel invader (Duyck et al. 2004). There are a number of factors that lead to the successful displacement of an already established pest, such as faster growth rate of the immature life stages, larger body mass, and subsequent monopolisation of finite resources (Fitt 1989; Fitt 1990; Duyck et al. 2004). These factors have resulted in established fruit fly species being limited to extremes of their fundamental niche, expressed as reproduction in fruit available earlier in the season or at higher altitude, or increased host specialisation in the presence of competition (DeBach 1966; Lux et al. 2003; Mwatawala et al. 2009b).

The Oriental fruit fly, *Bactrocera dorsalis*, previously recognised as *Bactrocera invadens* Drew, Tsuruta & White, was detected for the first time on the African continent in Kenya in 2003 (Lux et al. 2003). Recently, *B. invadens* and two other *Bactrocera* species (i.e., *B. papayae* and *Bactrocera philippinensis* (Drew & Hancock), were synonymised with *B. dorsalis* s.s. (Drew and Romig 2013; Schutze et al. 2015). Since the first detection of this pest in Africa, it has subsequently spread throughout sub-Saharan Africa (Khamis et al. 2009; De Meyer et al. 2010; Manrakhan et al. 2015; De Villiers et al. 2016). *Bactrocera dorsalis* is a highly polyphagous pest with multiple overlapping generations and high intrinsic rate of increase, making it of great economic concern (Ekesi et al. 2006; Stephens et al. 2007). In its natural range, *B. dorsalis* has been recorded infesting both cultivated and natural fruits from hosts spanning 22 species in 16 different plant families in Thailand (Clarke et al. 2001), and from 41 species spanning 20 different families in the Pacific Islands (Leblanc et al. 2012). Host surveys of *B. dorsalis* in West Africa have shown utilization of 46 species from 23 families, and in East Africa of 30 species from 13 families (Rwomushana et al. 2008; Mwatawala et al. 2009a; Goergen et al. 2011).

The severity of crop damage by *B. dorsalis* can be influenced by multiple extrinsic factors. In studies in and outside of Africa, populations have been observed to fluctuate sporadically in response to annual rainfall, with population size peaking throughout the rainy season (Tan and Serit 1994; Mwatawala et al. 2009b). However, populations are not completely dependent on the rainy season because the abundance of this polyphagous species can peak with host availability (Tan and Serit 1994; Mwatawala et al. 2009b). Fluctuations in the population size of *B. dorsalis* are typically monitored with the use of traps baited with methyl eugenol, to which males respond strongly (Tan and Serit 1994; Shelly et al. 2004). Females of *B. dorsalis* respond to food-based lures, but at a far lower level than males response to methyl eugenol (Barry et al. 2006).

Bactrocera dorsalis was first detected in South Africa in 2010, and despite a number of eradication and reintroduction events the pest was declared present in the northern regions of the country in 2013 (Manrakhan et al. 2015). An increase in *B. dorsalis* catches in methyl eugenol baited traps in the northern parts of South Africa between 2012 and 2013 (Manrakhan et al. 2015) was indicative of the pest population breeding in hosts present in these areas. To date though, there is still no information on the host utilization patterns for *B. dorsalis* in the northern parts of South Africa. In studies conducted in East and West Africa, a number of fruit types such as citrus and mango, which are cultivated commercially in the northern areas of South Africa for export, have been recorded as hosts for *B. dorsalis* (Mwatawala et al. 2006a; Vayssières et al. 2009; Migani et al. 2013). Consequently, it is important to quantify the natural infestation of commercial fruit species by *B. dorsalis* in South Africa. Additionally, as a basis for area-wide management of this new pest in the northern parts of South Africa, it is valuable to quantify the host status of indigenous fruit species for *B. dorsalis*.

This study determined the use of natural and cultivated fruiting plant species to establish the host range of *B. dorsalis* in its current distribution in South Africa. Population levels of the pest in these areas were also assessed and correlated with host presence and other extrinsic factors. Fruit infestation by indigenous fruit fly species was also recorded to identify the potential for current or future competitive displacement by *B. dorsalis*.

Materials and methods

Field sites

Field sites were located in Mpumalanga and Limpopo provinces of South Africa, where *B. dorsalis* is known to occur. Field sites consisted of three types: commercial orchards, interface (single orchard blocks surrounded by an equal area of natural vegetation) and natural habitat (Figure S1). In Limpopo province there were two commercial sites and two interface sites (Table S1). Both commercial sites in Limpopo were large-scale commercial citrus farms with routine bait spray treatments and well-maintained orchard sanitation that were located in the Letsitele valley. One interface site was a private farm located near the town of Tzaneen on which the only fruit fly control was the use of baited fruit fly traps in the mango orchards. The other interface site was a farm in the Thohoyandou district with a mixture of crops. The field sites in Mpumalanga comprised three commercial and two natural sites (Table S1). The commercial sites included well-maintained citrus farms with routine bait spray treatments and orchard sanitation. There were other types of cultivated crops in two of the commercial sites. The two natural sites in Mpumalanga province were a wildlife breeding farm relying on rainfall for water near Nelspruit, and the South African National Biodiversity Institute (SANBI) Lowveld National Botanical Gardens, hosting the largest biodiversity of plants in South Africa and using the Crocodile River for irrigation, also in Nelspruit. The large majority of both provinces fall within the savannah biome of southern Africa, which comprises widely spaced deciduous trees or shrubs with a well-developed understorey of grasses. Temperature and rainfall records for each site were obtained from the nearest meteorological station maintained by the ARC-Institute for Water, Climate and Soils and QMS AgriScience, Letsitele (Figure S2).

Adult population sampling

Three methyl eugenol baited Lynfield™ bucket traps (River BioScience, Port Elizabeth, South Africa) with Dichlorvos (Vapona Agricultural Strip, Acorn Products (Pty.) Ltd., North

Riding, South Africa) as the killing agent were placed at each field site, and serviced and re-baited on a monthly basis. Traps on each field site were at least 500 m apart. Trap captures were sorted and *B. dorsalis* males were identified and counted by C. D. Theron using published keys (Drew et al. 2005; White 2006). A reference sample of trap captures was placed in analytical grade ethanol (99.9%) and stored at Citrus Research International, Nelspruit.

