

# Comparative demography of *Bactrocera dorsalis* (Hendel) and *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) on deciduous fruit

## Research Paper

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### Abstract

*Bactrocera dorsalis* (Hendel) and *Ceratitis capitata* (Wiedemann) are highly polyphagous fruit fly species and important pests of commercial fruit in regions of the world where they are present. In South Africa, *B. dorsalis* is now established in the north and northeastern parts of the country. *B. dorsalis* is currently absent in other parts of the country including the Western Cape Province which is an important area for the production of deciduous fruit. *C. capitata* is widespread in South Africa and is the dominant pest of deciduous fruit. The demographic parameters of *B. dorsalis* and *C. capitata* on four deciduous fruit types *Prunus persica* (L.) Batsch, *Prunus domestica* L., *Malus domestica* Borkh. and *Pyrus communis* L. were studied to aid in predicting the potential population establishment and growth of *B. dorsalis* in a deciduous fruit growing environment. All deciduous fruit types tested were suitable for population persistence of both *B. dorsalis* and *C. capitata*. Development was fastest and survival highest on nectarine for both species. *B. dorsalis* adults generally lived longer than those of *C. capitata*, irrespective of the fruit types that they developed from. *B. dorsalis* had a higher net reproductive rate ( $R_0$ ) on all deciduous fruit tested compared to *C. capitata*. However, the intrinsic rate of population increase was estimated to be higher for *C. capitata* than for *B. dorsalis* on all fruit types tested primarily due to *C. capitata*'s faster generation time. Provided abiotic conditions are optimal, *B. dorsalis* would be able to establish and grow in deciduous fruit growing areas.

### Introduction

Biological invasions can be divided into at least three stages: arrival, establishment and spread (Liebhold and Tobin, 2008). For invasion to be successful, the arrival stage determined by propagule pressure and the establishment phase determined by abiotic and biotic factors should be favourable (Catford *et al.*, 2009). The life history characteristics of the invader highly influence invasion success (Sol *et al.*, 2012). When the founder population is small and the environment is favourable, a life history strategy that promotes fast population growth would enhance establishment (Sol *et al.*, 2012). Generally though, a successful invader is one which prioritizes longer adult life span with many reproductive events (Sol *et al.*, 2012). Resource availability is an important biotic factor which influences the establishment probability and population growth rate of an invading species (Chesson, 2000; Shea and Chesson, 2002). In communities where the invader and resident species utilize similar resources, establishment would be favoured if the invader has a superior ability to exploit available resources compared to the resident species (Sakai *et al.*, 2001).

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), (Diptera: Tephritidae) is an invasive species of Asian origin which invaded and expanded its range on the African continent since 2003 (Lux *et al.*, 2003, Drew *et al.*, 2005, Khamis *et al.*, 2009). In 2013, *B. dorsalis* invaded the northern parts of South Africa and is now present in the north and northeastern parts of South Africa (Manrakhan *et al.*, 2015) but is still absent in other areas of the country. A number of *B. dorsalis*-free regions in South Africa, including the Western Cape Province, were, however, deemed suitable for the establishment of *B. dorsalis* based on climatic models (Hill and Terblanche, 2014; De Villiers *et al.*, 2016). The Western Cape Province of South Africa is an important deciduous fruit growing region in the country (Anonymous, 2016). Most of the deciduous fruit being grown commercially are exported, bringing important revenues to the country and the region (Anonymous, 2016). Fruit flies are pests of phytosanitary concern for export fruit, including deciduous fruit markets from South Africa (Barnes *et al.*, 2015).

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), was found to be the dominant fruit fly pest on deciduous fruit in the Western Cape Province (Manrakhan and Addison, 2013). With the potential threat of introduction of *B. dorsalis* in the Western Cape Province, the questions that arise are (1) would deciduous fruit be a favourable host for *B. dorsalis* and, if so, (2) how would utilization of deciduous fruit as a host for *B. dorsalis* compare with *C. capitata*? Differences in the use of the deciduous fruit as a host between *B. dorsalis* and *C. capitata* would provide quantitative information on the establishment and growth potential of *B. dorsalis* should it arrive in the Western Cape Province.

*B. dorsalis* (Hendel) and *C. capitata* (Wiedemann) (Diptera: Tephritidae) are both multivoltine species and do not enter a diapause phase (Burk and Calkins, 1983; Chen et al., 2006; Goergen et al., 2011). *C. capitata*, a pest of Afrotropical origin (De Meyer et al., 2002), was recorded as the most widespread fruit fly pest species across South Africa (De Villiers et al., 2013). *C. capitata* and *B. dorsalis* both exhibit a high reproductive potential, are highly mobile and are opportunistic, broad range exploiters of fruit (Liquidó et al., 1990; Chen et al., 2006; Ekesi et al., 2007). Host plants play an important role in the ability of fruit fly species to survive and disperse (Bateman, 1972; Malacrida et al., 2007). In Africa, *B. dorsalis* has been recorded on more than 80 host plants (De Meyer et al., 2012). Mango appears to be its primary host in many African countries (Mwatawala et al., 2004; Ekesi et al., 2006), with guava (*Psidium guajava*; Myrtaceae) (Vargas et al., 2007; Ali et al., 2014; Hussain et al., 2015) and tropical almond (*Terminalia catappa*; Combretaceae) being suitable reservoir hosts for the pest (Mwatawala et al., 2006, 2009). For *C. capitata*, 353 plant species were listed as hosts (Liquidó et al., 1990; Radonjić et al., 2013). In the northern parts of South Africa where *B. dorsalis* has been present since 2013, a limited host range was recorded for this pest (Theron et al., 2017). In another recent survey on various indigenous fruits in the northern areas of South Africa, Grove et al. (2017) found that, of the 28 plant species sampled, *B. dorsalis* only emerged from one indigenous fruit – marula fruit (*Sclerocarya birrea* (A. Rich.) Hochst. (Anacardiaceae)). In that survey, however, *C. capitata* emerged from 12 of 28 indigenous plant species sampled (Grove et al., 2017).

