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RESEARCH ARTICLE

Role of developmental plasticity in tethered flight performance of the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae)

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This study investigated the effect of nutrition on development of wings and adult body condition of *Bactrocera dorsalis* (Hendel), an exotic pest of Asian origin and a species of economic importance in South Africa. Six host fruit types were used to rear *B. dorsalis*: mango, guava, orange, grapefruit, papaya and apple. One day after emergence, adults were used for tethered flight assessments using computerised flight mills. Additional flies were assessed in terms of wing morphology using geometric morphometrics, flight muscle mass, and lipid content. There were significant differences in the larval and pupal developmental time as well as larval and pupal survival amongst the tested host fruit, with orange tending to lead to poor performance in development and survival. Host fruit type and sex had a significant effect on the flight performance and wing morphology of *B. dorsalis*. There was a significant difference between female and male wing shapes, indicating the presence of sexual dimorphism. Females were more likely to fly than the males, and flies that developed on grapefruit covered the shortest distance. Host fruit type influenced both the lipid content and the flight muscle mass, with development in grapefruit leading to the lowest values. Our results show that variation in flight performance of *B. dorsalis* individuals can be associated with differences in resource quality during their development, and may lead to regional and temporal differences in the ability of the pest to disperse.

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INTRODUCTION

Dispersal through flight is a key component in insect population dynamics, and has implications for invasion biology, biogeography, population genetics and integrated pest management (Naranjo 2019). Insect survival and evolution depend on flight, with flying insects having an advantage when searching for food sources, evading predators, and colonising new habitats (Sane 2003). Pest insect flight capacity is a key consideration when determining the size of buffer zones protecting pest free areas, quarantine zones around incursions, and the extent of associated eradication programmes (EPPO 2021).

Variation in dispersal ability or flight performance between individuals is frequently associated with differences in individual phenotypes such as muscle mass, wing size (Dudley 2002) or life-history trade-offs (Hanski et al. 2006; Zera 2003). Flight performance can be significantly influenced by wing size through its effect on wing loading (body mass/wing area) (Ellington 1984; Rayner 1979). Individuals with larger wings decrease the power needed to offset their mass by generating more lift and can facilitate dispersal, but this could be at the cost of reduced manoeuvrability (Steenman et al. 2015). Thomas et al. (1998) have reported that there is more power available for flight among individuals with a larger thorax compared to body mass, resulting from a higher flight muscle ratio. Another way in which flight performance can be promoted is through the storage of energy reserves. Animals obtain nutrients from food for somatic maintenance, reproduction and growth but they also play a large role in tolerance of desiccation and starvation (Djawdan et al. 1998). Lipid stores represent the substrate from which flight energy is derived (Sacktor 1974). In general, there is a direct utilisation of fat reserves to support long-term insect flight (Beenakkers et al. 1985).

According to several studies, factors such as diet, gender or nutrition are known to influence the flight performance of true fruit flies (Diptera: Tephritidae). The flight capacity of tephritids can be influenced by physiological and environmental factors (Chen et al. 2015). Nutrition can result in changes in morphology. Pieterse et al. (2017) found that there were significant differences in the shape of the wings between the females and males of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). In addition, they found that the distance between corresponding landmarks among the wings of both species were significantly different when individuals were reared on plum, nectarine, apple or pear. They concluded that wing shape change might be a function of the plasticity of the species and therefore geometric morphometrics is an important tool to add to the methods used in the study of insects. However, they did not further explore the functional implications of wing morphology resulting from different host fruits, nor include tropical fruit hosts preferred by *B. dorsalis* in their study. Prior studies show that *B. dorsalis* exhibit a preference for host fruits like grapefruit (*Citrus x paradisi*), mango (*Mangifera indica*), loquat (*Eriobotrya japonica*) and guava (*Psidium guajava*) (Mwatawala et al. 2006). When *B. dorsalis* is developed in the above mentioned host fruits it leads to faster developmental period, bigger pupae size, larger fruit flies, and long-lived fruit flies. However, how the differences relate to the variety of host fruit they develop in is not well understood, although we know that the host fruits are rich in particular nutrients.

This study investigated how development in different host fruit affected flight in *B. dorsalis*. To achieve this aim, the effect of development in host fruit type on wing morphology, flight muscle weight, and the lipid content of *B. dorsalis* were measured. Furthermore, the effect of development in host fruit types on flight capacity of *B. dorsalis* was recorded based on laboratory flight recordings. The wing morphology, lipid content and flight muscle mass were related to the measurements obtained from tethered flight for six hours. The tethered flight variables included total distance flown, total flight duration, number of discrete flight bouts, duration of each flight bout, maximum flight speed and the mean flight speed. We predicted that development in host fruit considered preferred hosts for *B. dorsalis* (e.g., guava and mango) would lead to larger wings, heavier flight muscles, and higher fat reserves. We also predicted that *B. dorsalis* with larger wings, greater thorax:body ratio and heavier flight muscles would exhibit better tethered flight performance. Flies with larger quantities of stored lipids would be able to sustain flight for longer distances.

MATERIALS AND METHODS

Insect culture

The flies used in this study were obtained from a *B. dorsalis* culture maintained in the Department of Zoology and Entomology, University of Pretoria, South Africa. The *B. dorsalis* culture was established from flies reared from infested mangos collected near Nelspruit, South Africa and had been maintained in the laboratory for one year. Adults were kept in ventilated cages (30 × 30 × 30 cm) provided with sugar and hydrolysed yeast (HG000BX6.500, Merck, Wadesville, South Africa). The culture and all the experiments described below were kept in a climate room at a constant temperature of 24 ± 1 °C, a buffered relative humidity of 40–60%, and with a 14:10 (light:dark) photoperiod. The first and last hour of the light phase comprised 1 hour of simulated dawn and dusk to promote mating. This was achieved by the sequential turning on (dawn) or off (dusk) of 4W and 8W fluorescent tubes. The main room lights in the climate room were turned on at 06:00 and turned off at 18:00 (South African Standard Time; GMT+2).

Fruit inoculation and immature development

Six host fruit types were used to rear *B. dorsalis* for testing: mango (*Mangifera indica* L. var. Keitt), guava (*Psidium guajava* L. var Fan Retief), orange (*Citrus* × *sinensis* L. var Valencia), grapefruit (*Citrus* × *paradisi*. var Star Ruby), papaya (*Carica papaya* L. var. Papino), and apple (*Malus domestica* var. Golden Delicious). These host fruits were used in the rearing of fruit flies as Rwomushana et al. (2008) reported them as hosts of *B. dorsalis*. Golden Delicious apples were used as a control for this study due to wing geometric morphometrics of *B. dorsalis* having already been assessed in this variety (Pieterse et al. 2017). Fruit of each type were weighed (Denver Instrument MXX-123.1 Maxx Series Portable Balance, 120 g × 0.001 g, 115V) before being used in experiments.

The *B. dorsalis* eggs were harvested from stings in a Golden Delicious apple and allowed to hatch on moist black filter paper. First instar larvae were artificially inoculated into each fruit at a rate of 1 larva per 3.1 g of fruit. This step was required to remove the effect of female preference for fruit on the number of eggs laid and differences in fruit size. The rate of infestation was based on the number of *B. dorsalis* reared from host fruit under warm, humid conditions of 1 larva/3.1 g of fruit (Rwomushana et al. 2008) while also avoiding potential overcrowding. The mean number of eggs inoculated (± s.e.) into each fruit was 166.4 ± 4.0 for mango, 29.9 ± 2.2 for guava, 83.3 ± 2.1 for orange, 110.0 ± 2.9 for grapefruit, 107.4 ± 8.6 for papaya and 50.6 ± 1.3 for apple. Fruits were placed on a layer of washed sand in individual 1-L clear plastic buckets. The lid of the bucket had a section removed and replaced with white voile curtain fabric for ventilation. The sand in each box was sifted daily and the pupae from each fruit were recorded and placed in separate Petri dishes. These Petri dishes were placed into 5-L plastic cages with only water available until the emergence of adults. Survival to the pupal and adult stage were recorded. The time to complete larval and pupal development was also recorded. Survival and development time were recorded to give an indication of the suitability of the different host fruit for the development of *B. dorsalis*.