Fruit collection

Fruit were collected on a monthly basis from each site to sample a wide range of fruit types and cover various stages of ripeness of a particular fruit type. Fruit collected included those from naturally occurring vegetation, weeds, ornamental plants, and cultivated fruit. Fruit were sampled based on the methods of Copeland et al. (2002). Field sites were searched by vehicle for fruit. Any fruit from the same species collected within a 50 m radius on the same day were recorded as a single sample. The aim was to collect no less than 1 kg of fruit from natural vegetation, weeds and ornamental plants, and 2 kg of fruit from sampled commercial orchards. Fruit collected from separate orchard blocks were recorded as independent samples. Fruit collected from the tree and the ground were kept separate in brown paper bags and transported to the lab on shredded paper in boxes. Fruit samples were weighed, dipped in an antifungal agent (1ml/L; Sporekil Agricultural Disinfectant, Agritec Pty. Ltd., Carrim Downs, Australia) and incubated in a climate room at 26 (±1)°C at 70% relative humidity for 8 weeks. Fruit samples were checked daily for fruit fly emergence. At the end of the 8-week period, sand from the emergence box was sieved for any dead adults before being discarded. Photos of the plant and biological samples were collected and identified by a botanist at the SANBI Lowveld National Botanical Gardens in Nelspruit (W. Froneman).

Species identification

Fruit flies (Tephritidae) that emerged from collected fruit were placed in a separate container with water and food (sugar and yeast hydrolysate mixture [4:1]) for four days to allow full colour development, after which they were killed by freezing. *Bactrocera dorsalis* samples were identified using published keys (White 2006). Other fruit fly species were identified to either genus or species level using published keys (De Meyer 1998; De Meyer and Copeland 2005; De Meyer and Freidberg 2005).

Data analyses

All data were analyzed in R Studio (Version 0.99.902) running R (version 3.3.1) (R Core Team 2013). *Bactrocera dorsalis* adults caught by each trap in each month (flies/trap/month) were used as independent data points. Field sites were grouped into two types for all analyses: commercial, and natural and interface sites. This was done due to the relative size and proximity of interface sites to natural sites, and the very limited fruit fly control techniques applied at interface sites. There were few differences in temperature and rainfall across the sampled sites (Figure S2), so province was not included as a factor in any analyses. A linear model was used to determine the effects of site type and month, and their interaction, on adult trap captures. Trap captures were log-transformed [log(x+1)] so that model residuals were randomly distributed. Type III sums of squares, permitted by the 'car' library, were used to summarize model effects. Post-hoc Tukey multiple comparison tests were performed using 'multcomp'.

It was not possible to sample all developmental stages of fruit from all plant species. Despite these limitations, fruit infestation was recorded as the number of *B. dorsalis* flies emerging from a particular sample divided by the total weight of the fruit sample (i.e., flies per kilogram of fruit). Data for trap catches was analysed with a negative binomial distribution with a log link function with the farm type and province as independent variables. The p-values were then adjusted to represent the F-test. The effects of fruit type and month on fruit infestation by *B. dorsalis* were analysed in R using the libraries MASS (Ripley et al. 2015), multcomp (Hothorn et al. 2013) and lme4 (Bates et al. 2016). A negative binomial distribution was the best fit for the data providing the lowest residuals for error and degrees of freedom. Due to uneven availability of fruit over the period of the study, interactions could not be included in this model.

Time series analysis using the 'astsa' library in R was performed to cross-correlate overall mean *B. dorsalis* caught by each trap in each month with mean monthly minimum temperature, mean monthly maximum temperature, and total monthly rainfall for each site type. Mean monthly fruit infestation by *B. dorsalis* was also cross-correlated with mean monthly trap captures of *B. dorsalis* for each site type.

Results

Adult B. dorsalis abundance

There was a significant effect of site type ($F_{1,341}$=13.344, P<0.001), month ($F_{1,341}$=34.388, P<0.001), and the interaction of site type and month ($F_{1,11}$=2.987, P<0.001) on captures of adult *B. dorsalis* in traps. Captures of adult *B. dorsalis* per trap per month were generally higher at natural and interface sites in comparison with commercial sites. Overall, captures between July to December 2014 were low and did not differ significantly from each other. Relative to the low captures of *B. dorsalis* in December 2014, trap captures increased to peak in February 2015 in commercial sites, and March 2015 in natural and interface sites (Figure 1). The difference between these peaks in *B. dorsalis* trap captures in each site type was significant. After these peaks, trap captures declined to low levels by May 2015 in commercial sites, and by June 2015 in natural and interface sites. There was an overall upward trend in adult trap captures over the period July 2014- June 2015.

