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Oviposition Preference and Offspring Performance in Phytophagous Fruit Flies (Diptera: Tephritidae): The African Invader, Bactrocera invadens

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Abstract - Behavioral choices have been hypothesized to reflect fine-tuned evolutionary adaptation by the preference-performance hypothesis (PPH), which states that female insects will evolve to oviposit on hosts on which their offspring fare best. The extent to which this is true in the African invader, Bactrocera invadens (Diptera: Tephritidae) was assessed in this study. Five host-plant species: Terminalia catappa (Combretaceae), Persea americana (Lauraceae), Psidium guanjava (Myrtaceae), Mangifera indica (Anacardiaceae), and Citrus sinensis (Rutaceae), and 11 mango varieties: Tommy, Zillatte, Keitt, Kent, Kagogwa, Apple, Palvin, Dodo, Kate, Biire and Glen, were tested for their conformity to the PPH. The fruits were incubated, larvae reared, and the adults maintained on an artificial diet in the laboratory. There was significant variability in host species (P = 0.038) and variety (P = 0.015) preference in the orders: T.catappa > P.guanjava > M. indica > C. sinensis > P.americana; while Glen & Biire and Zillate & Tommy were the most and least preferred varieties, respectively. Offspring performance (development rate, survival, weights and sex ratio) differed significantly and followed a very similar trend only that for fruit species P.americana performed better than C. sinensis. The relationship between host preference and the offspring performance measures showed strong support for the PPH with overall coefficient of determination of 75.4% (P = 0.000) and 65% (P = 0.003) for host species and varieties, respectively. This study has generally increased the knowledge on the role of host species and varieties on the biology of the pest and re-affirmed the growing credence that host-specific variation in adult performance has an important role in shaping host preference of phytophagous insects, as proposed by PPH.

Keywords - Bactrocera invadens, Offspring Performance, Oviposition Preference, Tephritidae

1. Introduction

The linkage between preference of ovipositing females for certain plant species and growth, survival, and reproduction of offspring (performance) on those plants has been a central problem in the theory of insect/ plant interactions (Thompson, 1988). Consequently, the preference/ performance confront has been subject of several studies and debates over the evolution of host specificity, delimiting of enemy-free space, and host shifts in allopatric and sympatric insect populations (Lawton & McNeill, 1979; Thompson, 1988a,b; Cronin & Abbrahamson, 1999; Eben et al., 2000; Scheirs et al., 2004; Santos & Silveira, 2008; Bonebrake et al., 2010; Heard, 2012). Evolutionarily, the relationship between host preference and larval and adult performance has been related to understanding host-plant specificity, diet breadth, host-race formation, sympatric speciation, life-history evolution and the adaptive radiation of herbivore taxa (Mitter et al., 1991; Thompson, 1996). Nonetheless, there is a general paucity of understanding of insect/ plant interactions in terms of the preference-performance. For instance, among the tephritid fruit flies (Diptera: Tephritidae), this knowledge is mainly limited to geographic variation in host use (e.g Copeland et al., 2002; Rwomushana et al., 2008; Mwatawala et al., 2009), phenotypic or genetic variation within populations in preference or performance, and on selection to modify these characters (Aluja, 1986; Drew et al., 2008; Barr & McPheron, 2008; Khamis et al., 2008; Billah et al., 2008; Khan et al., 2011).

At the wider host preference and larval performance subject level, knowledge gained through the various studies has led to the suggestion of hypothesizes on this relationship (Thompson, 1988; Price, 1997), among which is the ideal free distribution theory (IFD) (Fretwell & Lucas, 1970). The IFD theory, which predicts how organisms distribute themselves in a heterogeneous environment, has served as an important foundation for several related theories in ecology (Thompson, 1988). The IFD theory assumes that habitat suitability decreases with increasing densities of organisms, but that for a given density, habitats differ in their suitability. It then predicts that if organisms have perfect knowledge of their environment and behave ideally, then they should distribute themselves so that the average fitness is approximately equal in all habitats (Ellis, 2008). Among the extensions of this theory, is the oviposition preference–offspring performance (P–P) hypothesis (Thompson 1988; Valladares & Lawton 1991; Nufio & Papaj 2004; Scheirs et al., 2004; Ellis, 2008; Santos & Silveira, 2008; Bonebrake et al., 2010; Heard, 2012). This hypothesis predicts how ovipositing females distribute their offspring in a heterogeneous environment (Schriber, 1983; Thompson, 1988; Valladares & Lawton, 1991; Nufio & Papaj, 2004). Specifically, it predicts that when insects utilize discrete hosts or environments, and have juveniles that have limited ability to disperse, females should evolve oviposition behaviors that maximize offspring growth and survival. The expected consequence is a positive correlation between preference and performance among the available host genotypes (Thompson, 1988).