The literature on the use of deciduous fruit by *B. dorsalis* is scarce. White and Elson-Harris (1992) listed *Prunus persica* (L.) Batsch (Nectarine), *Prunus domestica* L. (Plum), *Malus domestica* Borkh. (Apple) and *Pyrus communis* L. (Pear) as host plants for *B. dorsalis* in China from various sources, some unpublished. Ye and Liu (2005) found that apple was a less preferred host for *B. dorsalis* in China and pear was not infested as frequently as peach, *P. persica* (L.) Batsch. Peach was listed as a host fruit for *B. dorsalis* in Hawaii by Bess and Haramoto (1961). Apart from the information on the presence and degree of infestation of *B. dorsalis* on some deciduous fruit, demographic parameters of *B. dorsalis* on deciduous fruit have not been quantified. A comparison of the demographic parameters of *B. dorsalis* and *C. capitata* on deciduous fruit would provide an estimate of the suitability of such a landscape for the establishment of *B. dorsalis* as well as the likelihood of potential interactions between the two species on deciduous fruit.

The main objectives of this study were therefore to compare the development, reproduction and survival of *B. dorsalis* and *C. capitata* on the main deciduous fruit types typically cultivated in the Western Cape.

## Materials and methods

### Fruit fly species and rearing methods

Laboratory-reared *B. dorsalis* and *C. capitata* were used for all tests. *B. dorsalis* was reared in the Insect Quarantine Facility of the Agricultural Research Council in Stellenbosch. They were reared at 27°C (±1°C) and 70% (±5%) humidity in Perspex™ cages (30 × 30 × 40 cm, 36 l) with a fabric sleeve under natural light conditions and provided with perforated apple halves for oviposition as well as water and a mixture of sugar and yeast as food (Barnes et al., 2007). The culture was started from infested guavas collected near Thohoyandou in Limpopo Province, South Africa (23°3'49.70"S, 30°18'14.44"E) during March 2014 and wild flies from the same area were added once a year. The perforated apple halves provided for oviposition were removed every two days. Larvae were reared on an artificial larval rearing medium (Barnes et al., 2007) with the addition of 100 g carrot powder per kg of mix and kept in separate containers on vermiculite at 27°C (±1°C) for pupation. The vermiculite was sifted to remove the pupae which were placed in honey jars marked with the date collected. The flies that emerged were released into cages marked with the day of emergence and provided with water and a mixture of sugar and yeast as food (Barnes et al., 2007), but no oviposition substrate. The flies used in the experiments were 14 (±1) days old. *B. dorsalis* reared in a colony under laboratory conditions reaches sexual maturity between 10 and 15 days after emergence (Bess and Haramoto, 1961; Diatta et al., 2013).

*C. capitata* was reared in the insect rearing facility at Welgevalle experimental farm (Stellenbosch University) at 25°C (±1°C) and 70% (±5%) humidity in Perspex™ cages (800 mm<sup>3</sup>) under 12 h light/12 h dark conditions. Flies were provided with perforated apple halves for oviposition, water and a mixture of sugar and yeast as food (Barnes et al., 2007). Pupae to start the colony were obtained from colonies held at Citrus Research International (CRI) in Nelspruit. The perforated apple halves provided for oviposition were removed every 2 days. Larvae were reared on an artificial larval rearing medium (Barnes et al., 2007) and kept in separate containers on vermiculite at 25°C (±1°C) for pupation. The vermiculite was sifted to remove the pupae, which were placed in 250 ml plastic jars marked with the date collected. The flies that emerged were released into cages marked with the day of emergence and provided with water and a mixture of sugar and yeast as food (Barnes et al., 2007), but no oviposition substrate. The flies used in the experiments were 7 (±1) days old. *C. capitata* reared in a colony under laboratory conditions reaches sexual maturity between 4 and 6 days after emergence (Carey, 1984).

All experiments were conducted in a quarantine insectary at the Plant Quarantine Station of the Department of Agriculture, Forestry and Fisheries in Stellenbosch (at 26°C (±1°C) and 70% (±5%) humidity with a 12 h light/12 h dark cycle). The 11 h full light cycle was provided by eight 36 W Osram™ fluorescent light tubes delivering 3350 lumens each. One hour dawn and dusk was created by connecting two 40 W bulbs (delivering 450 lumens each) to a timer switch. The 40 W bulbs were switched on simulating 1 h dawn and 1 h dusk every day within the 12 h light cycle.

### Deciduous fruit tested

Four deciduous fruit types were used in all tests: *P. persica* (L.) Batsch, Nectarine 'Arctic Star' and Nectarine 'Mongreb'; *P. domestica* L., Plum 'Fortune'; *M. domestica* Borkh., Apple 'Golden delicious'; *P. communis* L., Pear 'Packham'. Tests were

carried out between December 2016 and June 2017, depending on fruit availability.

Fruit was purchased from a shop selling fruit grown under good agricultural practice, using integrated pest management principles to reduce chemical pesticide residues on the fruit. All fruit types used were at the mature ripe stage. Fruit was then kept at 25°C overnight before use.

### Development and survival of immature stages

This experiment was conducted in two separate parts: (1) determination of duration and viability of egg stages and (2) determination of larval and pupal development. In both parts of the experiment, five adult pairs (female and male) of each species were placed in 19 × 15 × 16 cm (4.5 l) aerated insect cages and provided with water and a mixture of sugar and yeast (enzymatic yeast hydrolysate, Separations, Johannesburg, South Africa) as food (in a 3:1 ratio). One test fruit was placed in each cage for 24 h. The test fruit was weighed before placement in the cage. In the first part of the experiment on egg stage development, the number of sting marks on the fruit was counted as well as the number of eggs per sting mark. All sting marks and egg pockets were dissected out and placed on moist black filter paper (9 cm in diameter, Macherey-Nagel GmbH & Co. KG) in sterile Petri dishes. The Petri dishes were kept at 25°C in a growth chamber (SMC Scientific Manufacturing, Table View, South Africa). Eggs were counted every hour for 8 h until all eggs had hatched or no further egg hatch occurred. The number of eggs that hatched was recorded. The experiment was repeated four times for each fruit type with a different cohort used for each repetition. In the second part of the experiment on larval and pupal development, the number of sting marks on the fruit was counted before placement of the entire fruit on vermiculite in individual 2 l plastic boxes with cloth in the lid for aeration, for pupation. After 7 days, the vermiculite was sieved daily and the numbers of pupae were recorded. The pupae were placed in honey jars with aerated lids for the adults to emerge. Adult emergence was recorded daily, noting the number of males and females emerging every day. The experiment was repeated four times for each fruit type with a different cohort used for each repetition.