One day after emergence, adults were used for tethered flight assessments. One-day-old flies were used because studies have found evidence for post-teneral dispersal of fruit flies (Chen et al. 2006; Fletcher 1974; Rwomushana et al. 2008) and adult feeding could influence lipid stores (Weldon et al. 2019) that would then mask host fruit effects on measured flight, morphological and physiological traits. Flies were transferred to pre-weighed, individual 1.5 ml microcentrifuge tubes, and body weight was measured using an analytical balance (to 0.0001 g; NewClassic MF Model # MS204S, Mettler-Toledo, Greifensee, Switzerland). Additional flies were also weighed and then immediately killed and stored in a freezer at −20 °C for later determination of morphological and physiological traits.

Recording of tethered flight

Flight mills were used to investigate the flight behaviour of insects. Flight mills provide an exact measurement of flight distance, speed, and duration, which are the most reliable parameters to understand the physiological basis of flight capacity (Chen et al. 2015). These flight parameters for each fly were related to variations in wing size and shape, and how this phenotypic plasticity may influence specific flight parameters as in Fraimout et al. (2018).

The effect of development in host fruit types on flight capacity of *B. dorsalis* was studied using flight mills attached to a 15-channel flight mill data acquisition (DAQ) system connected to a computer and placed on a shelf in a room where the temperature, relative humidity and photoperiod were the same as described for rearing (Makumbe et al. 2020). The DAQ and flight mills were built by the Vehicle Dynamics Group at the University of Pretoria based on the design developed by the USDA-ARS Arid Land Agricultural Research Centre in Maricopa, Arizona (Naranjo 1990). The flight mill DAQ comprised 15 inputs for 15 individual flight mills. Movement of the flight mill arm is recorded by a magnetic motion detector so that the time and number of flight arm revolutions can be recorded by the flight mill DAQ. The custom-designed DAQ interface ran on Java virtual machine on a laptop computer running Windows 7 Enterprise version 6.1. An Ethernet connector was used to connect the DAQ to the computer to download data after an experiment had been run. Live recordings of flight were displayed on the laptop using a web browser.

Before running the experiment, a day after emergence, 20 female and 20 male *B. dorsalis* adults from each host fruit were prepared for the flight experiments over multiple days as they emerged. One fly of known age (1 day old), weight and sex were cooled for exactly 2 minutes in a small (approximately 2.5 l) cooler box containing fine ice shavings. Once cooled, the fly was placed on a paper towel and a small drop of melted hot glue collected on the tip of a #1 insect pin was immediately placed on the centre of the thorax with the pin in an upright position and perpendicular to the thorax of the fly. The attached fly was left to recover for 2–5 minutes by sticking the pointed end of the attached pin into a Styrofoam board.

Only 10 flies that recovered from chill coma and tried to fly were attached to the flight mill. To do so, the insect pin attached to the thorax of the fly was then carefully inserted with its pointed end into the opening of the hypodermic tube of the flight arm of the flight mill to fit snugly enough to hold it in place without slipping. A very small amount of rubber-based reusable putty adhesive (Prestik, Bostik, Henkel S.A. (Pty) Ltd) was used to

ensure the pin did not slip out of the tube. A quantity of the same putty adhesive of equal weight to the fly was placed onto the head of another entomological pin on the opposite side of the flight mill arm to act as a counterbalance.

Each test was conducted for 6 h and each adult was tested once in their lifetime. Data that were recorded by the flight mill DAQ were the time of flight initiation and each half-revolution, and the number of mill half-revolutions that occurred. These data were downloaded as comma-separated values files to the laptop computer and stored. Knowing the radius of the flight mill arm, this data permitted the calculation of flight distance, speed, duration and the maximum speed of flight for each fly. Flights that were interrupted by a 5-min interval were considered as separate flights. Records of the date of experiment, host fruit, weight before flight, age and sex of fly, fly label, flight mill number and any other additional observations were noted. Following each flight trial, individual female and male *B. dorsalis* adults were detached from the flight mills and immediately placed in 1.5 ml microcentrifuge tubes. An appropriate label corresponding to each fly was written and placed in the tube. Any dead individuals detached from flight mills were discarded and excluded from the analyses.

Wing morphology

Following the flight mill observations, each fly was killed by being placed in a freezer (−20 °C) for storage until required. Later, the right wing (unless damaged, then the left wing) of each specimen was detached from the thorax using fine forceps and placed on a microscope slide. The wing was secured onto the slide using clear double-sided tape and a label was affixed to correspond with the fly identity. Wings from one flight mill session were placed on one slide to avoid any chance of misidentification. A second microscope slide was used to cover the wings. The same procedure was used to affix wings to slides from an additional 28 females and males reared on each host fruit type (i.e., total n = 38 females and 38 = males, reared on mango, orange, guava, grapefruit, papaya and apple; 456 in total).

Images of the wings of the 38 females and 38 males reared from each host fruit type were used to assess wing morphology. Differences in wing morphology were determined using a geometric morphometric approach. Wing image processing was done by positioning the microscope slide with wing samples on a stereo microscope with a low objective lens (1×) fitted with a digital camera (Dino-Eye AM7023CT, Dino-Lite, Almere, The Netherlands). A photograph of each wing was taken using DinoCapture® 2.0 software.

To collect wing landmark coordinates, the digital photographs were opened in ImageJ software (Schneider et al. 2012). Cartesian coordinates were then generated for the same 15 wing landmarks used by Pieterse et al. (2017), as well as the termination of vein A1 and Cu2, which is often used as a landmark in the tephritid literature for measurement of wing length (Figure 2, Table 1). The 15 landmarks were collected for the wings of all 76 individuals reared from each host fruit type. In addition, the landmarks of each wing were digitised an additional two times to quantify measurement error.

Flight muscle weight

To establish flight muscle weight, a combination of methods used by Helm and Davidowitz (2013) and Snelling et al. (2012) were used. From the same flies for which wing morphology and flight capacity were determined, ten flies from each fruit group were tested for flight muscle weight. For flight muscle mass, the wings, legs, head and abdomen of the fly were separated from the thorax. Each individual thorax was weighed on a microbalance (Sartorius CPA2P Micro Balance, Weender Landstrasse 94-108 37075 Goettingen, Germany). A razor blade was then used to cut the thorax longitudinally and then again horizontally into four pieces.

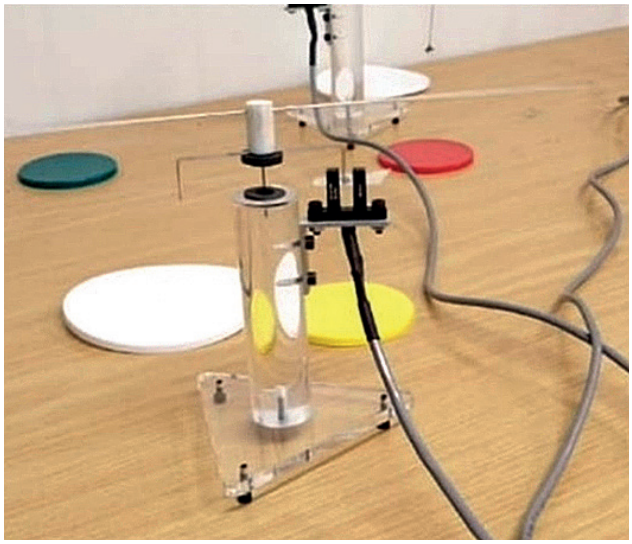

Figure 1: Flight mill setup for measurement of tethered flight in *Bactrocera dorsalis* reared from different host fruit types.

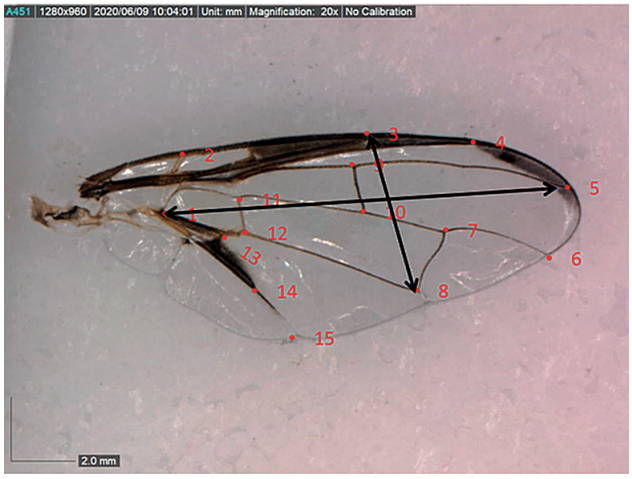

Figure 2: Dorsal view of the right-wing of *Bactrocera dorsalis*. Numbers indicate the location of 15 selected landmarks as described in Table 1.

Table 1: Positions of 15 anatomical landmarks used to characterise *Bactrocera dorsalis* wing geometry. Numbers on the table relate to landmarks shown in Figure 2.