Several previous studies have reported strong, positive preference-performance correlations in a number of herbivorous insects (Price et al., 1990; Rossi & Strong, 1991; Hanks et al., 1993). On the contrary, other studies reported results against this pattern: many insects preferentially oviposit on plant genotypes that do not yield highest fitness (Karban & Courtney 1987; Courtney & Kibota 1990; Horner & Abrahamson, 1992; Larsson et al., 1995). In response to these inconsistent results, a broad range of hypotheses have emerged to explain the lack of a positive preference-performance correlation. Among these, possible causes for the subvert occurrence of a one-to-one correspondence between preference and performance have included: host confusion and limited discriminatory ability of herbivores (Fox & Lalonde 1993; Larsson & Ekbom 1995), plant appearance (Chew & Courtney 1991), novel association between host plant and herbivore (Thompson 1988, 1996; Joshi & Thompson 1995; Larsson & Ekbom 1995), phenology of herbivore oviposition (Briese 1996), herbivore abundance (Wiklund, 1982), environmental predictability (Chew & Courtney 1991; Lalonde & Roitberg, 1992), and parasites and predators (Lawton & McNeill, 1979; Strong & Larsson, 1994). Earlier on, Jaenike (1986) and recently, Scheirs et al., (2004) too proposed the optima foraging theory as one of the reasons for the subvert occurrence. In this theory, females may select those hosts that are optimal for adult nutrition instead of those that are optimal for their offspring, and hence female insects maximize fitness through the optimization of adult performance. Consequently, there is need for more studies to understand this (PPH) linkage, especially for species where there is paucity of information on preference-performance relationship, such as the African invader, (Bactrocera invadens).

Bactrocera invadens (Drew, Tsuruta & White), an invasive species is an ideal organism for testing the preference-performance hypothesis. Bactrocera invadens is the most economically important fruit fly in the region and continent, where it infests over 44 known cultivated and wild hosts (Ekesi et al., 2006; Mwatawala et al., 2006; Rwomushana et al., 2008; Vayssières et al., 2009; Mwatawala et al., 2009). The highly polyphagous nature of B. invadens could be facilitated by the higher behavioral adaptation characteristics of polyphagous species. Such adaptations enable these species to oviposit in a wide range of fruit crops (Aluja & Mangan, 2008), offering an opportunity to assess its relative preference and performance in the various hosts. Although studies have suggested that B. invadens prefers certain fruit host types (Ekesi et al., 2006; Mwatawala et al., 2006; Rwomushana et al., 2008; Vayssières et al., 2009; Mwatawala et al., 2009; Geurts et al., 2012), or mango fruit varieties (Ambele et al., 2012), most have not adequately demonstrated differences in performance between the fruit species and varieties that may generate the selective pressures necessary for the evolution of these behaviors.

Therefore, the purpose of this study was to examine the effects of fruit species and variety on the performance of B. invadens. In this study, we tested the hypothesis that because of its polyphagous nature, B. invadens can obscure the expected positive correlation between adult oviposition preference and offspring performance. Specifically, the study aimed to: (1) establish patterns of oviposition in relation to resource type (fruit species and varieties) and (2) compare offspring performance among the resource types. Results were then used to provide information on the potential roles of resource type (fruit species and varieties) in determining the preference–performance relationship and the evolution of B. invadens oviposition preferences. This information may be used as an important means in planning a successful integrated pest management (IPM) program for B. invadens.

2. Materials and Methods

2.1. Study area

The study was conducted in the Lake Victoria Crescent (LVC) agro ecological zone, Uganda (Figure 1). This zone consists of hills and ridges dissected by streams and swamps. Altitude ranges from 1100 to 1400 metres above sea-level (masl). Typically, the soils of the area (ferralsols) are old, highly weathered and of low inherent fertility. Moderately deep, residual soils are located on hillcrests. When virgin, however, these soils have a high organic carbon content, which results in a good nutrient holding capacity. Rainfall in the area ranges between 700-2100mm. The main crops grown are bananas, coffee, beans and a variety of vegetables and root crops. Bananas and coffee are farmers' main source of income. The majority of these crops are grown in small-scale monoculture and/or polyculture fields that are integrated into the coffee-banana agroforest production systems where coffee and banana are the major crops. The zone is a mosaic landscape where "islands" of patches of natural habitats are found scattered within agricultural matrices dominated by linear and nonlinear features of semi-natural habitats that serve as field boundaries for a diversity of small-scale fields (Munyuli, 2012).