### Demographic parameters

For each fruit fly species tested, a pair of adult flies (female and male) was placed in an 11 × 12 × 18 cm (2 l) aerated insect cage and provided with water and a mixture of sugar and yeast (in a 3:1 ratio) as food. Flies for this experiment were reared for two generations from the same fruit on which they were tested. A 5 ml container (15 mm in diameter) with a 1 cm piece of test fruit covered with parafilm™ (pierced four times) was placed in each cage. The container with fruit was replaced daily and the number of sting marks, number of eggs and mortality of the adults were recorded daily for 90 days.

### Statistical analysis

Effects of species, fruit type and interactions thereof on oviposition (number of sting marks, number of eggs), survival (percentage egg hatch, total number of pupae, number of pupae per gram of fruit, percentage adult emergence and number of emerged adults) and development (hours until egg hatch and number of days to pupation) were analysed using a generalized linear

model (GLM) with a log link function assuming a Poisson distribution of the count data. Wald's  $\chi^2$  test was used in the model to determine the significance of the response variables. The interactions between the main effects of species, fruit type and time on the parameters measured were analysed, the main effects were analysed where interactions were not significant. In the adult demographic studies, time-series data on the number of eggs produced over 90 days were analysed using linear mixed-effects models (lme4 library in nlme package) in R v. 3.5.1 (R Development Core Team) using a Poisson distribution and log link function. The models were fitted by maximum likelihood, and Bayes' information criterion (BIC) was used to compare model fits by the difference in BIC scores (where  $\delta > 10$  was considered highly significant and lower BIC was better). The initial model had fruit type and fly species as fixed effects, and cage (replicates) as a random effect to determine if cage effects were a significant factor contributing to the model's variation. This was contrasted against the same model but that ignored the cage random effect. These models showed that the addition of a random cage term significantly worsened the models. In the case of GLZ analyses, over-dispersion was assessed in each case and corrected for, if necessary. The rate of adult death was analysed using the Cox Proportional-Hazards Regression for Survival Data in R. The graphs were drawn using Statistica 13.0 (Statsoft, Tulsa, USA).

### Life table parameters

Life table parameters of *B. dorsalis* and *C. capitata* on each fruit tested were determined based on data collected over 90 days. The egg load for the two species was not determined in these experiments. For *B. dorsalis* aged between 7 and 80 days with full access to protein, egg load was found to be  $20.7 \pm 2.7$  per female (Chou *et al.*, 2012). Egg load of 7-day-old *C. capitata* with access to protein was found to be 20 per female (Prokopy *et al.*, 1994). The net reproduction rate ( $R_0$ ) was determined using the following equation (Carey, 1982):

$$\sum_{x=1}^t l_x m_x$$

where  $l_x$  is the proportion of females alive on day  $x$ , and  $m_x$  is the total number of female progeny produced per female on day  $x$ .

The mean generation time ( $T$ ) was calculated using the following equation (Birch, 1948):

$$T = \frac{\sum_{x=1}^t l_x m_x x}{\sum_{x=1}^t l_x m_x}$$

where  $T$  is the time in days.

These values were subsequently used to obtain an initial estimate of the intrinsic rate of natural population increase ( $r_m$ ), a dimensionless measure of increase per capita as described and refined in Birch (1948) and Price (1984). The intrinsic rate of increase ( $r_m$ ) was estimated using iterations to solve the below equation (Watson, 1964):

$$\sum_{x=1}^t (e)^{-r_m x} L_x M_x = 1, \quad \chi = 1, 2, 3, \dots, t \text{ days}$$

The mean net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r_m$ ) and generation time ( $T$ ) were calculated for each fruit type and analysed using an ANOVA in Statistica 13.0 (Statsoft, Tulsa, USA).

**Table 1.** Mean ( $\pm$ SD): (1 and 3) number of eggs per female over 24 h and 90 days, (2 and 4) number of sting marks per female over 24 h and 90 days, (5) number of pupae per gram of fruit, (6) number of adults, (7 and 8) number of days to pupation and to adult emergence, (9) percentage egg hatch and (10) percentage eclosion of *C. capitata* and *B. dorsalis* on four different deciduous fruit types