Anatomic position of landmark	Description
1	Basal junction of veins of cell bm
2	Inner antero-distal corner of cell bc
3	Junction of vein R1 and costal vein
4	Termination of vein R2 + 3
5	Termination of vein R4 + 5
6	Termination of vein M
7	Juction of vein M and dm-cu
8	Juction of vein CuA1 and dm-cu
9	Juction of vein R4+5 and r-m cross-vein
10	Junction of vein M and r-m cross-vein
11	Juction of vein M and dm-bm cross vein
12	Junction of veinCuA1 and dm-bm cross vein
13	Junction of CuA1 and CuA2
14	Junction of veins A1 and CuA2
15	Termination of vein A1 and Cu2

The dissected thorax was placed into approximately 2 mL of 1 M NaOH for 24 hours to dissolve the flight muscle. The remaining cuticle was removed from the NaOH, rinsed with distilled water, dried between paper towel and then weighed on the microbalance. The difference between thorax weight and thoracic cuticle weight was used to approximate flight muscle weight.

Lipid content

The total amount of lipids in each insect was determined with the same vanillin colorimetric assay used by Weldon et al. (2019). Twenty individual flies (10 males and 10 females) from each fruit group were initially selected at random from the flies for which wing morphology and flight capacity were determined. Each insect was individually homogenised in 180 µl of lysis buffer with a single 3 mm, zirconium bead using a microtube homogeniser (BeadBug™ Three Position Bead Homogeniser, Benchmark Scientific Inc., Sayreville, NJ, USA) for 60 s at the maximum speed setting (4000 rpm). The lysis buffer consisted of 100 mM potassium dihydrogen phosphate, 1 mM DTT and 1 mM EDTA (pH 7.4). After homogenisation, the samples were centrifuged at 14 000 × g for 10 min at 4 °C. 4.5 µl of lysis buffer and 20 µl of 20% (w/v) sodium sulphate was added to the remaining sample homogenate (to reach a final volume of 200 µl). After 1500 µl of chloroform: methanol (1:2 v/v) was added to each sample, samples were vortexed vigorously and centrifuged at 14 000 × g for 10 min at room temperature (~20˚). Three hundred microliters of the supernatant were aliquoted for the lipid analysis.

Glyceryl trioleate (Sigma-Aldrich, St Louis, MO, USA) dissolved in chloroform:methanol (1:2 v/v) was used as a calibration standard (dilution range 0.1, 0.2, 1.0 and 2.0 µg/µl). One hundred microliters of standard or aliquoted supernatant were transferred to a 96-well microplate in duplicate. The samples were completely evaporated at 90 °C in the heating block (AccuBlock™ Digital Dry Bath, Labnet International Inc, NJ, USA), then 10 µl of 98% sulphuric acid was added before they were incubated at 90 °C for two minutes. After the samples had been cooled on ice, 190 µl of vanillin solution (1.2 g/L vanillin, ReagentPlus® 99%, Sigma-Aldrich, St Louis, MO, USA dissolved in 68% orthophosphoric acid) was added to each sample. The microplate was placed in a microplate spectrophotometer (Biotek Instruments. Winooski, VT, USA) and the shake function was used to mix the reaction mixture before incubation for 15 min at room temperature and subsequent measurement of optical density at 525 nm.

Data analyses

Unless otherwise stated, statistical analyses were computed using R version 3.5.1 (R Core Team 2013).

Development and adult body weight

The effect of host fruit type on larval and pupal development time was analysed using separate generalised linear models (GLZ) with normal distribution and identity link. Separate GLZs with binomial errors and logit link were also run to determine the effect of host fruit type on larval and pupal survival. In these cases, the response was a bivariate vector comprising the number completing and entering each life stage created using the 'cbind' function. Post-hoc multiple comparisons were performed using pair-wise Tukey's tests using the 'emmeans' package to identify which fruit groups differed from each other.

Wing morphology

Four parameters were derived to describe wing size of *B. dorsalis*: (i) centroid size; (ii) wing length (distance between the 1st and 5th landmark); (iii) wing width (distance between the 3rd and 8th landmark) (Figure 2); and (iv) wing area from the full set of wings. The centroid size, also called the 'configuration barycentre' is a global size (or multidimensional measurement) calculated as the square root of the sum of squared Euclidean distances between each landmark and the wing centroid. Centroid size was computed using PAST software V.3.09 (Hammer et al. 2001). Also, based on the adult weight parameter, the wing loading was calculated (in kg/m^2) using the formula: wl = mass/wing area (Ribak et al. 2017). To see whether error due to measurement could affect the study, unpaired *t*-test and MANOVA test were respectively performed by comparing the centroid size and the shape data of the first and second recordings.

To assess the effect of host fruit type and sex on the parameters described above for *B. dorsalis*, two-way analyses of variance (ANOVA) were run followed by post-hoc Student–Newman–Keuls (SNK) tests after checking the wing size parameters for normality using the Shapiro–Wilk test ($p > 0.05$) and the variance homogeneity using the Bartlet test ($p > 0.05$). To identify correlations between centroid size, wing length, wing width, wing area, adult weight, wing loading, flight muscle mass and lipid content, a separate principal component analysis (PCA) was performed for the host fruit type.

Wing shape variation

To assess wing shape variation across the different host fruit types, the raw landmark Cartesian coordinates of the full set of wings were imported into MorphoJ software (Klingenberg 2011). This software was first used to perform a generalised Procrustes analysis to extract shape information from the data and eliminate differences in orientation, position and isometric size. Afterwards, a separate multivariate analysis of variance (MANOVA) was done to compare wing shapes (Cartesian coordinates) across the different host fruit types (guava, mango, navel orange, papaya, grapefruit and apples) and sex. Using PAST software, a thin plate spline analysis was performed to visualise wing shape deformations. Using MorphoJ, a canonical variate analysis combined with discriminant analysis was used to analyse the relative similarities and dissimilarities of the different wing groups. To determine the significance of pairwise differences in mean shapes, permutation tests were performed (10 000 rounds) with Mahalanobis distances and Procrustes distances. To assess the effect of wing size on wing shape (allometry), a linear regression between the Procrustes coordinates and the log (centroid size) was fitted, using a permutation test with 10 000 randomisations.

Flight performance

As noted in the results, one outlier from the flight distance, duration and speed was recorded for a single male fly reared from guava. For the analysis of flight performance, this individual was removed. Flight propensity was determined as the probability whether the flies flew on the flight mill or not. Flew with two responses of zeros and ones, with zero no and one yes. A GLZ model with binomial errors was performed to determine the list of zeros and ones. A GLZ with binomial errors was performed to determine the main effects of fruit type and sex and their interaction on the flight propensity. The scores for dimension 1 and dimension 2 from the wing morphology analysis were extracted for flies for which tethered flight. These were included as covariates in GLZs with Gaussian errors and identity link were performed to determine the main effects and interaction of fruit type and sex on flight parameters (flight distance, flight duration, flight speed). The minimum adequate model was determined using backwards stepwise regression ('step') to reduce the number predictors in the model. The 'step' procedure removes the least significant effect from a model until there is no further significant change in model fit as indicated by Akaike's information criterion (AIC). Analysis of deviance was performed to summarise whether effects significantly affect flight propensity or not and the flight parameters. Post-hoc multiple comparisons were performed using Tukey's tests to identify which fruit types differed from each other.

Flight muscle weight

Flight muscle weight was analysed using GLZ with normal distribution, with host fruit type, sex, their interaction and thorax weight as covariates. A backwards step-wise regression using 'step' was performed to identify the minimal adequate model. Post-hoc multiple comparisons were performed using pair-wise Tukey's tests to establish which fruit groups differed from each other.

Lipid content

Lipid content was analysed using a GLZ with the effects of host fruit type, sex, and their interaction, and body weight as a covariate. The response variable (lipid content) was log-transformed as it was not normally distributed, with variance increasing with the mean. The minimum adequate model was determined using 'step'. Post-hoc multiple comparisons were performed using pair-wise Tukey's tests to identify which fruit groups differed from each other.

RESULTS

Immature development

Development in different host fruit had a significant effect on the larval development time of *B. dorsalis* (GLZ: Wald $\chi^2 = 148.69$, df = 5, $p < 0.001$). The fastest larval development was recorded from grapefruit, mango and papaya (Figure 3A). Tukey's tests indicated that larval development was significantly longer in oranges than grapefruit, mango and papaya, although there was considerable variability in development from oranges. Larval development was longest in apple and guava. Pupal development time of *B. dorsalis* was also significantly affected by host fruit (GLZ: Wald $\chi^2 = 49.207$, df = 5, $p < 0.001$). Development time was shortest for pupae reared from apple, mango, grapefruit and papaya, which did not differ significantly from each other (Figure 3B). Pupal development time was then significantly longer from orange than guava.