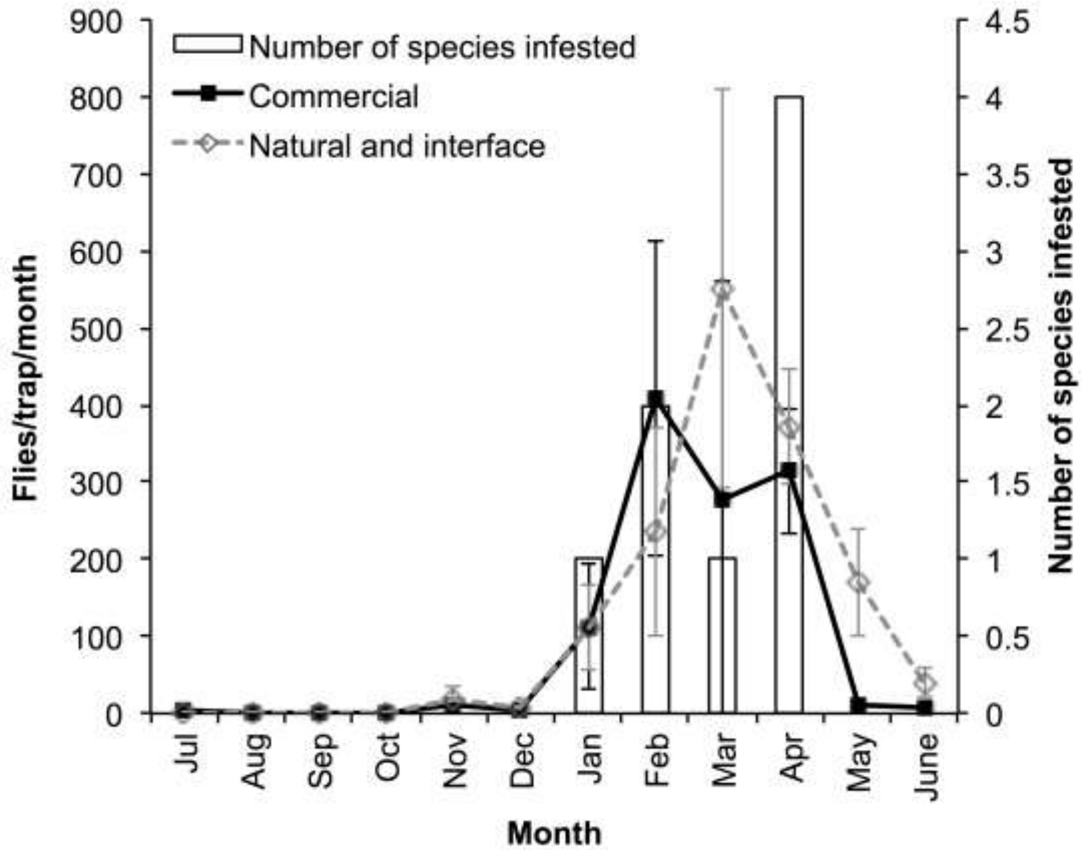

Figure 1. Mean (± 1 s.e.) trap captures of *B. dorsalis* for commercial and natural and interface sites, and the number of fruit species from which *B. dorsalis* were reared between July 2014- June 2015.

Fruit infestation

During the 12-month period over 160 fruit samples were collected from the designated field sites. Fruit samples covered more than 50 different species from 23 families collected from both commercial and natural vegetation (Table 1). Similarly, collected fruit were rarely infested with *B. dorsalis*. *Bactrocera dorsalis* (Hendel) was reared from seven different species spanning six families of fruit from commercial and non-commercial field sites (Table 1) in Limpopo and Mpumalanga provinces in South Africa.

Table 1. Host species collected from commercial and natural and interface sites infested with *Bactrocera dorsalis*. Values represent range (and mean) of infestation (flies per kg fruit) recorded between July 2014-June 2015 for *B. dorsalis* and other Tephritidae.

Family	Species	Common name	Collected	Infestation (flies per kg)	
				Tephritidae	*Bactrocera dorsalis*
Anacardiaceae	*Mangifera indica* (L.)	Mango cv Tommy Atkins	Ground	19.80-653.52 (180.56)	12.73-72.54 (34.07)
	Anacardium occidentale (L.)	Cashew	Ground	5.35*	4.46*
Kiggelariaceae	*Xylotheca kraussiana* (Hochst.)	African dogrose	Tree	291.34*	39.37*
Myrtaceae	*Psidium guajava* (L.)	Guava	Tree	6.78*	0.48*
Rubiaceae	*Vangueria infausta* (Burchell)	Wild medlar	Ground	30.28*	6.34*
Rutaceae	*Citrus sinensis* (Osbeck)	Valencia	Tree	0	3.3*
Solanaceae	*Solanum mauritianum* (Scop.)	Bug weed	Tree	0	20.41*

* Values from a single sample

Bactrocera dorsalis adults were reared from seven fruit species, two commercially cultivated species: mango (*Mangifera indica*) (L.), and *Citrus sinensis* cv. Valencia (Osbeck); and five non-commercially cultivated species: guava (*Psidium guajava*) (L.), cashew (*Anacardium occidentale*) (L.), *Solanum mauritianum* (Scop.), *Vangueria infausta* (Burch.) and *Xylotheca kraussiana* (Hochst.) (Table 1). There was a significant difference in infestation levels (measured as flies/kg fruit) between these fruit types (F_{42}=1.746, P= 0.017) and months (F_{11}=3.419, P<0.001). Fruit infested with *B. dorsalis*, were collected from both the tree and ground (Table 1 and S2). Fruit infested by *B. dorsalis* often showed damage and exposed pulp. Fruit infested by *B. dorsalis* and collected from the tree were always at the ripe stages (Table 1 and S2). Valencia oranges, infested by *B. dorsalis* were also infested with false codling moth, *Thaumatotibia leucotreta* (Meyrick) (Lepidoptera:Tortricidae). The fruit from which *B. dorsalis* emerged were often also infested with *Ceratitis* species including *C. cosyra* (Walker), *C. rosa* (Karsch) and *C. capitata* (Wiedemann) (Table S2).

Cross-correlation of adult B. dorsalis with weather and fruit infestation

There was significant (p<0.05) cross correlation between average temperature and average minimum temperature with mean catch of *B. dorsalis* per month in both site types (Figure 2a). Mean *B. dorsalis* trapped per month increased positively after a lag of one to two months following an increase in average maximum and minimum temperature at commercial and natural and interface sites (Figure 2b). At commercial sites, mean *B. dorsalis* trapped per month was not significantly cross correlated with monthly rainfall, but at natural and interface sites, *B. dorsalis* trapped per month was positively correlated with increasing rainfall after a lag of three and four months respectively (Figure 2c).

Increases in mean *B. dorsalis* trapped per month were significantly correlated with fruit infestation (Figure 2d). At commercial sites, peak trap captures of *B. dorsalis* followed peak fruit infestation by one month. At natural and interface sites, there was a delay of three months from peak fruit infestation and peak trap captures of *B. dorsalis*. In both cases, the detection of infested mangoes occurred prior to peaks in the adult population. However, it was also apparent that infestation of mangoes did not occur until adult population levels reached a certain threshold. For example, at Tzaneen Country Lodge, ripe mango fruit (*Mangifera indica* cv Tommy Atkins) were collected from the ground in November and December 2014. From these samples, only *Ceratitis cosyra* emerged (87.83 flies/kg fruit and 260.42 flies/kg fruit, respectively). The *B. dorsalis* population at the site was very low at these times (0.38 and 20.38 flies per trap month, respectively). It was only after adult *B. dorsalis* population levels increased above 50 flies per trap month that they were reared from