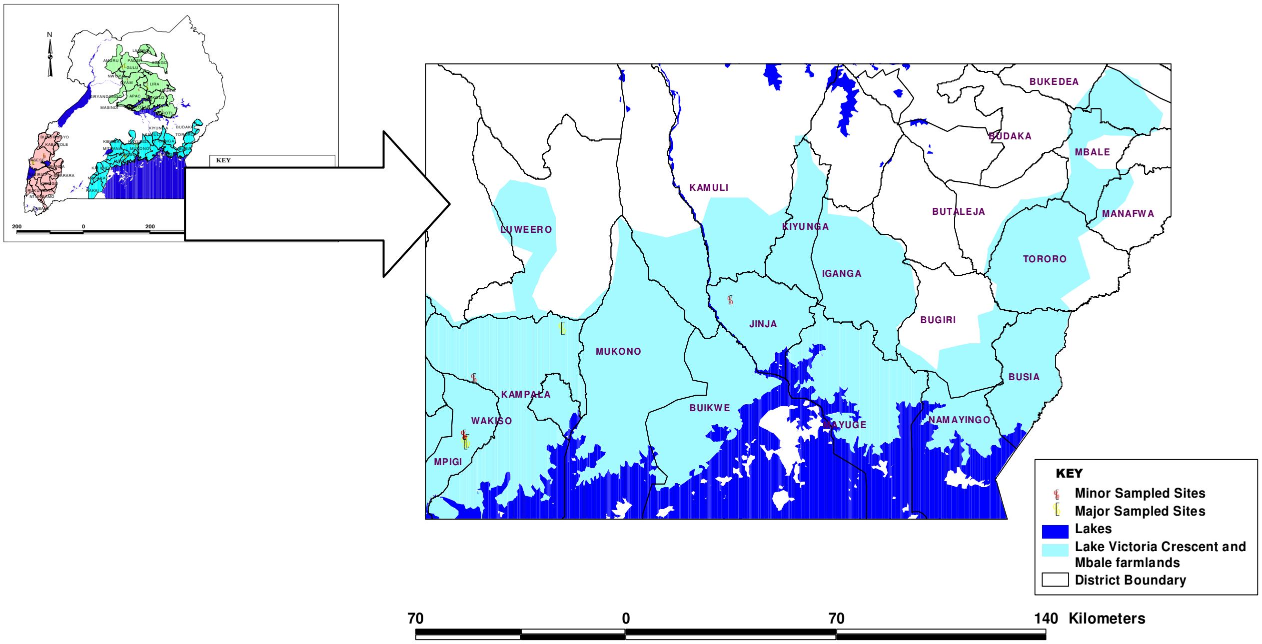


Figure 1: Map of Uganda showing the location of Lake Victoria Crescent, and the details of the zone with the respective sampling sites.

2.2. Host plants

Five host plants were used in this study, including sweet orange (Citrus sinensis (L.) Osbeck), tropical almonds (Terminalia catappa L.), avocado (Persea americana Miller, variety 'Local'), guava (Psidium guajava L., variety 'common guava') and mango (Mangifera indica L., variety 'Mixed'). These fruits were selected because they are some of the most important economic fruits and are primary host plants of B. invadens. Tropical almonds were included on this list mainly because of its best B. invadens host status in the area (Isabirye et al., unpublished data). The selected mango varieties included: Tommy, Zillatte, Keitt, Kent, Kagogwa, Apple, Palvin, Dodo, Kate, Biire and Glen. The five species of host plants, including varieties for the mango host, were randomly sampled in the LVC mainly Wakiso, Luwero and Jinja districts (Figure 1). The protocol for collecting, transporting and rearing, of fruit flies followed the methodology developed by the African Fruit fly Programme at ICIPE (Lux et al., 2005), while sample labeling was done according to the protocol described by Copeland et al. (2002) .

2.3. Host oviposition preference and larval development

Fruit host preference for oviposition was determined by incubating fruits naturally infested by B. invadens in the field. For this reason, a few (3) of the fruits were infested by B. invadens and some Ceratitis species, which on emerging were excluded from the study records for consistence. Collected fruits were transported to the rearing unit at the National Agricultural Research Laboratories (NARL), where they were washed with soap and rinsed, and allowed to air dry before being kept in individual rearing buckets and provided with appropriate medium for pupation as recommended by Copeland et al. (2002). Each container was capped with a plastic lid containing two screened 5- by 7-cm ventilation holes, which were covered by a 0.3 mm nylon screen mesh. Containers were placed in an outdoor screen house insectary. The insectary was 15 by 13 m, with half block walls and screen windows and doors. The building was covered with a corrugated iron roof, which provided some degree of shading from ambient sunlight. Temperature conditions in the insectary were very comparable to conditions outside, but experiments were sheltered from wind and precipitation. Temperature was monitored with an onsite thermometer, which gave morning, afternoon and evening readings to average for the day. Conditions at the rearing unit averaged 28 ± 2^0C (range 25.0-30.1^0C) and 58±5% relative humidity over the experimental period.

Newly hatched larvae and tenneral adults that emerged were carefully removed and handled following methods described by White & Elson-Harris (1992). The adults were fed with an artificial diet consisting of 10% honey-water solution through a cotton ball in separate plastic transparent buckets (22 X 33cm). These buckets were maintained on countertop space in the laboratory. The larvae and tenneral adults, which varied in number because of differences in emergencies, were monitored for development and mortality at 12-h intervals. In the meantime, the dishes were cleaned, and new cotton ball were replaced as needed. The adults were sexed and separately weighed. Developmental time of development stages was measured as time (days) for each larvae to develop into pupae stage. The study was repeated using similar methods for mango varieties (2.2) only that in this case adults were not sexed and weighed, mainly for logistical reasons.