Proportional larval survival of *B. dorsalis* was significantly affected by different fruit types (GLZ: Wald $\chi^2 = 308.33$, df = 5, $p < 0.001$). The highest proportional larval survival was recorded from guava, then grapefruit (Figure 4A). Proportional larval survival from these fruit types was significantly higher than from apple, mango and papaya. The lowest larval survival was recorded from orange. Host fruit type also had a significant effect on the proportional pupal survival of *B. dorsalis* (GLZ: Wald $\chi^2 = 148.01$, df = 5, $p < 0.001$). The highest proportional pupal survival was recorded in apple (Figure 4B). Pupal survival was the lowest when reared on mango, orange and papaya, which did not differ significantly from each other.

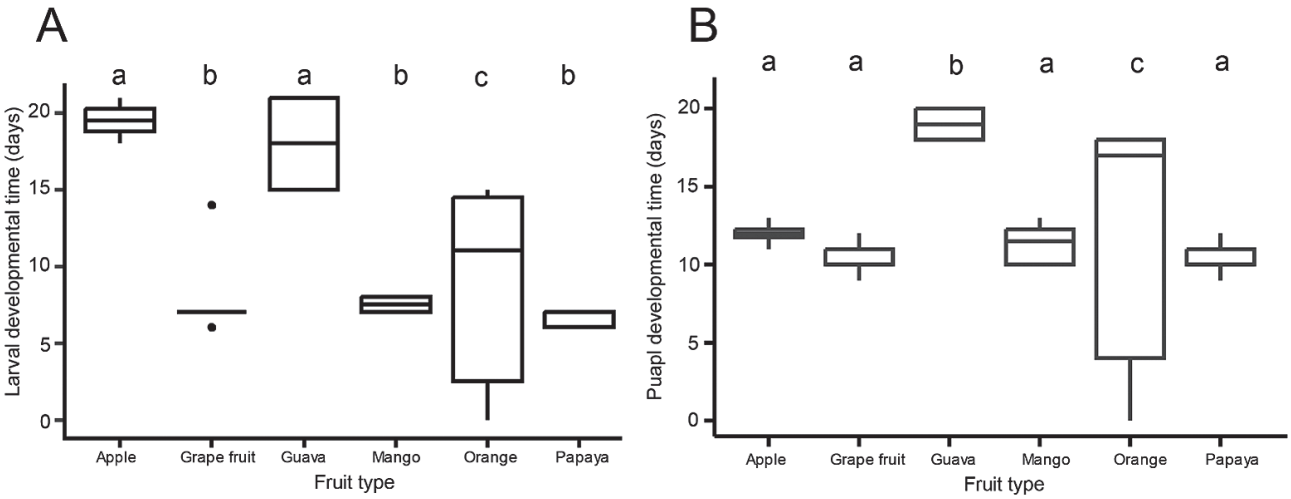

Figure 3: Boxplots displaying variation in (A) larval development time and (B) pupal development time of *Bactrocera dorsalis* when reared in different host fruit (ANOVA followed by post-hoc Tukey tests: $p < 0.05$).

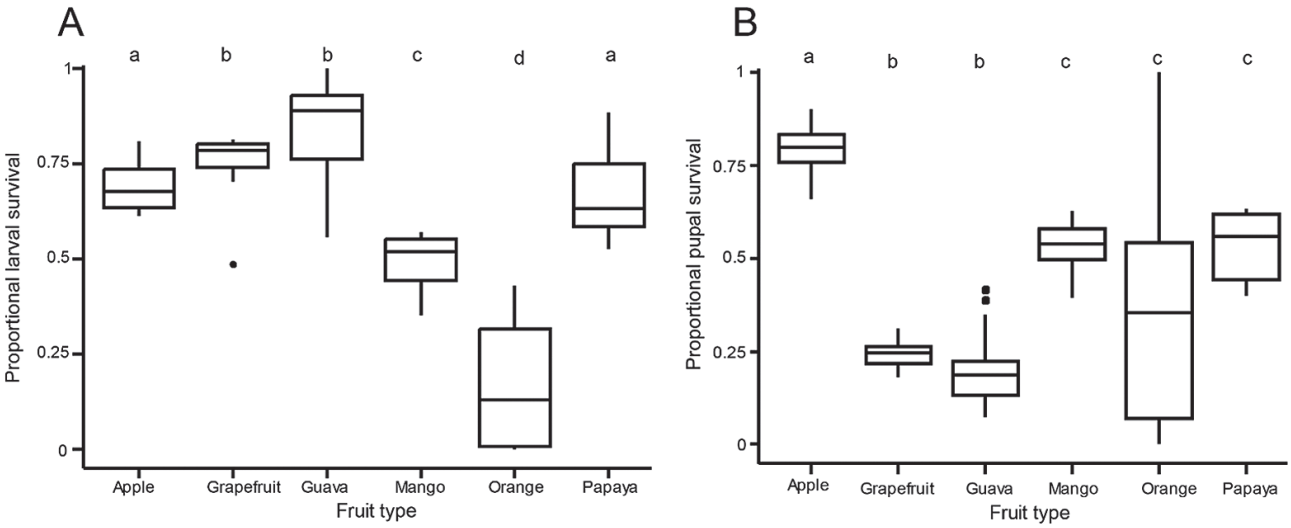

Figure 4: Boxplots displaying variation in (A) larval survival and (B) pupal survival of *Bactrocera dorsalis* when reared in different host fruit. Boxplots with different letters show significant differences (ANOVA followed by post-hoc Tukey tests: $p < 0.05$).

Wing morphology, lipid reserves and flight muscle

All the *p*-values obtained when comparing the centroid size and the shape data for the first and second recordings were above 0.95, suggesting that any change in wing size and shape derived from the effect of sex and host fruit will have an effect on the flight performance.

Host fruit type had a significant effect on the centroid size, wing length, wing area, wing loading, adult weight, flight muscle mass and lipid content, while sex significantly affected the centroid size, wing width, wing length and wing area (Table 2). The interaction between host fruit and sex did not affect the *B. dorsalis* adult traits. Wing size of *B. dorsalis* were significantly affected by host fruit with flies reared on mango and papaya having the longest wing length compared to the flies reared on apple (Figure 5). Body weight varied among the fruit types with flies reared from orange having the highest body weight, while flies reared from papaya had the lowest body weight (Figure 5E). Lipid content and flight muscle mass were significantly affected by host fruit type with flies reared on grapefruit having the lowest quantity of lipids and lowest flight muscle mass (Figure 4F and Figure 4G).

The principal components analysis accounted for 60.75% of the total wing size variation (Figure 6A). The principal component biplot showed that there were differences between *B. dorsalis* flies reared on different host fruit, with the polygon depicting apple being separated from mango and papaya. PC1 explained 32.19% (Figure 6B) of the total variation with wing loading and body weight as the main contributors, and lipid content and centroid size to a lesser extent (Figure 5C). PC2 accounted for 28.56% of the total variation with wing area and wing length as the major contributors (Figure 6D). The PC results are important for the analysis of flight, as PC1 relates mostly to fly body conditions while PC2 relates mostly to wing morphology.

Canonical variate analysis (Figure 7) and discriminant analysis (supplementary material) separated *B. dorsalis* wing shapes according to the host fruit in which flies developed. Canonical variate analysis explained 65.81% of the total female *B. dorsalis* wing shape variation (Figure 7A; CV1 = 42.5% and CV2 = 23.31%) while canonical variate analysis explained 59.49% of the total male *B. dorsalis* wing shape variation (Figure 7B; CV1 = 31.40% and CV2=28.09%).

The effect of host fruit type on wing shape of *B. dorsalis* was found to be significant (MANOVA, $F = 2.69$, Pillai's trace = 0.74, $p < 0.001$), while there was a further significant difference between male and female wing shape, indicating the presence of sexual shape dimorphism (MANOVA, $F = 40.61$, Pillai's trace = 0.72, $p < 0.001$). This is clearly shown in the thin plate spline deformation grid (Figure 8). The flies that were reared from orange, papaya, guava and apple, experienced expansion movement of landmarks 11, 12, 13 and 14 relative to the average wing shape, whereas flies reared on grapefruit and mango experienced contraction movement for the same landmarks. The fruit and sex interaction were significant (MANOVA, $F = 1.42$, Pillai's trace = 0.42, $p = 0.001$) indicating that the fruit kind and sex did influence the differences between the wings of individual flies. For instance, female flies reared on mango experienced a contraction while the male flies experienced expansion for landmarks 3, 9 and 10, and female flies reared on grapefruit experienced contraction for landmarks 3, 11, 12 and 13 while the male flies experienced contraction for the same landmarks.