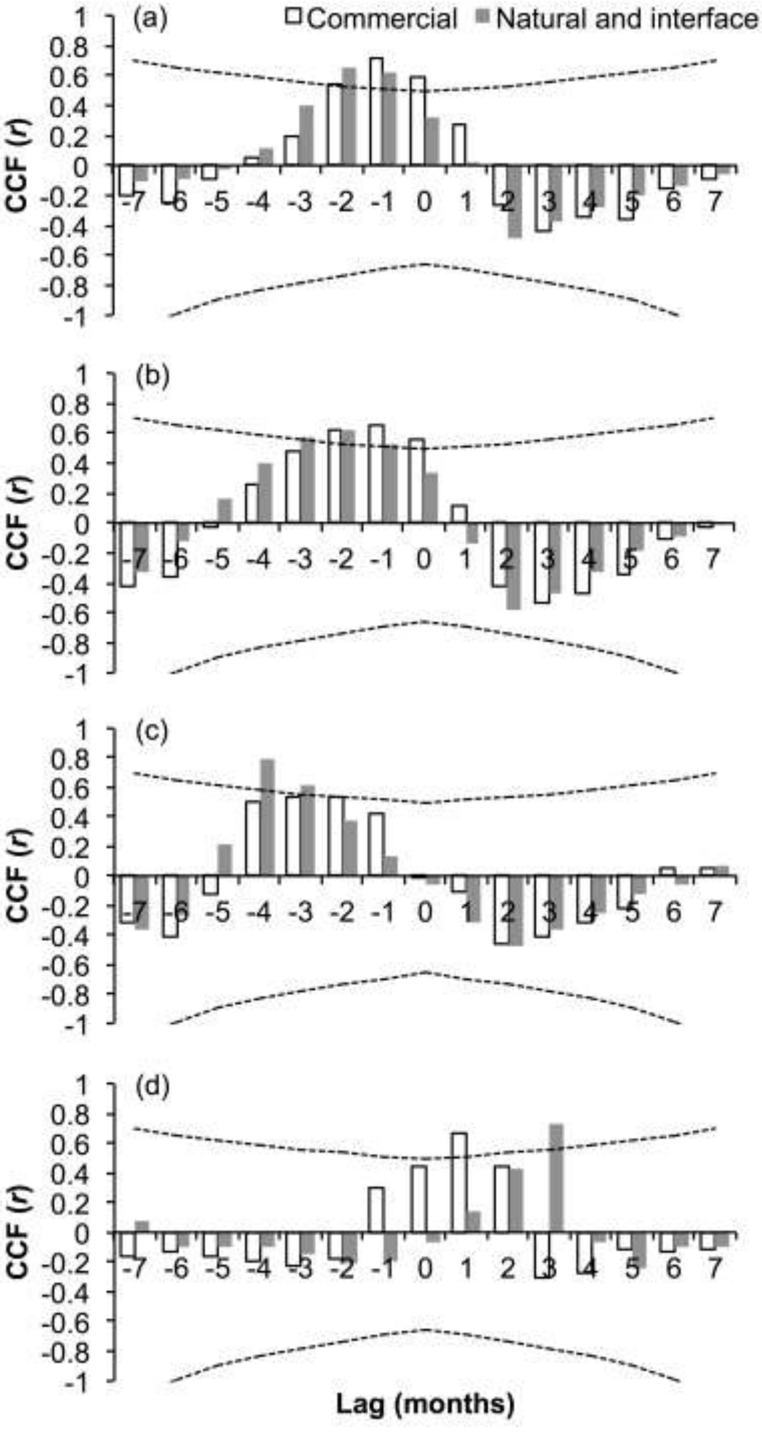

Figure 2. Cross correlation of mean adult captures of *B. dorsalis* (flies/trap/month) with mean monthly maximum temperature (a), mean monthly minimum temperature (b), monthly rainfall (c), and mean larval infestation (d) at commercial and natural and interface sites. White bars: commercial sites; grey bars: natural and interface sites. Dotted lines represent the upper and lower 95% confidence interval for the sample cross correlation function (r) at each time lag. If there is a significant correlation of *x* (e.g., mean maximum temperature) versus *y* (e.g., mean adult captures) at a negative time lag, this is interpreted as *x* leading *y* [as illustrated in (a)]. The alternative, where the correlation of *x* (e.g., mean adult captures) follows *y* (e.g., mean larval infestation) is represented by a positive time lag [as illustrated in (d)].

Tommy Atkins mangoes (72.54 flies/kg fruit) in conjunction with *Ceratitis cosyra* (653.52 flies/kg fruit). When the population pressure was at its highest in February 2015, *B. dorsalis* was reared from ripe mangoes (*Mangifera indica*) collected from the ground.

Discussion

This study detected *B. dorsalis* infesting fruit from only seven different species covering six plant families. This is a low diversity of host species compared with other locations in Africa (Rwomushana et al. 2008; Mwatawala et al. 2009a; Goergen et al. 2011), but infestation of *Vangueria infausta* and *Xylotheca kraussiana* by *B. dorsalis* represents the first records of their kind. Considering the wide spread of host species across plant families, it is suspected that *B. dorsalis* has not yet reached its full host range in these areas. The degree of infestation by *B. dorsalis* was found to vary between different fruit types which indicates a preference for some host plant species over others as shown in laboratory based studies by Rwomushana et al. (2008).

The presence of other *Ceratitis* species in the same fruit as *B. dorsalis* can be related to other studies showing interspecific competition. In Tanzania the number of *Ceratitis* species reared from fruit with *B. dorsalis* present were much lower in comparison to this study and the number of *B. dorsalis* was much higher when comparing flies per kilogram in mangoes (Mwatawala et al. 2006b). The number of *B. dorsalis* per kilogram of mango in this study (72.5 flies/kg fruit) is only slightly lower than the infestation rates found in the coastal provinces of Kenya (91.2 flies/kg fruit). However, no report was made on the abundance of *Ceratitis* species in these samples (Rwomushana et al. 2008). Adult captures of *B. dorsalis* in South Africa recorded on a monthly basis are currently well below those recorded in Tanzania (Mwatawala et al. 2009b). This may explain the limited host range of this fly in South Africa and it may expand if population numbers were to increase to higher levels. To determine if the *B. dorsalis* population is outcompeting the local *Ceratitis* species, a long-term survey involving trapping and fruit collection is needed.

Other host studies performed in the native and African invasive range of *B. dorsalis* have not specified if fruit were collected from the ground or tree (Ekesi et al. 2006; Rwomushana et al. 2008; Mwatawala et al. 2009a; Mwatawala et al. 2009b). This study shows higher levels of infestation by *B. dorsalis* in fruit collected from the ground. Future monitoring is required to determine if commercial fruit would still be susceptible to this pest before being picked at the recommended export grade. In South Africa, mangoes are picked for export when the flesh is still green (0.3 on colour index; Agricultural Products Standards Act 119 of 1990). *Bactrocera dorsalis* was not reared from green or ripe mangoes that were collected from the tree in this study. However, one sample of green, damaged mangoes collected from the ground was infested by a *Ceratitis* species.