2.4. Data Analysis

To compare fruit species and varieties preference, infestation rates were calculated according to Cowley et al., (1992). The infestation index values were tested for normality using Anderson and Darling tests and when strongly skewed, they were transformed (log(x +1) prior to analyses if necessary to meet the assumption of normality and homogeneity of variances. Means were separated using the post-hoc Tukey (HSD) Significant differences test at $\alpha < 0.05$. The Kaplan–Meier estimator was used to estimate the survival function from species and varieties fruit fly emergent lifetime data, construct hazard plots and to estimate mean survival times. To test for equality of the survival distribution functions of the Kaplan–Meier survival function, Log-rank tests at $P < 0.05$ were used. For all emergence data, cumulative adult emergence curves over time were constructed. Because cumulative emergence curves were sigmoid, all data were transformed using the inverse cumulative normal distribution function (Addinsoft, 2010). This function transformed the sigmoid proportion data to a linear relationship with time, relating the data to a normal distribution of 3 (for zero) through 3 (for 1), with 0.5 cumulative emergences set equal to zero (the mean of a normal distribution) (Myers et al., 2007). Linear regression analysis was conducted on the transformed cumulative emergence data versus time.

To make pair wise comparisons of regression slopes, t values were calculated using the following formula:

$$\boldsymbol{T} = \frac{(\mathrm{m}1-\mathrm{m}2)-\square\mathrm{m}1-\mathrm{m}2}{\mathrm{Sqrt}\ ([\mathrm{SEm}\ 1]^2+[\mathrm{SEm}\ 2]^2)}$$

Where T is t value, m1 is slope of regression line 1, m2 is slope of regression line 2, $\square\mathrm{m}1 - \mathrm{m}2$ is the hypothesized difference in slopes, SEm1 is standard error of regression slope 1, and SEm2 is standard error of regression slope 2 (Myers et al., 2007). Slopes were considered significantly different if t value probability derived from T distribution was less than 0.05 (Zar, 1999). To test for the effect of host species on B. invadens adult weight, one-way analysis of variance (ANOVA), followed by Tukey HSD's multiple range test at $P<0.05$ was used, while effect on sex ratio was tested using Kruskal-Wallis test and multiple post-hoc analysis done using Steel-Dwass-Critchlow-Fligner test after application of a Bonferroni correction (Addinsoft, 2010). Linear regression and one-way Multivariate Analysis of variance (MANOVA) were used to test for the ultimate relationship between B. invadens host preference and offspring performance indicators (Cronin & Abrahamson, 1999; Scheirs et al., 2004; Santos & Silveira, 2008). All these analyses were done using PAST computer program (Oyvind, 2002) and XLSTAT2012 (Addinsoft, 2010).

3. Results

3.1. Fruit Host Preference for Oviposition

In the natural field conditions, numbers of larvae per fruit oviposited by B. invadens females on the five fruit types differed significantly ($F = 2.759$; df = 4, 60; $P = 0.038$) (Figure 2A). B. invadens oviposited tropical almond fruit the most (17.38±7.3 larvae, range 0 - 73), followed by guava (13.77±5.8, 0 - 75), and the least on avocado (2.46±1.2, 0 - 13). Tropical almond did not differ significantly with guava, but was preferred more significantly ($P = 0.000$) than mango, avocado and orange (citrus).

Mango and guava were not significantly different, but differed significantly with citrus and avocado, which were not different themselves. Similarly, fruit fly oviposition on the 11 mango varieties differed significantly (F = 2.211; df = 10, 2031; P = 0.015) (Figure 2B). B. invadens oviposited the most on Glen mango fruits (57.8±23.7), followed by Biire (43.1±5.5) and Kate (37.1±8.3), and the least on Zillatte (13.3±5.2) and Tommy (12.0±4.8). Glen, Biire and Kate were significantly different (P = 0.000) from Zillatte and Tommy, but only Glen and Biire differed significantly with Kagogwa, Kent and Keitt. The latter three were not significantly different from Kate, Dodo, Palvin and Apple varieties. Consequently, the 11 varieties formed three discrete groups: Glen and Biire (most susceptible), Zillate and Tommy (least susceptible), while the rest of the varieties were intermediates in susceptibility.