Differences in Mahalanobis scores for corresponding landmarks on the wings of female *B. dorsalis* were highly significant in most pairwise comparisons between host fruit (Table 3; 10 000 rounds, $p < 0.016$). The only exception was the comparison of wing landmarks for females reared from mango and papaya. With Procrustes distance estimators, there was a significant difference in wing shapes of females reared from apple and all other tested host fruit, guava in comparison with orange and papaya, and orange in comparison with papaya (Table 3; 10,000 rounds, $p < 0.001$). Comparison of Mahalanobis scores for corresponding landmarks on wings of male *B. dorsalis* were highly significant for comparisons between all host fruit (Table 4; 10 000 rounds, $p < 0.001$). Procrustes distance showed that there was a significant difference in wing shapes in flies reared from apple and all other tested host fruit, grapefruit and all other host

Table 2: Analysis of variance summaries for the effect of host fruit and sex on variation in wing size parameters, adult weight, muscle mass, and lipid content of *Bactrocera dorsalis*.

	Predictors	df	Mean Sq	*F*	*p*
Centroid size	Host fruit	5	0.08355	53.68	< 0.001
	Sex	1	0.1424	91.48	< 0.001
	Host fruit*Sex	5	0.00251	1.61	0.156
Wing width	Host fruit	5	12842	46.562	< 0.001
	Sex	1	9403	34.094	< 0.001
	Host fruit*Sex	5	992	3.597	0.0034
Wing length	Host fruit	5	66936	63.77	< 0.001
	Sex	1	83632	79.68	< 0.001
	Host fruit*Sex	5	1091	1.04	0.394
Wing area	Host fruit	5	1.66E+10	53.119	< 0.001
	Sex	1	2.96E+10	95.041	< 0.001
	Host fruit*Sex	5	3.68E+08	1.181	0.317
Lipid content	Host fruit	5	1074024	36.809	< 0.001
	Sex	1	16719	0.573	0.45
	Host fruit*Sex	5	17656	0.605	0.696
Flight muscle mass	Host fruit	5	2.68E-06	26.909	< 0.001
	Sex	1	6.73E-07	6.76	0.0107
	Host fruit*Sex	5	1.82E-07	1.828	0.114

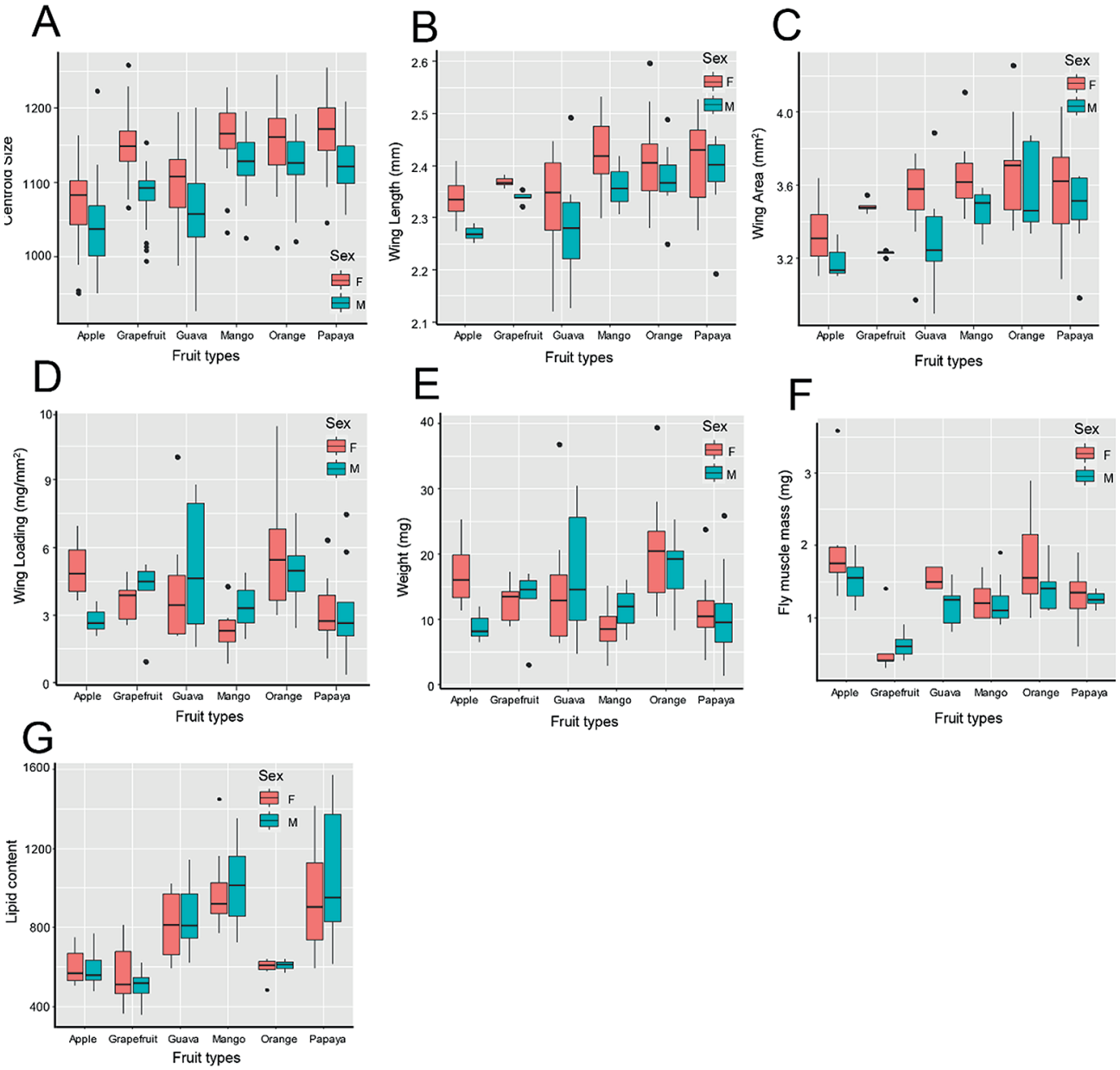

Figure 5: Wing size and adult weight of *Bactrocera dorsalis* is significantly affected by different host fruit. Boxplots depicting variation in (A) wing centroid size, (B) wing length, (C) wing area, (D) wing loading, (E) adult weight, (F) flight muscle mass, and (G) lipid content across the different host fruit.

fruit, guava in comparison with orange and papaya, mango in comparison with orange and papaya, and orange in comparison with papaya (Table 4; 10 000 rounds, $p < 0.001$). The multivariate regression of Procrustes coordinates on log-transformed centroid size showed a significant relationship between wing size and shape (permutation test, 10 000 rounds, $p = 0.0346$). Wing size accounted for 0.99% of the total shape variation, indicating a weak but significant allometric effect. This means that wing shape varies slightly with size, but most of the observed shape differences among *B. dorsalis* are likely driven by host-related developmental effects rather than allometry.

Tethered flight

Host fruit type had a significant effect on flight propensity of *B. dorsalis* (GLZ: Wald $\chi^2 = 21.98$, df = 5, $p < 0.0005$). Flight propensity differed among the fruit types; flies reared on mango were least likely to fly. Females were more likely to fly than males GLZ: Wald $\chi^2 = 8.28$, df = 1, $p < 0.0039$) (Figure 9). A maximum flight distance of only 103.3 m was recorded, but average flight distance was affected by fruit type, with flies reared from grapefruit covering the shortest distance and there was no significant effect of sex on flight distance GLZ: Wald $\chi^2 = 7.42$, df = 5, $p < 0.1910$) (Figure 10A). Flight duration on average was 132.8 seconds, and there was no significant effect of fruit type or sex on flight duration GLZ: Wald $\chi^2 = 1.75$, df = 5, $p < 0.8829$) (Figure 10B). Average flight speed was quite low, at only 0.254 m/second. There was no significant effect of fruit type or sex on flight speed GLZ: Wald $\chi^2 = 5.15$, df = 5, $p < 0.3977$) (Figure 10C).