Parameters tested	Fruit fly species	Nectarine	Plum	Pear	Apple
<i>Mean numbers of</i>					
1. Eggs per female (24 h)	<i>B. dorsalis</i>	40.3 <sup>b</sup> $\pm$ 5.3	53.25 <sup>a</sup> $\pm$ 17	54.5 <sup>a</sup> $\pm$ 4.5	44.35 <sup>ab</sup> $\pm$ 13.5
Means per fruit type	<i>C. capitata</i>	25.75 <sup>c</sup> $\pm$ 3.5	18.5 <sup>cd</sup> $\pm$ 2.7	8.9 <sup>d</sup> $\pm$ 4.2	38.5 <sup>b</sup> $\pm$ 5.5
		33.01 <sup>AB</sup> $\pm$ 8.8	35.9 <sup>AB</sup> $\pm$ 21.7	31.7 <sup>B</sup> $\pm$ 24.7	41.45 <sup>A</sup> $\pm$ 10.0
2. Sting marks per female (24 h)	<i>B. dorsalis</i>	7.8 <sup>a</sup> $\pm$ 2	1.05 <sup>c</sup> $\pm$ 0.4	0.95 <sup>c</sup> $\pm$ 0.4	0.9 <sup>c</sup> $\pm$ 0.3
Means per fruit type	<i>C. capitata</i>	3.7 <sup>b</sup> $\pm$ 0.7	3.95 <sup>b</sup> $\pm$ 2.6	1.3 <sup>c</sup> $\pm$ 1	1.25 <sup>c</sup> $\pm$ 0.3
		5.7 <sup>A</sup> $\pm$ 2.6	2.5 <sup>B</sup> $\pm$ 2.3	1.1 <sup>C</sup> $\pm$ 0.7	1.1 <sup>C</sup> $\pm$ 0.4
3. Eggs per female (90 days)	<i>B. dorsalis</i>	6.9 <sup>b</sup> $\pm$ 17.2	7.7 <sup>b</sup> $\pm$ 20.1	15.2 <sup>a</sup> $\pm$ 28.8	7.4 <sup>b</sup> $\pm$ 12.6
Means per fruit type	<i>C. capitata</i>	4.2 <sup>c</sup> $\pm$ 14.3	6.8 <sup>b</sup> $\pm$ 15.5	4.8 <sup>c</sup> $\pm$ 15.5	0.7 <sup>d</sup> $\pm$ 3.7
		5.5 <sup>c</sup> $\pm$ 15.9	7.2 <sup>B</sup> $\pm$ 17.9	10.0 <sup>A</sup> $\pm$ 23.7	4.1 <sup>D</sup> $\pm$ 9.9
4. Sting marks per female (90 days)	<i>B. dorsalis</i>	0.60 <sup>c</sup> $\pm$ 1.2	0.56 <sup>c</sup> $\pm$ 1.2	0.90 <sup>b</sup> $\pm$ 1.4	1.17 <sup>a</sup> $\pm$ 1.4
Means per fruit type	<i>C. capitata</i>	0.34 <sup>d</sup> $\pm$ 1.3	0.57 <sup>c</sup> $\pm$ 1.2	0.29 <sup>d</sup> $\pm$ 0.8	0.13 <sup>e</sup> $\pm$ 0.5
		0.5 <sup>C</sup> $\pm$ 0.02	0.6 <sup>B</sup> $\pm$ 0.02	0.6 <sup>AB</sup> $\pm$ 0.02	0.7 <sup>A</sup> $\pm$ 0.02
5. Mean number of pupae per gram of fruit	<i>B. dorsalis</i>	1.08 <sup>ab</sup> $\pm$ 0.69	0.86 <sup>bc</sup> $\pm$ 0.51	0.29 <sup>cd</sup> $\pm$ 0.15	0.19 <sup>d</sup> $\pm$ 0.03
Means per fruit type	<i>C. capitata</i>	1.66 <sup>a</sup> $\pm$ 0.78	0.37 <sup>cd</sup> $\pm$ 0.21	0.37 <sup>cd</sup> $\pm$ 0.18	0.4 <sup>cd</sup> $\pm$ 0.25
		1.4 <sup>A</sup> $\pm$ 0.7	0.6 <sup>B</sup> $\pm$ 0.4	0.3 <sup>B</sup> $\pm$ 0.2	0.3 <sup>B</sup> $\pm$ 0.2
6. Mean number adults	<i>B. dorsalis</i>	97.5 <sup>b</sup> $\pm$ 43.3	45 <sup>bc</sup> $\pm$ 23.2	42.5 <sup>bc</sup> $\pm$ 24	25 <sup>c</sup> $\pm$ 4.3
Means per fruit type	<i>C. capitata</i>	162.2 <sup>a</sup> $\pm$ 83	18.7 <sup>c</sup> $\pm$ 9.94	62.5 <sup>bc</sup> $\pm$ 33.79	46.5 <sup>bc</sup> $\pm$ 31.5
		130 <sup>A</sup> $\pm$ 70.6	31.9 <sup>B</sup> $\pm$ 21.7	52.5 <sup>B</sup> $\pm$ 29.2	35.8 <sup>B</sup> $\pm$ 23.8
7. Mean no. of days to pupation	<i>B. dorsalis</i>	8.3 <sup>e</sup> $\pm$ 0.9	11 <sup>cd</sup> $\pm$ 0.0	12 <sup>c</sup> $\pm$ 2.3	18.7 <sup>b</sup> $\pm$ 2.6
Means per fruit type	<i>C. capitata</i>	9 <sup>de</sup> $\pm$ 0.0	12.2 <sup>c</sup> $\pm$ 0.5	11.7 <sup>c</sup> $\pm$ 1.7	23 <sup>a</sup> $\pm$ 3.4
		8.6 <sup>C</sup> $\pm$ 0.7	11.6 <sup>B</sup> $\pm$ 0.7	11.9 <sup>B</sup> $\pm$ 1.9	20.9 <sup>A</sup> $\pm$ 3.6
8. Mean no. of days to adult emergence	<i>B. dorsalis</i>	17.9 <sup>d</sup> $\pm$ 0.9	20.2 <sup>c</sup> $\pm$ 0.5	21.8 <sup>c</sup> $\pm$ 2.3	27.5 <sup>b</sup> $\pm$ 2.8
Means per fruit type	<i>C. capitata</i>	17.7 <sup>d</sup> $\pm$ 0.5	21 <sup>c</sup> $\pm$ 0.8	19.9 <sup>c</sup> $\pm$ 1.5	31.2 <sup>a</sup> $\pm$ 3.8
		17.8 <sup>C</sup> $\pm$ 0.7	20.6 <sup>B</sup> $\pm$ 0.7	20.8 <sup>B</sup> $\pm$ 2.1	29.4 <sup>A</sup> $\pm$ 3.7
<i>Mean percentage of</i>					
9. Egg hatch for fruit (24 h)	<i>B. dorsalis</i>	88% <sup>abc</sup> $\pm$ 5.9	81% <sup>bc</sup> $\pm$ 11.3	73% <sup>c</sup> $\pm$ 6.5	47% <sup>d</sup> $\pm$ 23.2
Means per fruit type	<i>C. capitata</i>	97% <sup>a</sup> $\pm$ 1	91% <sup>a</sup> $\pm$ 3.5	89% <sup>abc</sup> $\pm$ 13.3	94% <sup>ab</sup> $\pm$ 2.1
		92.3% <sup>A</sup> $\pm$ 6.5	86.2% <sup>AB</sup> $\pm$ 9.5	80.9% <sup>BC</sup> $\pm$ 12.7	70.4% <sup>C</sup> $\pm$ 29.2
10. Pupal eclosion (24 h)	<i>B. dorsalis</i>	95.4% <sup>a</sup> $\pm$ 3.3	95.1% <sup>a</sup> $\pm$ 2.6	91% <sup>ab</sup> $\pm$ 8.2	95% <sup>a</sup> $\pm$ 3.9
Means per fruit type	<i>C. capitata</i>	94.7% <sup>a</sup> $\pm$ 4.75	92.3% <sup>a</sup> $\pm$ 5.29	94% <sup>a</sup> $\pm$ 7.15	84.4% <sup>b</sup> $\pm$ 4.69
		95.1% <sup>A</sup> $\pm$ 3.7	93.7% <sup>AB</sup> $\pm$ 4.1	92.5% <sup>AB</sup> $\pm$ 7.4	89.6% <sup>B</sup> $\pm$ 6.8