The adult population of *B. dorsalis* in South Africa was found to be more influenced by temperature, than the abundance of host fruit in the areas that were sampled in this study. With an increase in temperature there was an increase in adult population. Rainfall had no effect on the adult population in commercial sites, but there was an effect on the population in natural and interface sites, with populations showing an increase four months after rainfall. A lack of an effect of rainfall in commercial sites may suggest a role for routine irrigation in the survival of adults, as has been modelled for the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Dominiak et al. 2006). This is due to *B. dorsalis* survival being susceptible to dry conditions (Stephens et al. 2007). The lag detected between fruit infestation and adult population levels is one month in commercial sites and three months in natural and interface sites. This implicates fruit present in December-January, such as early season *Mangifera indica* (L.) cv. (Tommy Atkins) and *Anacardium occidentale* (L.) as the main hosts contributing to increases in population levels in Limpopo and Mpumalanga provinces.

Host use and adult population trends in this study highlight the importance of sanitation in an orchard. *Bactrocera dorsalis* was found only in fruit on the ground, whereas intact fruit attached to the tree were not infested at current population levels in the sampled areas. In line with this observation, commercial sites, in which orchard sanitation was maintained to a high standard, had lower numbers of adult *B. dorsalis*. The suppression of *B. dorsalis* populations is also critical in preventing the spread of this species to new hosts. Allowing population size to reach levels similar to those in East and West Africa may lead to the exploitation of a wider array of commercially grown fruit and other hosts (Ekesi et al. 2006; Mwatawala et al. 2009b; Vayssieres et al. 2015). An increase in population levels could also allow *B. dorsalis* to outcompete *Ceratitis* species, which has been found to occur in Kenya (Ekesi et al. 2009).

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Supplementary material

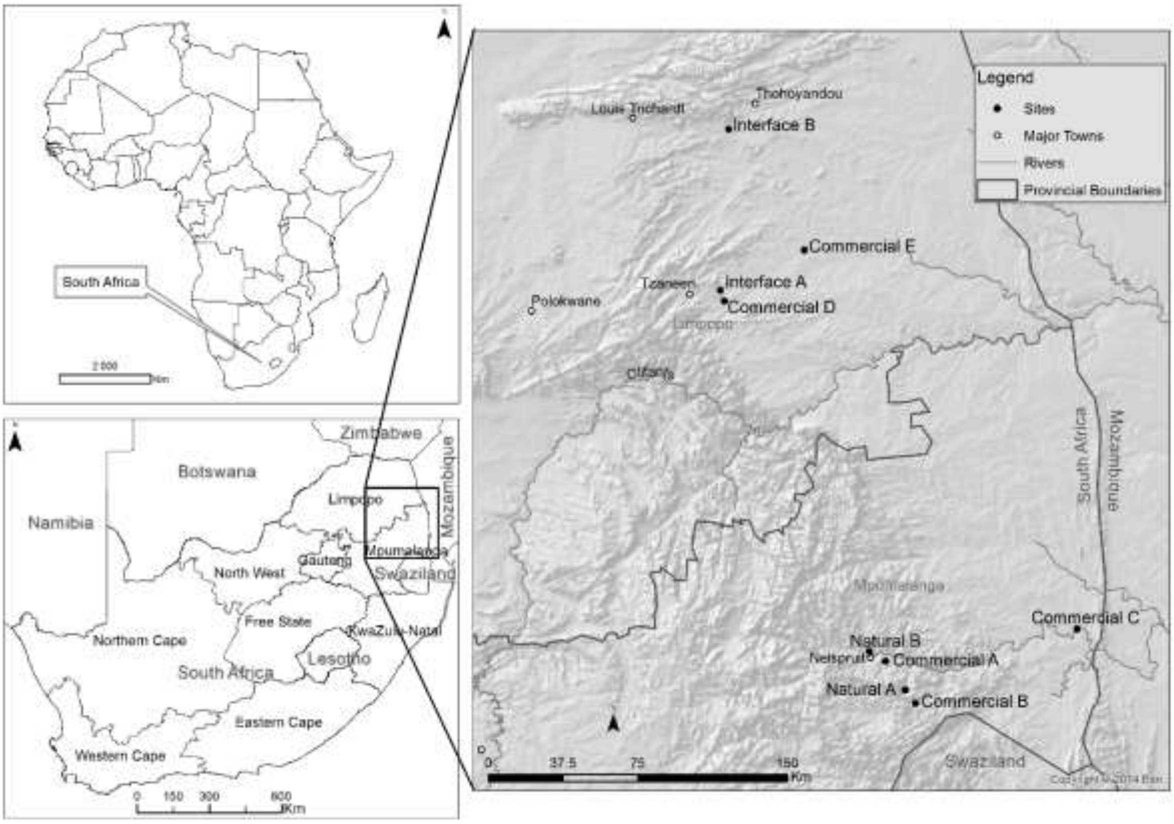

Figure S1. Field sites sampled in Mpumalanga and Limpopo provinces in South Africa. Commercial A: Crocodile Valley Citrus Co.; Commercial B: Siyalima Boerdery; Commercial C: Vergenoeg (Komati Fruits); Commercial D: Letaba Estates; Commercial E: Constantia (Gustav van Veijren). Natural A: Paradors Game Farm; Natural B: Lowveld National Botanical Gardens. Interface A: Tzaneen Country Lodge; Interface B: Tshakuma Community Farm.