DISCUSSION

Taking all measured developmental traits into account, papaya followed by mango led to the fastest development and highest juvenile development. Larval development in apple was extended relative to mango, papaya and even grapefruit, but the larvae and pupae reared from apples exhibited high survival to the next life stage. In contrast, individuals reared on grapefruit and guava had a low likelihood of surviving the pupal stage. These results corroborate others from *B. dorsalis* and *Ceratitis fasciventris* where larval performance varies considerably when reared on different host fruit (Ekesi et al. 2014). The developmental time, survival, larval growth and the number and fitness of adult fruit flies are

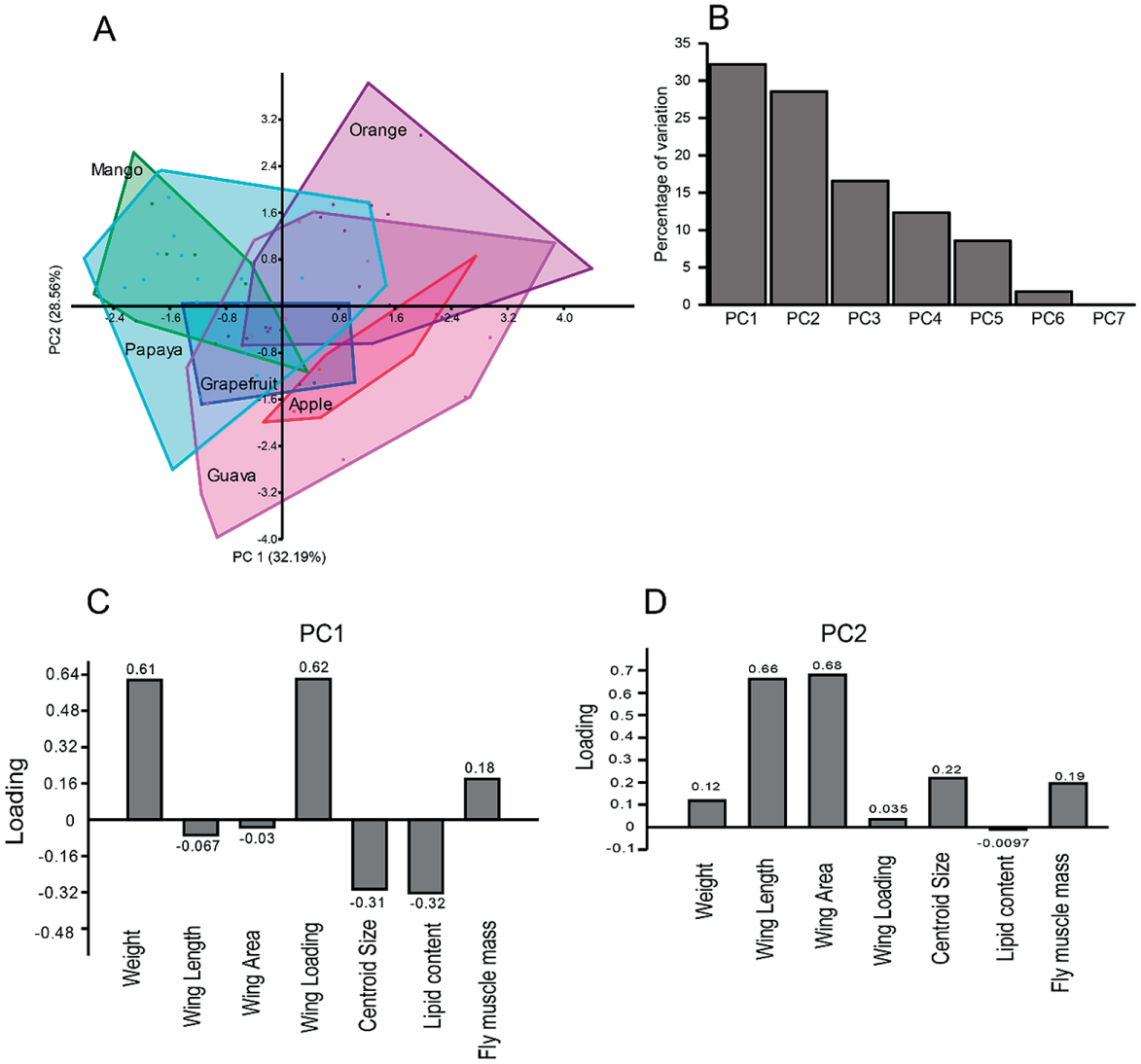

Figure 6: Output from principal components analysis summarising variation in *Bactrocera dorsalis* morphological traits when reared on different host fruit types. (A) Biplot presenting the similarities (or dissimilarities) existing between *B. dorsalis* flies reared on different host fruit, (B) bar graph displaying the percentage of variation accounted for by each principal component, (C) bar graph displaying the effect of morphological traits on PC1, and (D) bar graph displaying the effect of morphological traits on PC2.

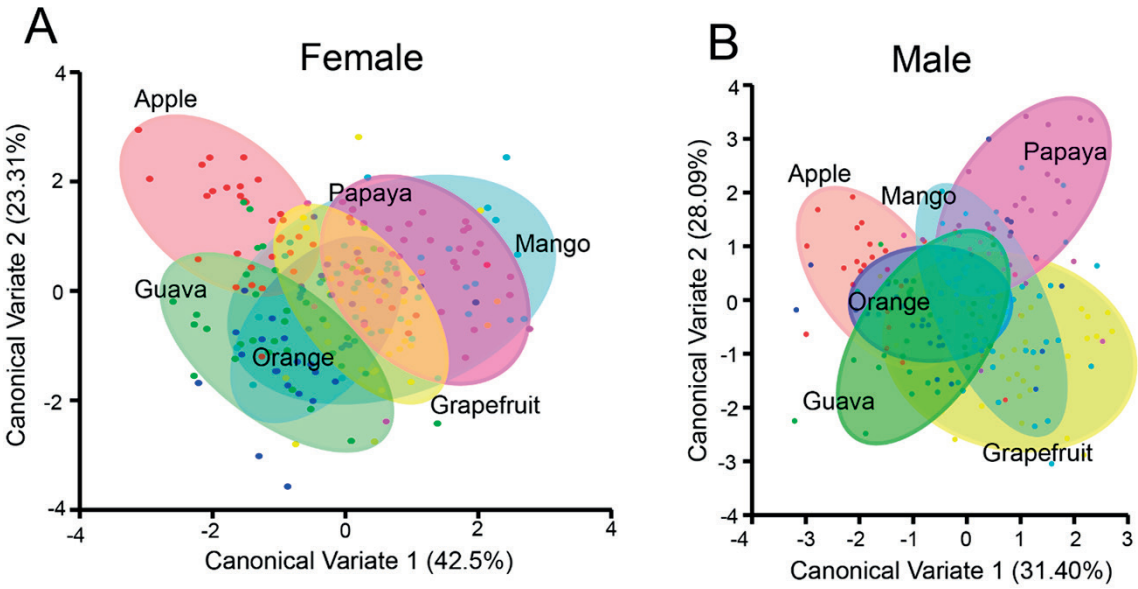

Figure 7: Wing shape of *Bactrocera dorsalis* is significantly affected by host fruit type. (A) Differences in the shape of *B. dorsalis* female wings that were reared on different host fruits along the first two canonical variate axes [cv1 (42.5%) and cv2 (23.31%)] with 90% confidence ellipses. (B) Difference in the shape of *Bactrocera dorsalis* male wings that were reared on different host fruits along the first two canonical variate axes [cv1 (31.40%) and cv2 (28.09%)] with 90% confidence ellipses.