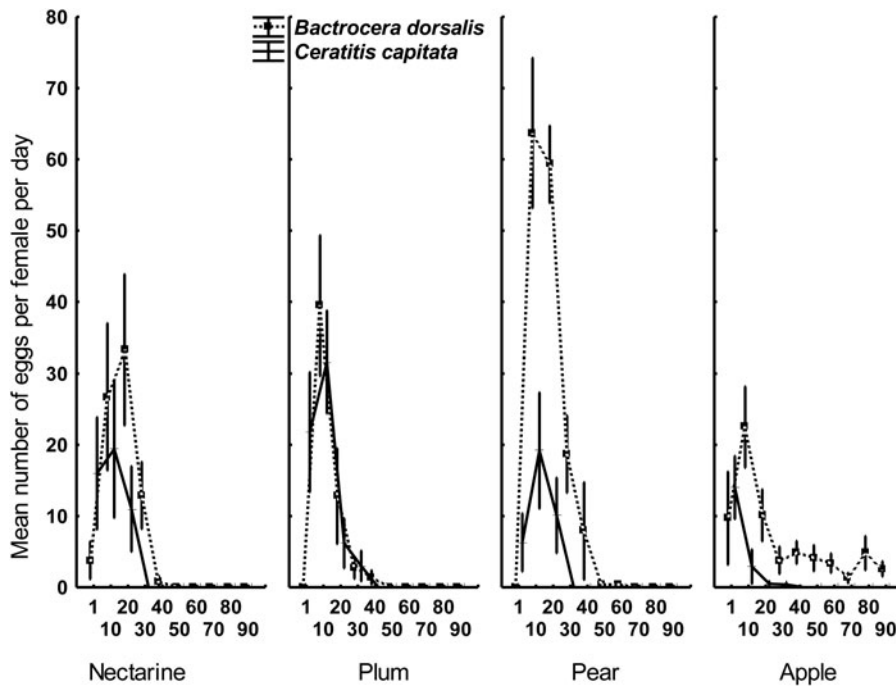
Development and survival of immature stages (5–10) were determined following a 24 h exposure to fruit. For each parameter, means followed by the same lowercase letters are not significantly different at the 0.05% probability level. For each parameter, means per fruit type followed by the same uppercase letters between columns within the same row are not significantly different at the 0.05% probability level.

## Results

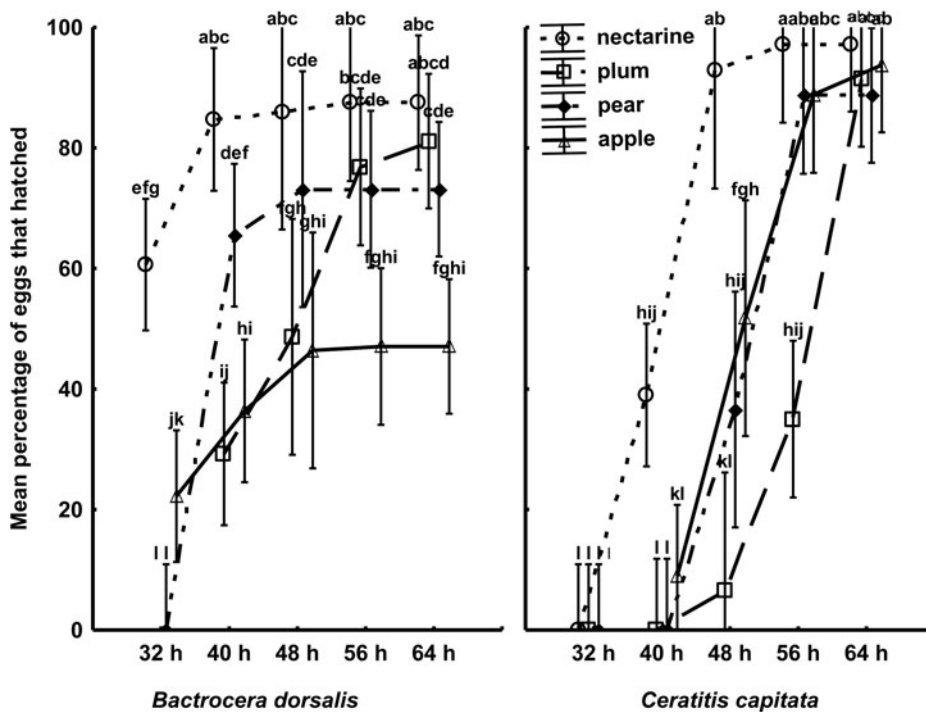
### Oviposition and egg development

There were significant effects of fruit fly species and fruit on egg laying and sting marks for both time periods: 24 h (eggs: DF = 3, Wald's  $\chi^2 = 41.0$ ,  $P < 0.001$ ; sting marks: DF = 3, Wald's  $\chi^2 = 25.671$ ,  $P < 0.001$ ) and 90 days (eggs: DF = 3, Wald's  $\chi^2 = 41.373$ ,  $P < 0.001$ ; sting marks: DF = 3, Wald's  $\chi^2 = 49.769$ ,  $P < 0.001$ ). Over 24 h, *B. dorsalis* laid more eggs per female than *C. capitata* on all deciduous fruit types (table 1). On apple,

differences in the number of eggs laid over 24 h between *B. dorsalis* and *C. capitata* were not statistically significant. Fewer eggs were laid in pear over 24 h by both species. When exposed to fruit sections over 90 days, *B. dorsalis* produced more eggs than *C. capitata* on all fruit types except on plum (table 1 and fig. 1). The number of sting marks on fruit represented oviposition attempts. In contrast to egg laying, differences in the number of oviposition attempts over 24 h between species only occurred on the stone fruit types: nectarine and plum. On nectarine, *B. dorsalis* had more oviposition attempts while the reverse occurred on



**Figure 1.** The pattern of egg laying of *B. dorsalis* and *C. capitata* females on four different deciduous fruit types over 90 days. On day 1 of this study, *B. dorsalis* females were 14 ( $\pm 1$ ) days old whilst *C. capitata* females were 7 ( $\pm 1$ ) days old. Vertical bars denote  $\pm 0.95$  confidence intervals.