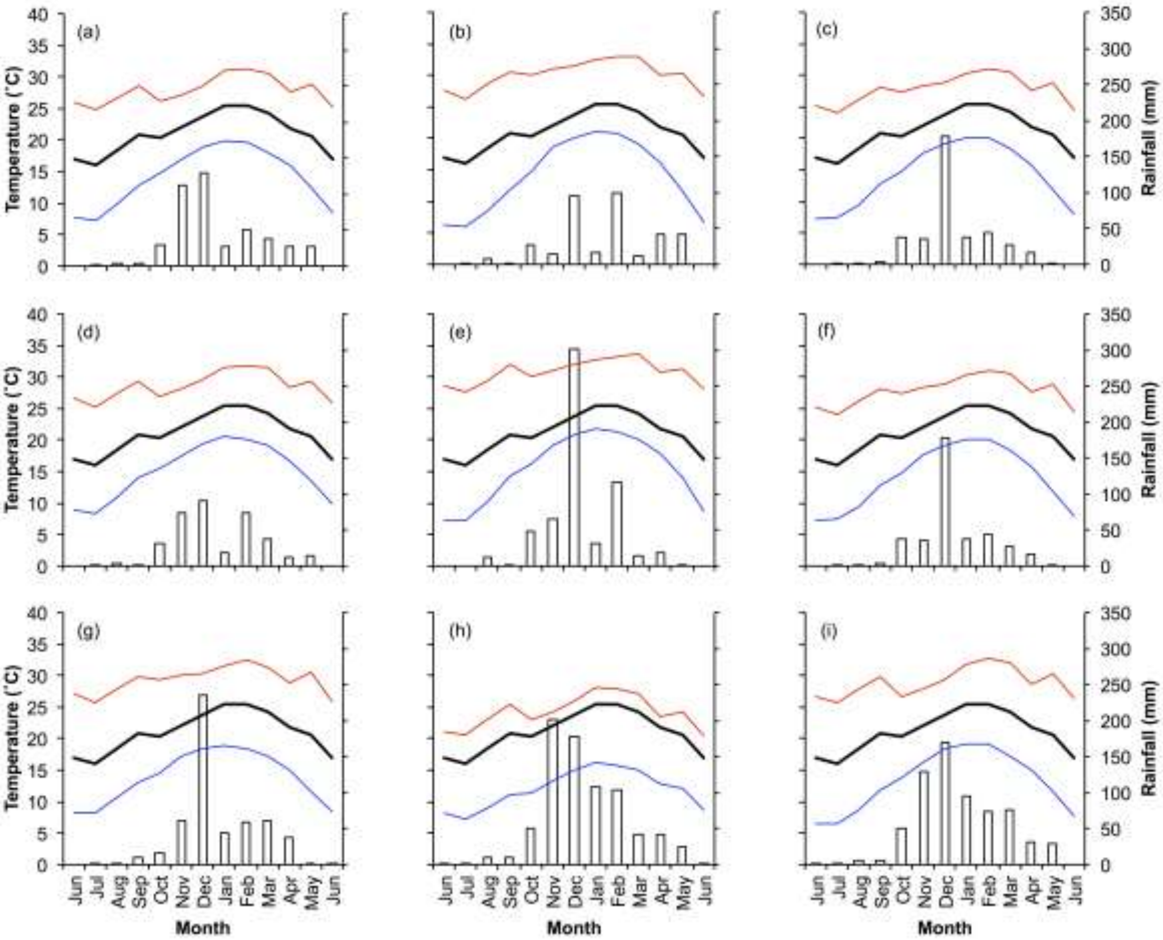

Figure S2. Mean monthly maximum and minimum temperatures, and monthly total rainfall at sampling site between July 2014- June 2015. Commercial sites: (a) Crocodile Valley Citrus Co., (b) Constantia (Gustav van Veijren Farm), (c) Letaba, (d) Siyalima Boerdery, (e) Vergenoeg (Komati Fruits); Interface sites: (f) Tzaneen Country Lodge, (g) Tshakuma Community Farm; Natural sites: (h) Paradors Game Farm, (i) Lowveld National Botanical Gardens. Red line: mean monthly maximum temperature; blue line: mean monthly minimum temperature; black line: mean average monthly temperature; bars: total monthly rainfall.

Table S1. Field site description and classification of fruit collection sites in Mpumalanga and Limpopo provinces, South Africa.

Province	Site	GPS Co-ordinates	Classification	Description	Fruit fly management
Mpumalanga	Crocodile Valley Citrus Co.	25° 29" 23S 31° 02" 38E	Commercial A	Large scale Citrus production (*Citrus sinensis* [Osbeck] cv Valencia)	Routine aerial bait sprays, bait stations, ground bait sprays
	Siyalima Boerdery	25° 40" 44S 31° 10" 45E	Commercial B	Large scale mixed crops (Citrus [*Citrus sinensis* [Osbeck] cv Valencia], Mangoes [*Mangifera indica* [L.]cv Tommy Atkins, Sensation, Keitt], Green peppers [*Capsicum annuum*])	Routine ground bait sprays, bait stations
	Vergenoeg (Komati Fruits)	25° 20" 39S 31° 54" 26E	Commercial C	Large scale mixed crops (Citrus [*Citrus paradisi* [Macfad.] cv Star Ruby, Marsh], Bananas [*Musa paradisiaca* (L.) cv Asdia])	Seasonal ground bait sprays
	Paradors Game Farm	25° 37" 06S 31° 07" 57E	Natural A	Natural Bushveld	None
	Lowveld National Botanical Gardens	25° 26" 37S 30° 58" 13E	Natural B	Highest species diversity of natural vegetation in South Africa	Irrigation scheme
Limpopo	Letaba	23° 52" 01S 30° 19" 04E	Commercial D	Large scale Citrus production (*Citrus sinensis* [L.][Osbeck] cv Valencia) and some Bananas (*Musa paradisiaca* [L.] cv Asdia)	Routine aerial bait sprays, bait stations, ground bait sprays, orchard sanitation
	Constantia (Gustav Van Veijren Farm)	23° 38" 11S 30° 40" 42E	Commercial E	Large scale Citrus (*Citrus sinensis* [L.][Osbeck] cv Valencia, *C. paradisi* (Macfad.) cv Star Ruby) some mangoes (*Mangifera indica* [L.] cv Tommy Atkins)	Routine aerial bait sprays, bait stations, orchard sanitation
	Tzaneen Country Lodge	23° 49" 07S 30° 18" 03E	Interface A	Small blocks of mango orchards (*Mangifera indica* [L.] cv Tommy Atkins, Sensation, Keitt, Kent) separated by indigenous savannah vegetation of equal size	Bait stations, orchard sanitation
	Tshakuma Community Farm	23° 05" 32S 3° 20" 12E	Interface B	Mixed orchards (*Citrus sinensis* [L.][Osbeck] cv Valencia, Guavas (*Psidium guajava* [L.]), Avocados	Bait stations in selected orchards, sporadic maintenance in selected orchards, largely

Province	Site	GPS Co-ordinates	Classification	Description	Fruit fly management
				[*Persea americana* [Mill] cv Pinkerton, Ryan, Hass], Bananas (*Musa spp*.), Macadamias (*Macadamia integrifolia* [Maiden & Betche]), Naartjies (*Citrus reticulata* [Blanco]), Mangoes (*Mangifera indica* [L.] cv Tommy Atkins)	lacking sanitation

Table S2. Fruit collected from each field site, including information on fruit phenology (Ripeness), location of fruit (Tree/Ground), the total weight of each sample, and emergence of Tephritidae from the sample (Y = yes, N = no). Tephritidae from each sample are divided between other Tephritidae and *Bactrocera dorsalis*. The identity of other Tephritidae that emerged is also presented.