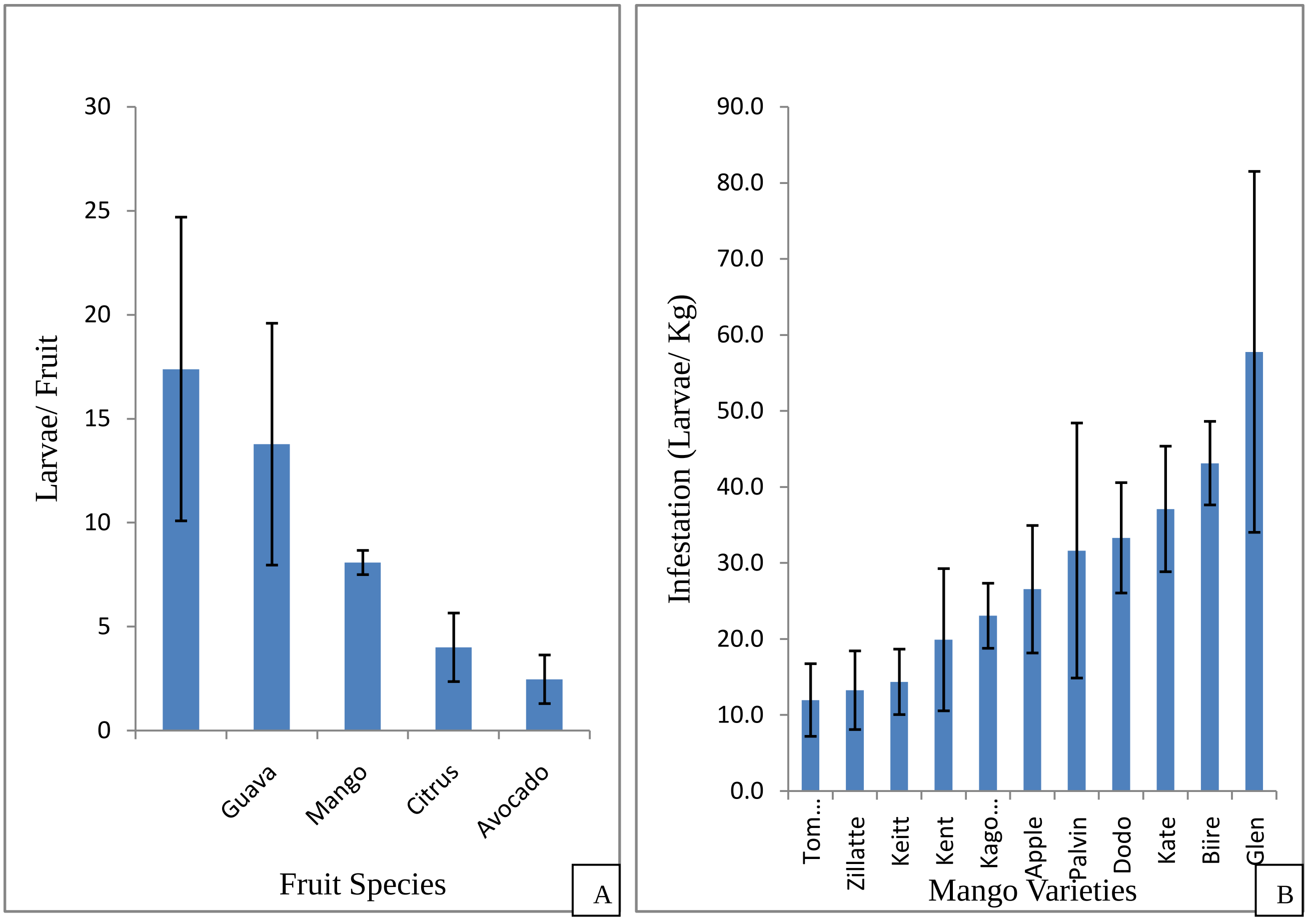


Figure 2: Bactrocera invadens larvae relative emergence Mean (±SE) per host plant species (A) and mango host variety (B)

3.2. Fruit fly relative host performance

3.2.1. Effect of host plants on larval development

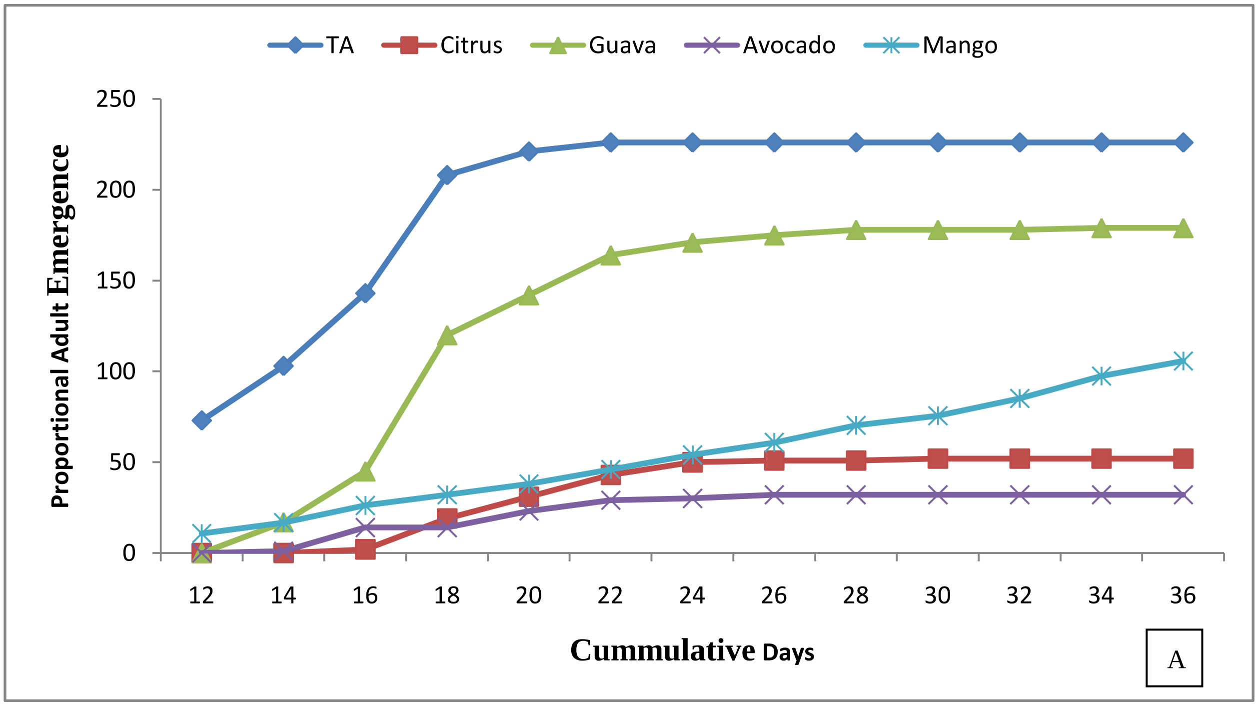
Overall, larval development was significantly affected by host plants (F = 111.1; df = 4, 60; P = 0.000), and fruit variety (F = 123.12; df = 10, 132; P = 0.000), with highly susceptible fruits recording faster development rates (Figure 3A&B). Transformation of adult emergence curve data from larval studies resulted in highly significant linear relationships between time (accumulated days) and cumulative emergence for all fruit species and mango varieties (Table 1). The slope of the transformed emergence curves indicated that development occurred significantly faster on tropical almonds (Slope = 0.832±0.256) and least on citrus (0.404±0.025) (Table 1). Post-hoc analysis of the host species effect on emergency time showed that cumulative development time was not significantly different between tropical almonds vs guava, or mango, and guava vs mango (T_{22} = 0.287, P > 0.05, T_{22} = 0.392, P > 0.05, T_{22} = 0.212, P > 0.05, respectively). Similarly, guava vs mango or avocado were not significantly different (T_{22} = 0.212, P > 0.05, T_{22} = 1.568, P > 0.05), while mango vs avocado were also not significantly different (T_{22} = 0.871,