**Figure 2.** The mean percentage egg hatch recorded for *Bactrocera dorsalis* and *Ceratitis capitata* on four different deciduous fruit types over 64 hours at 25 °C.  $\pm$  Vertical bars denote 0.95 confidence intervals. Values indicated by the same letter do not differ significantly at  $p = 0.05$ .

plum. Over 90 days, there were generally more oviposition attempts by *B. dorsalis* than by *C. capitata* on all fruit except plum (table 1). Over 90 days there were more oviposition attempts on apple than other fruit types for *B. dorsalis*. For *C. capitata*, there were more oviposition attempts on plum compared to other fruit types over 90 days similar to egg-laying patterns. There was no significant interaction between day  $\times$  species  $\times$  fruit when analysing the mean number of oviposition attempts (DF = 3, Wald's  $\chi^2 = 7.082$ ,  $P = 0.139$ ), but there was a significant

interaction between day  $\times$  species  $\times$  fruit when analysing the mean number of eggs deposited by a single female on the four fruit types over 90 days (DF = 3, Wald's  $\chi^2 = 12.790$ ,  $P < 0.001$ ). Egg laying by *C. capitata* peaked between days 16 and 38 in their adult life (fig. 1). Egg laying by *B. dorsalis*, on the other hand, peaked between days 23 and 45 in their adult life (fig. 1). After day 30 in the experiment (*C. capitata* at 38 days and *B. dorsalis* at 45 days), there were no significant differences in numbers of eggs laid between fruit types for both species.

The eggs of *B. dorsalis* generally hatched sooner (after 32 h) than those of *C. capitata* (after 40 h) (fig. 2). Averaged over all fruit types, the percentage egg hatch was higher for the eggs of *C. capitata* than those of *B. dorsalis* (table 1). There was a significant interaction between time × species × fruit when analysing the mean percentage of eggs that hatched ( $F_{(12, 96)} = 13.822, P < 0.001$ ) (fig. 2). Eggs of both species hatched the fastest on nectarine (fig. 2) and average percentage egg hatch was higher on nectarine for both fly species, but this was only significantly different when compared with apple for *B. dorsalis* (table 1). Percentage egg hatch was also highest on nectarine for *C. capitata*, but this was not significantly different from any of the other fruit kinds (table 1).

**Development to pupal and adult stages**

Both *B. dorsalis* and *C. capitata* produced the highest mean numbers of pupae, pupae per gram of fruit and mean number of adults on nectarine (table 1). *B. dorsalis* produced fewer pupae and adults than *C. capitata* on nectarine (table 1). In contrast, on plum, pear and apple, *B. dorsalis* produced higher numbers of pupae than *C. capitata* (table 1). On plum, *B. dorsalis* also had a higher number of adults than *C. capitata* (table 1). This was not the case on the pome fruit types: pear and apple, where *C. capitata* had a higher number of adults compared to *B. dorsalis* (table 2). There were no significant interaction effects between fruit type and number of days to pupation for the two species (DF = 6, Wald’s  $\chi^2 = 6.979, P = 0.323$ ). Development (mean number of days to pupation and adult emergence) was faster on nectarine and slowest on apple for both *C. capitata* and *B. dorsalis* (table 1). Larvae of *C. capitata* took significantly longer than those of *B. dorsalis* to pupate on apple. Adult emergence was over 90% on all crops for both species, except for *C. capitata* on apple which was at 84% (table 1). The ratio of male:female flies was approximately 50:50 for both species on all fruit types.

**Adult survival**

There was a significant interaction between fruit × species × sex (DF = 3, Wald’s  $\chi^2 = 19.671, P < 0.001$ ) when analysing the survival of *B. dorsalis* and *C. capitata* adults on the different fruit types (table 2).

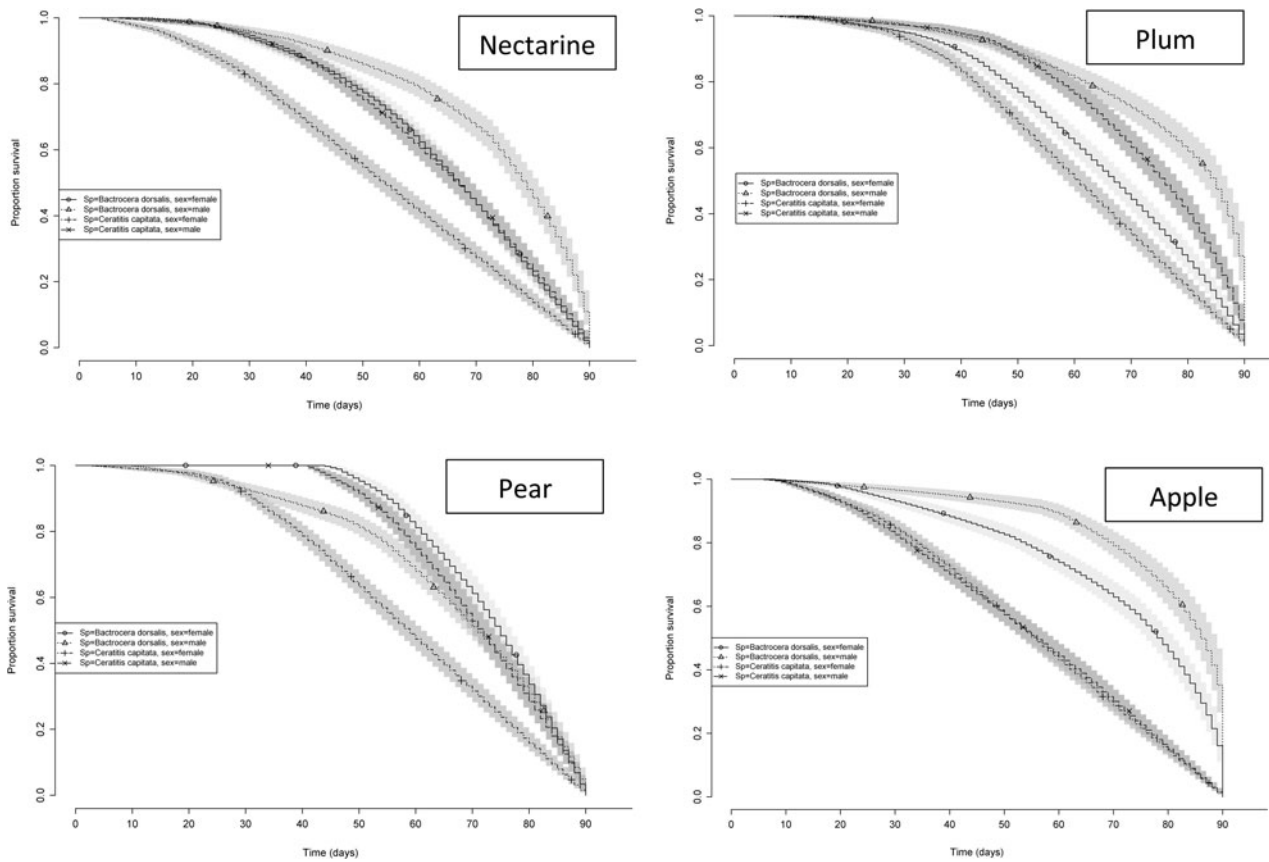
*B. dorsalis* lived longer than *C. capitata* on all deciduous fruit types tested except for males on pear (table 2). On pear, there were no significant differences in the lifespan of males between the two species (table 2). *B. dorsalis* reared from apple survived longer than those reared on any of the other crops ( $Z = -20.7, P < 0.001$ ), (table 2 and fig. 3). On all other crops, *B. dorsalis* and *C. capitata* had similar adult survival rates (table 2 and fig. 3). Males lived longer than females on all deciduous fruit types for both species (table 2).