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
Limpopo	Deerpark	Interface	*Mangifera indica (L.)*	Mango	Ripe	Ground	7.177	N	N
	Gustav van Veijren (Constantia Farms)	Commercial	*Anacardium occidentale (L.)*	Cashew	Ripe	Ground	1.121	Y *C. cosyra*	Y
			Anacardium occidentale (L.)	Cashew	Ripe	Ground+Tree	0.866	N	N
			Carissa edulis (L.)	Numnum berry	Ripe	Tree	0.295	Y *C. capitata*	N
			Citrus paradisi (Macfad) cv. Star Ruby	Grapefruit	Picking	Ground	9.339	Y *C. capitata*	N
			Citrus paradisi (Macfad) cv Star Ruby	Grapefruit	Picking	Tree	2.149	N	N
			Citrus sinensis (Osbeck)	Sweet orange	Picking	Ground	12.813	N	N
			Citrus sinensis (Osbeck) cv. Turkey Valencia	Sweet orange	Ripe	Ground	1.875	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Citrus sinensis (Osbeck) cv. Turkey Valencia	Sweet orange	Ripe	Tree	2.66	N	N
			Ficus sycomorus subsp sycomorus (L.)	Fig	Green	Tree	0.402	N	N
			Ficus sycomorus subsp sycomorus (L.)	Fig	Ripe	Ground	0.467	N	N
			Mangifera indica (L.)	Mango	Picking (10% colour in flesh)	Ground	5.559	Y *C. cosyra*	N
			Sclerocarya birrea subsp caffra (Rich)(Hoschst)	Marula	Ripe	Ground	12.152	Y *C. cosyra*	N
			Unknown	unknown	Mixed	Tree	0.037	N	N
	Letaba Estates	Commercial	*Citrus paradisi (Macfad)*	Grapefruit	Colour break	Tree	2.095	N	N
			Citrus paradisi (Macfad)	Grapefruit	Ripe	Ground	2.062	N	N
			Citrus paradisi (Macfad)	Grapefruit	Ripe	Tree	1.864	N	N
			Citrus sinensis (Osbeck)	Sweet orange	Colour break	Tree	2.123	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Mixed	Ground	1.356	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Mixed	Tree	1.563	N	Y
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Ground	13.31	N	N
			Citrus sinensis (Osbeck) cv. Navel	Sweet orange	Picking	Tree	2.25	N	N
			Syzigium jambos (L.)(Alston)			Tree	0.897	N	N
			Unknown	Wild cucumber	Ripe	Tree	3.761	N	N
	Tshakuma Community Farm	Interface	*Carica papaya (L.)*	Pawpaw	Green	Tree	2.095	N	N
			Citrus limon (L)(Burm.f.)	Lemon	Ripe	Ground	0.688	N	N
			Citrus reticulata (Blanco)	Mandarin	Colour break	Tree	2.002	N	N
			Citrus reticulata (Blanco)	Mandarin	Picking	Tree	2.727	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Tree	9.303	N	N
			Lantana camara (L.)	Lantana	Mixed	Tree	0.172	N	N
			Musa sp. (L.)	Banana	Over ripe	Ground	2.042	N	N
			Musa sp. (L.)	Banana	Over ripe	Tree	2.008	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Persea americana (Mill)	Avocado	Unknown	Ground	3.935	N	N
			Persea americana (Mill)	Avocado	Unknown	Tree	2.088	N	N
			Psidium guajava (L.)	Guava	Colour break	Tree	1.439	N	N
			Psidium guajava (L.)	Guava	Green	Ground	0.923	Y *C. capitata*	N
			Psidium guajava (L.)	Guava	Green	Tree	0.822	N	N
			Psidium guajava (L.)	Guava	Over ripe	Ground	1.81	N	N
			Psidium guajava (L.)	Guava	Over ripe	Tree	1.556	N	N
			Psidium guajava (L.)	Guava	Picking	Tree	4.43	N	N
			Psidium guajava (L.)	Guava	Ripe	Ground	0.983	N	N
			Solanum mauritianum (Scop.)	Bugweed	Green	Tree	0.291	N	N
			Solanum mauritianum (Scop.)	Bugweed	Mixed	Tree	0.698	N	N
			Cucurbita pepo (L.)	Courgette	Green	Tree	0.054	N	N
			Unknown	Wild cucumber	Ripe	Tree	0.218	N	N
			Passiflora edulis (Sims)	Passion Fruit	Yellow	Ground	0.215	N	N
			Musa sp. (L.)	Banana		Tree	2.692	N	N
			Carica papaya (L.)	Pawpaw	Picking	Tree	4.97	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Citrus reticulata (Blanco)	Mandarin	Picking	Tree	3.12	N	N
			Citrus reticulata (Blanco)	Mandarin	Mixed	Ground	0.872	N	N
			Citrus reticulata (Blanco)	Mandarin	Mixed	Tree	0.864	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Over ripe	Ground	1.848	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Over ripe	Tree	0.574	N	N
			Psidium guajava (L.)	Guava	Over ripe	Ground	1.42	N	N
			Psidium guajava (L.)	Guava	Over ripe	Tree	0.804	N	N
			Solanum mauritianum (Scop.)	Bugweed	Ripe	Tree	0.06	N	N
	Levubu- Adam Hugo	Commercial	*Solanum betaceum (Cav.)*	Tree tomato	Ripe	Ground	1.6	N	N
			Solanum betaceum (Cav.)	Tree tomato	Ripe	Tree	1.166	N	N
	Levubu- Fritz	Commercial	*Citrus limon (L)(Burm.f.)*	Lemon	Ripe	Ground	3.041	Y *Ceratitis spp.*	N
			Citrus limon (L)(Burm.f.)	Lemon	Ripe	Tree	3.187	N	N
			Citrus limon	Lemon	Green	Tree	0.949	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			(L)(Burm.f.)						
	Rotambo Farm	Interface	Unknown	Cucurbits (Invasive)	Green	Tree	0.44	N	N
	Tzaneen Country Lodge	Interface	*Antidesma venosum (Tul)*	Tasselberry	Mixed	Tree	0.177	N	N
			Antidesma venosum (Tul)	Tasselberry	ripe	Tree	0.131	N	N
			Carissa edulis (L.)	Numnum berry	Mixed	Tree	0.03	N	N
			Ficus sur (Forssk)	Fig	Picking	Tree	2.24	N	N
			Ficus sur (Forssk)	Fig	Ripe	Tree	0.228	N	N
			Ficus sycomorus (L.)	Fig	Ripe	Ground	0.265	N	N
			Mangifera indica (L.)	Mango	Green	Tree	2.801	Y *C. cosyra*	N
			Mangifera indica (L.)	Mango	Ripe	Ground	2.127	Y *C. cosyra* and *Ceratitis (Ceratalaspis) spp.*	Y
			Mangifera indica (L.)	Mango	Turning	Ground	3.993	Y *C. cosyra*	N
			Phyllanthus reticulatus (Poir.)	Potatobush	Green	Tree	0.208	N	N
			Psidium guajava (L.)	Guava	Over ripe	Tree	2.066	Y	Y