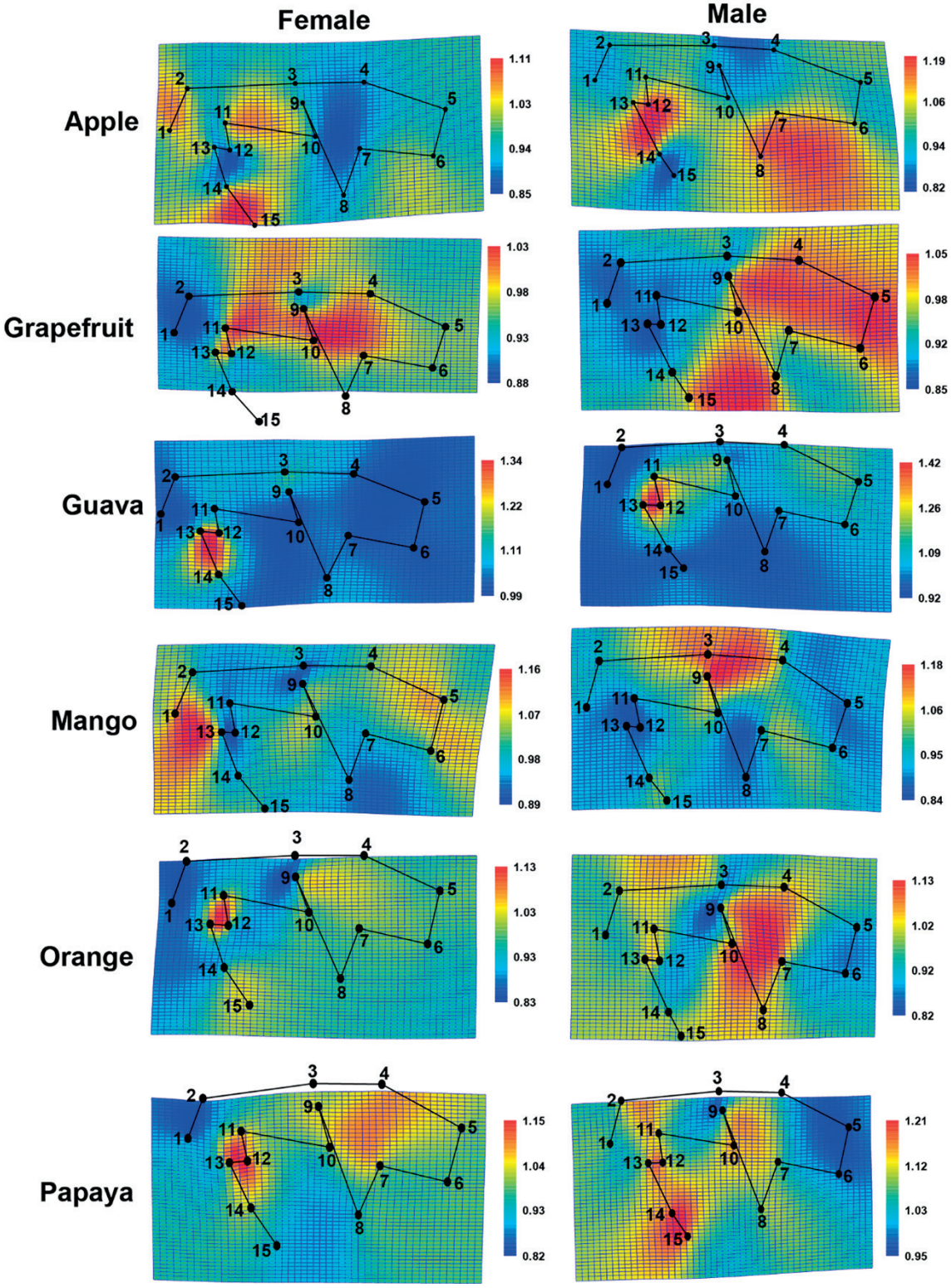

Figure 8: Thin plate spline deformation grids modelling the difference of *Bactrocera dorsalis* wing shape across the sexes and different host fruit types. The number shown on each grid represents the landmark positions. Yellow to orange-red colours indicate landmark expansions, while the light- to dark-blue indicates landmark contraction in (mm).

influenced by the nutritional content of the larval diet (Ekesi et al. 2007; Kaspi et al. 2002; Krainacker et al. 1987). Differences in development of *B. dorsalis* seen in this study may be due to physiochemical qualities, such as fruit size (Wang et al. 2009), firmness and ripeness (Am et al. 2017), nutrients (Chapman 2009; Murphy 2007; Scriber and Feeny 1979) and pH (Papachristos et al. 2008). High variation in the performance of larvae and pupae reared from orange may be a consequence of within-fruit differences in solutes and sugars, although larvae can move to select the more nutritious lower parts of a fruit (Fernandes-da-Silva and Zucoloto 1993).

Using the wing landmark-based geometric approach, we confirmed that the size and shape of *B. dorsalis* wings display phenotypic plasticity in response to development in different host fruit. As reported by Pieterse et al. (2017), who investigated the effects of nectarine, plum, pear, citrus and apple on wing shape variation in *B. dorsalis* and *C. capitata*, there was little variation in the centroid size, but fly sex and host fruit led to differences in

Table 3: Difference in wing shape of female *Bactrocera dorsalis* right wings reared from different host fruit. *p*-values (above the diagonal); distances between populations (below the diagonal). $p < 0.05$ denotes a significant difference.

	Mahalanobis distances						Procrustes distances					
	Apple	Grapefruit	Guava	Mango	Orange	Papaya	Apple	Grapefruit	Guava	Mango	Orange	Papaya
Apple	–	< 0.0001	0.0002	< 0.0001	< 0.0001	< 0.0001	–	0.0048	< 0.0001	0.0106	< 0.0001	< 0.0001
Grapefruit	2.2994	–	< 0.0001	0.0149	0.0001	0.0017	0.0167	–	0.0771	0.9064	0.08086	0.7818
Guava	1.6935	2.070	–	< 0.0001	< 0.0001	< 0.0001	0.0136	0.0135	–	0.4736	0.0034	< 0.0001
Mango	2.3288	1.565	1.979	–	< 0.0001	0.1147	0.0250	0.0172	0.0186	–	0.4483	0.5685
Orange	2.0556	1.663	1.773	2.0178	–	< 0.0001	0.0147	0.0097	0.0107	0.0185	–	0.0018
Papaya	2.3317	1.584	2.378	1.4169	2.1136	–	0.0162	0.0107	0.0151	0.0183	0.0123	–

Table 4: Difference in wing shape of male right wings from *B. dorsalis* reared from different host fruit. *p*-values (above the diagonal); distances between populations (below the diagonal). $p < 0.05$ denotes a significant difference.

	Mahalanobis distances						Procrustes distances					
	Apple	Grapefruit	Guava	Mango	Orange	Papaya	Apple	Grapefruit	Guava	Mango	Orange	Papaya
Apple	–	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.000	-	< 0.0001	< 0.0001	< 0.0001	0.0002	0.0045
Grapefruit	2.4192	–	< 0.0001	0.0029	< 0.0001	< 0.000	0.0243	–	0.0047	0.0432	< 0.0001	< 0.0001
Guava	2.2587	2.3472	–	< 0.0001	< 0.0001	< 0.000	0.0215	0.0143	–	0.0512	0.0352	< 0.0001
Mango	2.2445	1.5565	2.0133	–	0.0004	0.000	0.0203	0.0100	0.0123	–	0.0004	0.0005
Orange	2.0594	2.1340	1.8975	1.7163	–	< 0.000	0.0185	0.0184	0.0132	0.0132	–	< 0.0001
Papaya	2.2613	2.5861	2.8610	1.8122	2.5285	–	0.0170	0.0199	0.0228	0.0151	0.0184	–

wing size and shape. Phenotypic plasticity is known to influence the flight capacity of insects. In *Drosophila suzukii*, developmental temperature has a strong effect on both wing size and shape, with correlated differences in flight velocity and acceleration (Fraimout et al. 2018). In particular, the fastest flies had a narrower proximal section and broader tip of the wing (Fraimout et al. 2018). Wing stiffness or flexibility is due to venation patterns and how the wing responds to the mechanical forces in flight (Combes and Daniel 2003; Wootton 1992). Therefore, the observed differences in landmark positions induced by different host fruit from the current study, might change wing deformability and aerodynamics.

We predicted that the fruit type leading to the best development and traits for flight would result in the best tethered flight performance. Consequently, fruit such as mango and papaya were expected to result in *B. dorsalis* individuals with traits associated with better flight. Our results did show that *B. dorsalis* flies reared on mango and papaya had longer wings. A study by DeVries et al. (2010) found that individuals with longer wings are more capable of flying than individuals with shorter wings. Insects with longer wings can also fly greater distances at a higher speed (Berwaerts et al. 2002; Hoffmann et al. 2007). Host fruit type also affected flight muscle mass in *B. dorsalis*, with flies reared on apple having the greatest flight muscle mass, with mango and papaya leading to only marginally less muscle mass. Diet quality can affect the development and metabolism of flight muscle, which then explains larval diet-induced changes in flight ability (Gunn and Gatehouse 1988; Portman et al. 2015). For example, tobacco hornworm, *Manduca sexta* L. (Lepidoptera: Sphingidae) larvae fed on inbred horsenettle plants with compromised antiherbivore defences, developed into adults with higher flight metabolic rate and associated flight muscles with a troponin t isoform composition different from those fed outbred plants (Portman et al. 2015).