**Life table parameters**

*B. dorsalis* had a higher net reproductive rate ( $R_0$ ) on all deciduous fruit tested compared to *C. capitata* (table 3). The value of  $R_0$  was the lowest for *C. capitata* on apple and highest on plum. For *B. dorsalis*,  $R_0$  was lowest on apple and highest on pear. *C. capitata* had a shorter generation time ( $T$ ) on all deciduous fruit types tested compared to *B. dorsalis*.  $T$  for *C. capitata* was shortest on apple and longest on pear.  $T$  for *B. dorsalis* was longest on apple.  $T$  for *B. dorsalis* on fruit types other than apple was more or less similar (table 3). *C. capitata* had a significantly

**Table 2.** The influence of deciduous fruit type on adult formation, sex ratio and lifespan of *B. dorsalis* and *C. capitata*

	Nectarine			Plum			Pear			Apple		
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD
Number of adults <i>B. dorsalis</i>	50	153	97.8% ± 43.4%	22	77	45 ± 23.2	19	67	42.5 ± 24	19	29	25 ± 4.3
% Male <i>B. dorsalis</i>	28	60.37	48.27 ± 14.03	42.85	62.16	50.68 ± 8.61	40	50.73	48.45 ± 6.26	36	59.25	43.82 ± 10.6
% Female <i>B. dorsalis</i>	39.62	72	51.72 ± 14.03	37.83	57.14	49.31 ± 8.61	46.2	60	51.54 ± 6.26	40.74	64	56.17 ± 10.6
Number of adults <i>C. capitata</i>	47	245	162.25 ± 83.03	10	33	18.75 ± 9.8	35	111	62.5 ± 33.8	18	84	46.5 ± 31.5
% Male <i>C. capitata</i>	48.57	57.71	53.22 ± 5.61	30	66.66	50.73 ± 15.22	46.6	51.42	49.39 ± 2.17	26.08	58.33	46.15 ± 14.67
% Female <i>C. capitata</i>	42.28	51.42	46.77 ± 5.16	33.33	70	49.26 ± 15.22	48.5	53.33	50.60 ± 2.17	41.66	73.91	53.84 ± 14.67
Male lifespan (days) <i>B. dorsalis</i>	13	89	38.1 ± 24.5	14	89	41.4 ± 25.9	10	89	33.5 ± 23.1	6	89	42.3 ± 25.3
Male lifespan (days) <i>C. capitata</i>	7	89	27.4 ± 20.6	10	89	35.5 ± 23.5	41	88	28.6 ± 18.8	6	65	17.6 ± 16.2
Female lifespan (days) <i>B. dorsalis</i>	11	71	25 ± 17.02	12	89	29.1 ± 21.9	44	81	30.4 ± 19	8	89	40.03 ± 25.7
Female lifespan (days) <i>C. capitata</i>	4	31	12 ± 8.2	7	46	17.5 ± 11.1	3	42	15.5 ± 9.8	7	39	13.5 ± 9.6



**Figure 3.** Kaplan–Meier plots showing the survival of *B. dorsalis* (14-day-old flies) and *C. capitata* (7-day-old flies) males and females on four different fruit types (apples, nectarines, pears and plums). Shaded areas of each line represent 95% confidence intervals of the mean proportion of survivors.

higher intrinsic rate of population increase ( $r_m$ ) compared to *B. dorsalis* on all fruit types.

**Discussion**

In this study, both *B. dorsalis* and *C. capitata* completed their life cycles successfully on all the deciduous fruit tested. *B. dorsalis* was able to survive longer as adults on deciduous fruit, made more oviposition attempts and laid more eggs than *C. capitata*. There were differences in larval and pupal survival rates between *C. capitata* and *B. dorsalis* according to the deciduous fruit tested. On all deciduous fruit types, the eggs of *B. dorsalis* hatched earlier than those of *C. capitata*, giving the developing *B. dorsalis* larvae a competitive edge over *C. capitata* larvae. Based on survival and reproduction data recorded in this study, a higher net reproductive rate ( $R_0$ ) was estimated for *B. dorsalis* than for *C. capitata* on all deciduous fruit types. Based on developmental rates, *B. dorsalis* was found to have a significantly lower intrinsic rate of increase ( $r_m$ ) and generation time ( $T$ ) than *C. capitata* on all deciduous fruit types tested. The life history patterns of *B. dorsalis* and *C. capitata* obtained in this study are in agreement with findings from previous studies where the two species were compared in similar environments (Carey and Vargas, 1985; Vargas *et al.*, 2000). Life-history traits of *B. dorsalis* were previously suggested as being mixed between r-selected (high fecundity) and K-selected (longer generation times and longer life span) while traits of *C. capitata* fitted to r-selected species (higher intrinsic rates of increase, short generation times) (Vargas *et al.*, 2000).

The traits of both species were preserved on the four deciduous fruit types evaluated in this study. While r-selected species are capable of rapid development, K-selected species would have greater competitive ability (Pianka, 1970). The K-selected traits of *B. dorsalis* on deciduous fruit indicate the latter would possibly out-compete *C. capitata*. Growth of populations of *B. dorsalis* would however be limited by temperature (Pieterse *et al.*, 2017) and the latter would possibly be the determining factor in competitive outcomes between the two species.