$P > 0.05$). B. invadens on tropical almonds ($T_{22} = 3.776$, $P < 0.05$) and guava ($T_{22} = 3.067$, $P < 0.05$) developed significant faster than on citrus, but paradoxically the latter did not differ in B. invadens development rates with mango ($T_{22} = 1.334$, $P > 0.05$) and avocado ($T_{22} = 0.481$, $P > 0.05$).

Table 1. Effect of five host species, mango fruit variety and susceptibility levels on B. invadens larval development rates

			Regression statistics-summary					
Fruit Type	**Susceptibility**	**Species/ Varieties**	**Slope***	**SE Slope**	**R² (%)**	**df**	**F value**	**P value**
Species	Very high	Tropical almonds	0.830	0.256	67.8	11	10.545	0.023
	High	Guava	0.750	0.110	92	11	46.171	0.002
	Medium	Mango	0.698	0.219	63	11	10.203	0.019
	Low	Avocado	0.472	0.139	59	11	11.493	0.009
	Very low	Citrus	0.404	0.025	95.9	11	260.021	0.000
Varieties	Medium	Apple	0.032	0.004	93.5	12	157.238	0.000
	High	Biire	0.029	0.003	82.3	16	69.597	0.000
	Medium	Dodo	0.032	0.003	85.4	16	87.436	0.000
	High	Glen	0.020	0.004	37.7	16	9.069	0.009
	Medium	Kagogwa	0.008	0.002	66.9	16	30.253	0.000
	Medium	Kate	0.011	0.002	66.5	16	29.76	0.000
	Medium	Keitt	0.025	0.003	85.1	16	85.619	0.000
	Medium	Kent	0.009	0.002	49.1	16	14.479	0.002
	Medium	Palvin	0.019	0.006	42	16	10.84	0.005
	Low	Tommy	0.004	0.001	67.3	16	30.891	0.000
	Low	Zillatte	0.006	0.001	68.2	16	32.144	0.000

*Cumulative development values transformed by inverse cumulative normal distribution function to a linear relationship with time.