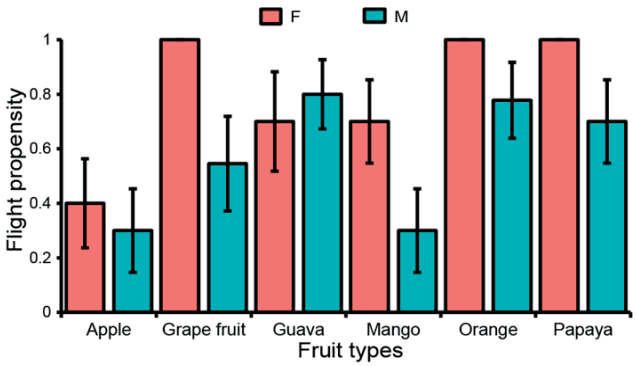

Figure 9: Flight propensity graph displaying different distances between female and male *Bactrocera dorsalis* within each fruit type (post-hoc Tukey tests: $p < 0.05$).

While there is some evidence for *B. dorsalis* having traits that should benefit their flight when reared on fruit that also supports survival and development, this did not extend to better tethered flight performance. However, our results did show that individuals emerging from grapefruit, a host that led to poor pupal survival, had the worst flight distance. The lower proportion of *B. dorsalis* that reached adulthood had shorter wings, lighter flight muscle mass, and low lipid reserves compared to flies reared from all other fruit types. The overall low tethered flight performance may be a consequence of testing flight in flies that had emerged only one day earlier. This was done to ensure that potentially subtle effects of host fruit on flight and associated body traits were not masked by adult conditions, but it likely limited baseline flight performance. In *B. dorsalis* females, flight performance improves with age (Chen et al. 2015; Makumbe et al. 2020) in association with

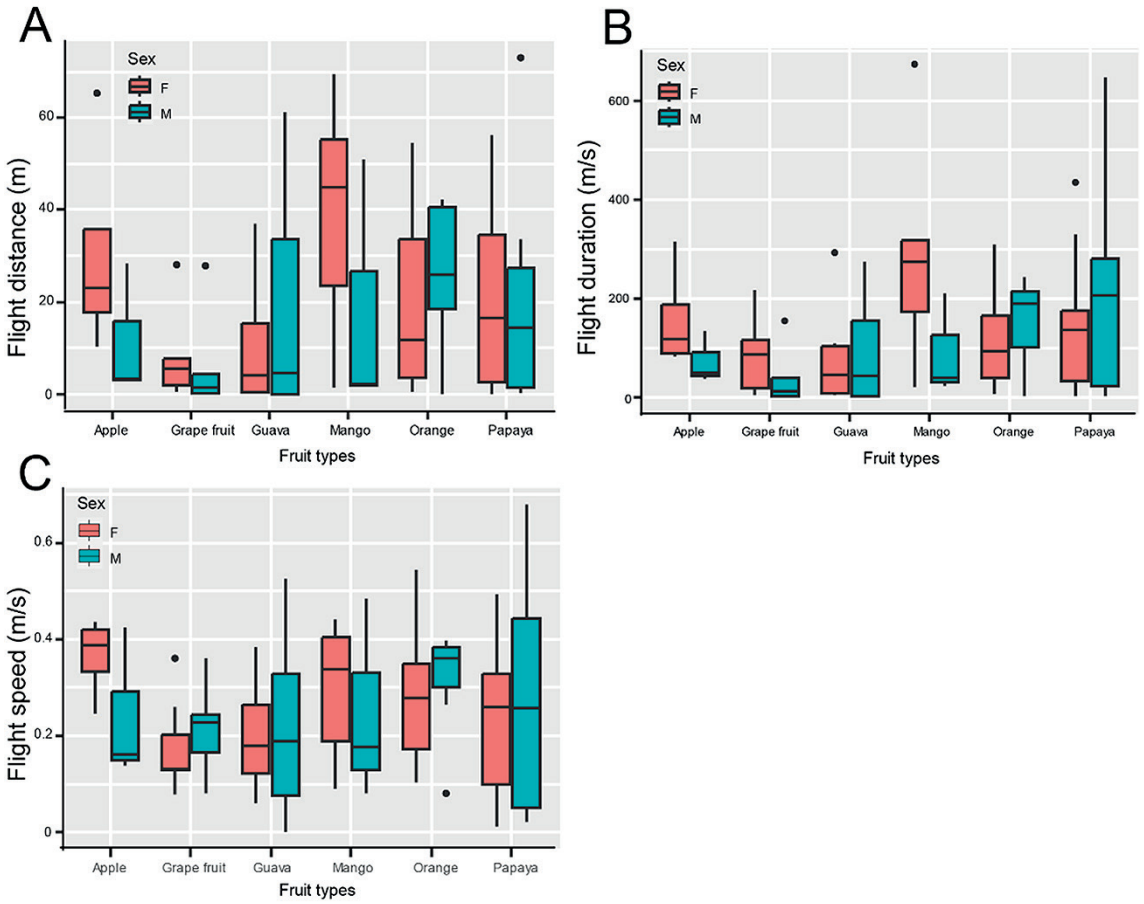

Figure 10: Boxplots displaying variation in flight parameters (A) flight distance, (B) flight duration, and (C) flight speed of *Bactrocera dorsalis* when reared in different host fruit for males and females (post-hoc Tukey tests: $p < 0.05$).

ultrastructural changes that improve flight muscle contraction (Chen et al. 2015). At five days after adult emergence, *B. dorsalis* flight muscles have thinner myofibrils (i.e., less generation of force during contraction), longer sarcomeres (i.e., with less overlap of thick and thin filaments to generate tension during contraction), and fewer mitochondria (i.e., less resistance to muscular fatigue) than when flight performance is optimal at 15 days after adult emergence (Chen et al. 2015).

Our results showed that females were better fliers than males. Similar results were found in other studies on *B. dorsalis* (Chen et al. 2015). Sharp et al. (1975a) reported that *B. dorsalis* females were better fliers with flight abilities varying with adult ages based on flight mill experiments. Females having better flight performance than males is also a pattern seen in other Diptera such as the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Cecidomyiidae) (Hao et al. 2013). Survival and persistence of *B. dorsalis* populations rely on the flight ability of females (Chen et al. 2014). Variability in flight with age and associations with sexual maturity are also evident in the males of *Bactrocera* species: it is assumed that younger males display better flight performance than older males as part of a post-teneral dispersal phase (Drew et al. 1984; Fletcher 1973; Froerer et al. 2010).

In the range currently invaded by *B. dorsalis*, flies emerging from citrus (orange and grapefruit) will perform worse compared to the flies emerging from mango and guava, based on our data. Our results showed that flies reared from mango had low wing loading. According to Makumbe et al. (2020), in some studies high wing loading has been related to faster flight, but this was not observed in our study. However, our results showed that body mass was associated with flight distance similar to the results found by Makumbe et al. (2020). Our results differed from the ones of Bloem et al. (1994) and Makumbe et al. (2020) who reported that the flight performance of larger *C. capitata* and *B. dorsalis* was better than that of smaller flies. Heavier pupae resulting in the emergence of larger sterile flies have greater flight ability leading to a better dispersal ability when released during SIT programmes, according to Dominiak et al. (2008) and Fanson et al. (2014). According to Lehmann (2002), *B. dorsalis* with a greater body mass might explain the faster flight ability through larger, more effective asynchronous flight muscles that can create better wingbeat amplitude during their oscillatory contractions (Ellington 1985; Lehmann 2002).

To conclude, understanding the flight capacity of *B. dorsalis* will allow for better prediction of *B. dorsalis* potential dispersal and help in the development of prevention and control management. We have contributed new information on how wing shape is affected by development in preferred fruit relative to those that have been studied previously. We also provided more detailed information about how host fruit affects flight muscle mass and lipid reserves which can potentially affect flight. We tried to link the variation in wing shape to flight performance, and although we did not find a strong relationship, this does form a basis for future studies. Flies with a higher flight propensity should be considered in cultures used for sterile insect release techniques as it could increase the effectiveness of the SIT programme.

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AUTHOR CONTRIBUTIONS

TPM: data curation, formal analysis, investigation, visualisation, writing - original draft, writing - review & editing
SBSB: formal analysis, methodology, supervision, validation, writing - original draft, writing - review & editing
CWW: conceptualisation, funding acquisition, methodology, project administration, resources, supervision, writing - original draft, writing - review & editing

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