The demographic parameters of *B. dorsalis* on deciduous fruit obtained in this study are similar to those obtained on mango (recorded by Ekesi *et al.*, 2007), the preferred host of this fruit fly species (Ekesi *et al.*, 2006). Ekesi *et al.* (2007) compared the demographic parameters of *B. dorsalis* reared on mango to those reared on an artificial diet. They found that larval development takes 10 days under similar rearing conditions, as was found in the present study, and that about 80% of the eggs and pupae emerged. Ekesi *et al.* (2007) recorded a lower number of eggs (per ten females) than was recorded in the present study on deciduous fruit (per five females). This is an indication that *B. dorsalis* could maintain similar or higher populations on deciduous fruit as on mango under suitable climatic conditions.

In the present study, males of *C. capitata* and *B. dorsalis* generally lived longer than con-specific females. This is similar to findings of Papadopoulos *et al.* (2002) on *C. capitata* and Ekesi *et al.* (2006) on *B. dorsalis*. The impact of food restriction on the longevity of male and female *Anastrepha ludens* (Loew) was investigated by Carey *et al.* (2008). The authors discussed the

**Table 3.** Life table parameters (mean net reproductive rate,  $R_0$ ; mean intrinsic rate of increase  $r_m$ ; mean generation time  $T \pm SD$ ) for *C. capitata* and *B. dorsalis* on four different deciduous fruit types

Parameter	<i>C. capitata</i>				<i>B. dorsalis</i>			
	Nectarine	Plum	Pear	Apple	Nectarine	Plum	Pear	Apple
$R_0$	227.28 ± 89.61 <sup>b</sup>	276.59 ± 54.15 <sup>b</sup>	212.31 ± 58.47 <sup>b</sup>	30.41 ± 11.81 <sup>c</sup>	273.15 ± 54.98 <sup>b</sup>	279.53 ± 57.94 <sup>b</sup>	499.54 ± 31.75 <sup>a</sup>	155.73 ± 31.80 <sup>bc</sup>
$r_m$	0.28 ± 0.03 <sup>bc</sup>	0.37 ± 0.02 <sup>a</sup>	0.33 ± 0.04 <sup>ab</sup>	0.25 ± 0.05 <sup>bcd</sup>	0.18 ± 0.02 <sup>de</sup>	0.19 ± 0.02 <sup>de</sup>	0.20 ± 0.01 <sup>cde</sup>	0.14 ± 0.02 <sup>e</sup>
$T$ (days)	14.93 ± 1.81 <sup>b</sup>	15.35 ± 1.58 <sup>b</sup>	16.10 ± 1.65 <sup>b</sup>	13.76 ± 2.34 <sup>b</sup>	28.70 ± 2.14 <sup>a</sup>	25.98 ± 2.30 <sup>a</sup>	31.62 ± 1.44 <sup>a</sup>	31.18 ± 3.36 <sup>a</sup>

costs of reproduction in male flies (energy spent during courtship-calling and mating) and they did not find any differences in lifespan of males and females along different food gradients. The differences in adult lifespan between males and females where food was not restricted could be due to the physiological cost of producing eggs (Vargas and Carey, 1989), also discussed by Carey *et al.* (1995).

Larval development success of *B. dorsalis* and *C. capitata* differed between types of deciduous fruit. For both species, nectarine offered the best larval environment compared to the other deciduous fruit types in terms of the numbers of pupae and adults produced. Development of pupae and emergence of adults took significantly longer on apple for both *C. capitata* and *B. dorsalis*. *P. persica* (peach and nectarine) and *P. domestica* (plum) have previously been found to be good hosts for *B. dorsalis* (Ye and Liu, 2005) and *C. capitata* (Liquido *et al.*, 1990; Ovruski *et al.*, 2003). *Malus pumila* (apple), on the other hand, was not found to be a good host for *C. capitata* when compared to apricot, peach and orange (Papadopoulos *et al.*, 2002). No larvae of *C. capitata* survived in apple during the host demographic studies of Carey (1984), who suggested that the flesh of the apple fruit was too firm for the larvae to feed on. Survival and development of other fruit fly species have been found to differ between fruit types which are within their host ranges (Hafsi *et al.*, 2016). Hafsi *et al.* (2016) found that the nutritional contents, especially the carbohydrate, lipid and fibre content of fruit, influenced larval development of polyphagous fruit flies. They used the survival rate, development time and pupal weight of larvae as indicators of performance on the fruit they tested. According to the National Nutrient Database for Standard Reference of the United States Department of Agriculture (2018) (<https://ndb.nal.usda.gov>), lipid and protein contents of nectarine and plum are higher than that of apple and pear. It is likely that the larval development of both *B. dorsalis* and *C. capitata* is limited by lipid and protein. Lipid and protein were found to be constantly utilized in different phases of larval-adult transition for *C. capitata* (Nestel *et al.*, 2003). This would probably also be the case for *B. dorsalis*. The presence of phenolic components in fruit was found to decrease larval development by exerting an anti-nutritive effect (Birke and Aluja, 2018). Apples (343 mg/100 g) and pear (305 mg/100 g) contain higher concentrations of phenolic components than plum (122 mg/100 g) and nectarine (154 mg/100 g) (Gil *et al.*, 2002; Imeh and Khokhar, 2002; Lombardi-Boccia *et al.*, 2004).

Host fruits with longer larval development times represent potential overwintering hosts for fruit flies until environmental conditions improve again (Papadopoulos *et al.*, 2002). Papadopoulos *et al.* (1996) found that apple, as opposed to other fruit such as pear, stay more intact and provide a refuge for larvae that protects them from the elements. In this study, a long period of egg production was found on apple for *B. dorsalis*. Apples could therefore represent ideal bridging hosts for *B. dorsalis* to survive until other fruits become available, such as citrus fruits, and suitable environmental conditions are restored.

*B. dorsalis* would be able to sustain its population in deciduous fruit growing areas under favourable climatic conditions. Given that *B. dorsalis* immatures were found to develop faster than those of *C. capitata* at a temperature of 26°C, competitive interactions at the larval stages between the two species can be expected. The results of this study imply that early detection and elimination of any *B. dorsalis* propagules are of utmost importance to protect the deciduous fruit growing area of the Western Cape from a potentially damaging pest.



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