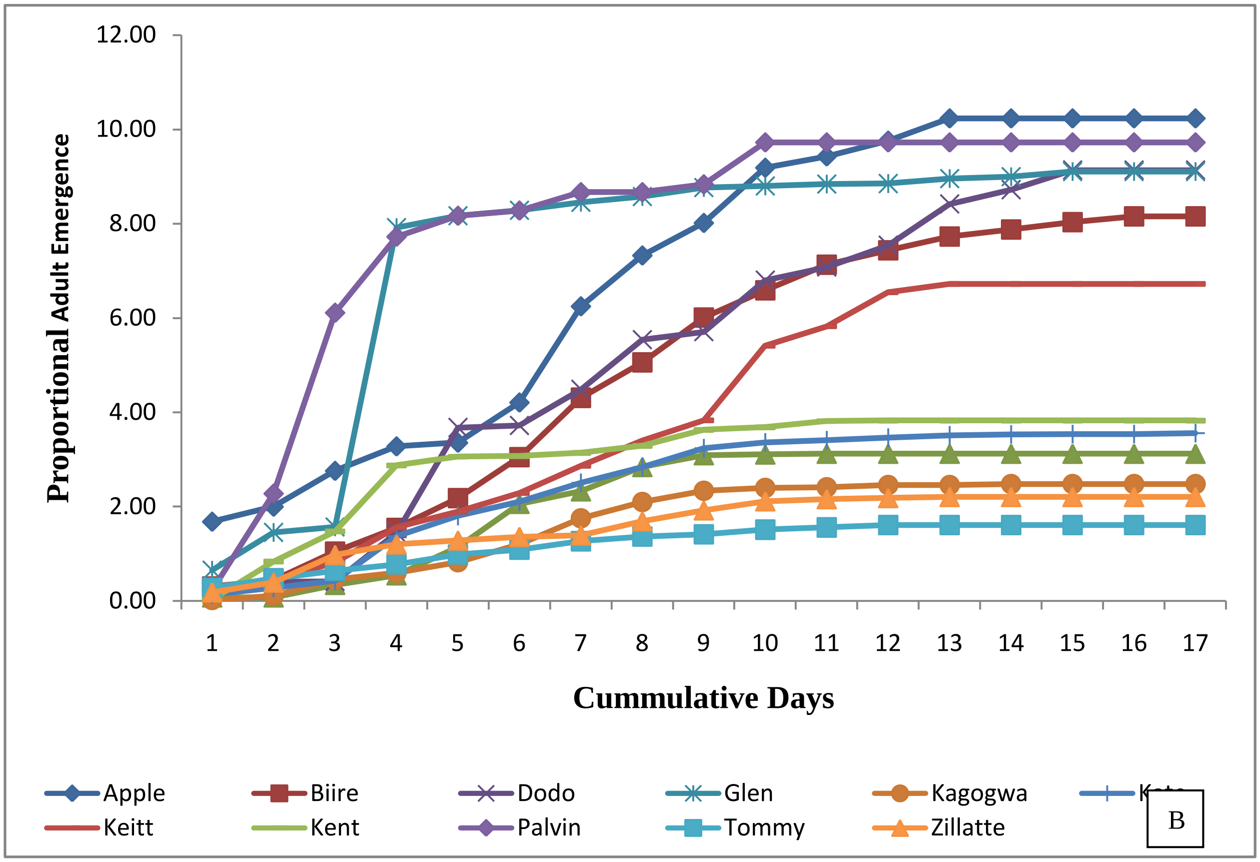


Figure 3. Proportional B. invadens larval development rates for the five host types (A) and 11 mango fruit varieties (B).

In terms of mango varieties, emergence was most rapid on Apple, Dodo and Biire (0.032, 0.032 and 0.029, respectively), while the least were in Tommy, Zillatte and Kent (0.004, 0.006 and 0.009, respectively; Table 1; Figure 3B). Post-hoc analysis of mango variety effect on emergency time showed that cumulative development rates were not significantly different among Apple, Dodo, Biire, Palvin, Keitt and Glen ($P > 0.05$), Kate, Kent and Kagogwa ($P > 0.05$), and between Zillate and Tommy ($P > 0.05$). B. invadens development was significantly fastest between Apple or Dodo vs Tommy ($T_{32} = 6.791$, $P < 0.05$), followed by the two (Apple &Dodo) vs Zillate ($T_{22} = 6.306$, $P < 0.05$). Moreover, Kent Kate and Kagogwa did not record significantly ($P > 0.05$) better development rates, while Biire, Keitt, Palvin, and Glen recorded better development rates ($P < 0.05$) than Tommy and Zillatte. Although not significantly different ($K = 4.755$; $df = 2$; $P = 0.073$), B. invadens on highly susceptible varieties developed faster (slope = 0.025±0.005), as compared to medium susceptible varieties (0.019±0.004) and the least susceptible group (0.005±0.001).