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
								C. capitata	
			Rhoicissus tridentata (Lam.)(Wild & R.B. Drumm)		Green	Tree	0.281	N	N
			Sclerocarya birrea subsp caffra (Rich)(Hoschst)	Marula	Ripe	Ground	2.631	N	N
Mpumalanga	Lowveld National Botanical Gardens	Natural	*Cordia caffra*		Ripe	Tree	0.358	N	N
			Dovyalis caffra (Harv.)	Kei-apple	Ripe	Tree	0.021	N	N
			Dovyalis longispina (Harv.)	Coastal Kei-apple	Ripe	Ground	0.6	N	N
			Mystroxylon aethiopicum schlechteri (Thunb.)(Loes)	Kooboo-berry	Picking	Tree	0.07	N	N
			Mystroxylon aethiopicum schlechteri (Thunb.)(Loes)	Kooboo-berry	Ripe	Ground	0.495	N	N
			Psychotria kirkii (Hiern)		Ripe	Tree	0.068	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Unknown		Ripe	Tree	0.039	N	N
			Vangueria infausta subsp infausta (Burch.)	Wild medlar	Mixed	Ground	1.42	Y *C. rosa*	N
			Walburgia salutaris (Bertol.f.)(Chiov.)		Over ripe	Ground	0.006	Y *C. cosyra*	Y
			Xylotheca kraussiana (Hochst.)	African dogrose	Ripe	Tree	0.127	Y *C. rosa* and *C. quilicii*	Y
			Cordyla africana (Lour)	Wild mango	Ripe	Ground	0.759	N	N
	Crocodile Valley Citrus Co.	Commercial	*Citrus sinensis (Osbeck)* cv. Navel	Sweet orange	Picking	Ground	8.489	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Ground	7.64	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Tree	3.425	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Ground	0.61	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Tree	4.145	N	N
			Ficus sur (Forssk)	Broomcluster fig	Red/ green	Tree	1.355	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Ficus sycomorus subsp sycomorus (L.)	Sycomore fig	Purple	Tree	0.231	N	N
			Melia azedarach (L.)	Seringa	Ripe	Tree	0.328	N	N
			Strychnos madagascariensis (Poir.)	Black monkey-orange	Green/ Yellow	Tree	0.473	N	N
			Strychnos madagascariensis (Poir.)	Black monkey-orange	Yellow	Ground	0.76	N	N
	Paradors Game Farm	Natural	*Carica papaya (L.)*	Papino	Picking	Tree	5.806	N	N
			Citrus reticulata (Blanco)	Mandarin	Ripe	Tree	0.653	N	N
			Ficus sycomorus subsp sycomorus (L.)	Sycomore fig	Picking	Tree	1.26	N	N
			Unknown	Wild cucumber	Green	Tree	0.41	N	N
	Siyalima Boerdery	Commercial	*Citrus limon (L)(Burm.f.)*	Lemon	Green	Tree	0.649	N	N
			Citrus limon (L)(Burm.f.)	Lemon	Picking	Tree	2.285	N	N
			Citrus limon (L)(Burm.f.)	Lemon	Ripe	Ground	7.471	N	N
			Citrus sinensis (Osbeck) cv. Navel	Sweet orange	Colour break	Tree	2.07	N	N

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Colour break	Tree	2.115	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Green	Tree	1.694	N	N
			Citrus sinensis (Osbeck) cv. Navel	Sweet orange	Picking	Tree	2.419	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Tree	2.781	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Ground	5.027	N	N
			Citrus sinensis (Osbeck) cv. Navel	Sweet orange	Ripe	Tree	0.508	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Tree	1.95	N	N
			Ficus sycomorus subsp sycomorus (L.)	Sycomore fig	Ripe	Ground	4.3	N	N
			Mangifera indica (L.)	Mango	Ripe	Ground	8.434	Y *C. cosyra*	Y
			Mangifera indica (L.)	Mango	Ripe	Tree	4.696	N	N
			Sclerocarya birrea subsp caffra (Rich)(Hoschst)	Marula		Ground	2.344	Y *C. cosyra*	N
			Solanum mauritianum	Bugweed	Mixed	Tree	0.245	N	Y

Province	Farm/area	Type	Fruit	Common name	Ripeness	Tree/ Ground	Total weight	Other Tephritidae (*Ceratitis* species)	*B. dorsalis*
			(Scop.)						
	Residential	Non-Commercial	*Annona senegalensis (Pers)*	Custard Apple		Tree	1.35	N	N
	Vergenoeg (Komati Fruits)	Commercial	*Citrus paradisi (Macfad)* cv. Star Ruby	Grapefruit	Picking	Ground	1.94	N	N
			Citrus paradisi (Macfad) cv. Star Ruby	Grapefruit	Ripe	Ground	3.636	N	N
			Citrus paradisi (Macfad) cv. Star Ruby	Grapefruit	Ripe	Tree	3.152	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Picking	Ground	1.35	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Ground	1.271	N	N
			Citrus sinensis (Osbeck) cv. Valencia	Sweet orange	Ripe	Tree	2.038	N	N