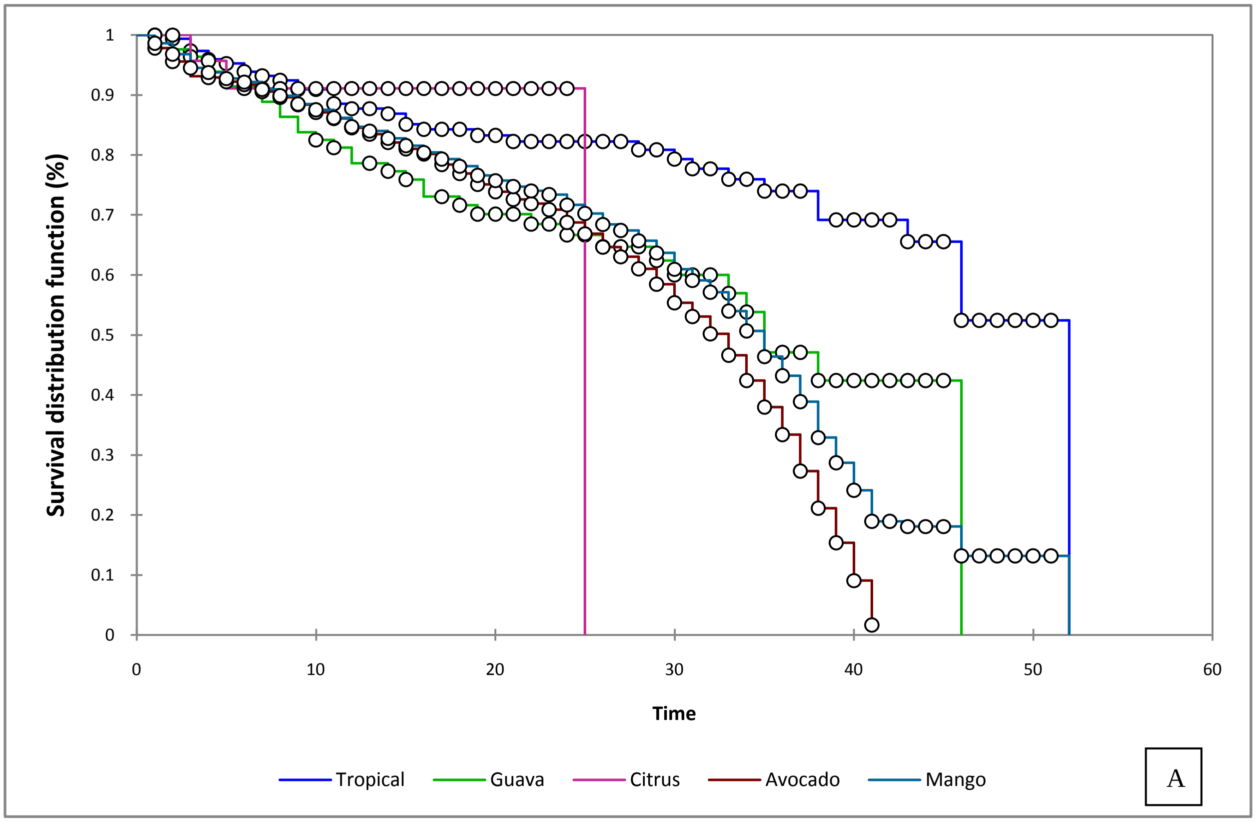
3.2.2. Effect of host plants on Bactrocera invadens adult fly survival

The survival rates of B. invadens adults varied significantly on the five host plants (Table 2; Figure 4A). The overall, accumulated survival rates of B. invadens adults on the four host plants differed significantly (Log-rank = 54.044, df = 4, $P = 0.0001$) (Figure 4A), and the highest was on tropical almonds (41.065±1.61 d), followed by that on guava (31.291±1.94 d), and least on citrus (23.133±1.55 d) (Table 2). Of the five species, with the exception of guava and mango, the survival rates of B. invadens were significantly different (Table 2). Similarly, accumulated survival rates of B. invadens adults on the eleven mango host varieties differed significantly (Log-rank = 42.268, df = 10, $P = 0.0001$) (Figure 4B), and the highest was on Biire (36.347±2.00 d), followed by Glen (34.095±1.85 d), Kate (33.976±1.70 d), and the least on Tommy (23.580±2.18 d) and Apple (23.609±2.07 d) (Table 2). Biire variety conferred significantly more longevity to adult flies than the rest of the varieties, followed by Glen and Kate, the latter two not recording significant differences in life longevity ($P > 0.005$). Kagogwa (31.630±1.72 d) was significantly ($P < 0.05$) a better host than Tommy, Apple and Keitt, although it did not differ significantly with Palvin, Dodo, Zillatte and Kent ($P > 0.05$). The latter four varieties recorded varied survival rates, but the difference was not significant ($P > 0.05$).

Table 2. Effect of five host species and mango fruit variety on B. invadens adult censorship frequency and life longevity

(Mean days±SD), means within the groups with similar letters are not significantly different (ANOVA followed by Tukey HSD's multiple range test, P<0.05)

Fruit Type	Fruits	Sample size	Total Failed	Total Censored	Mean survival time (Days±SD)	Boundaries (95%)
Species						
	Citrus	25	3	22	23.133±1.55d	20.104 - 26.161
	Avocado	451	240	211	28.098±0.63c	26.870 - 29.327
	Mango	715	311	404	31.306±0.67b	29.995 - 32.617
	Guava	84	34	50	31.291±1.94b	27.485 - 35.097
	Tropical almonds	155	34	121	41.065±1.61A	37.904 - 44.227
Varieties						
	Biire	41	4	37	36.347±2.00A	32.420 - 40.275
	Glen	41	12	29	34.095±1.85B	30.461 - 37.728
	Kate	41	13	28	33.976±1.70B	30.637 - 37.314
	Kagogwa	41	18	23	31.630±1.72C	28.258 - 35.001
	Palvin	41	23	18	28.838±1.85CD	25.219 - 32.457
	Dodo	41	24	17	28.722±1.79CD	25.221 - 32.222
	Zillatte	41	26	15	26.223±2.09CD	22.122 - 30.324
	Kent	41	27	14	25.018±2.18CD	20.746 - 29.291
	Keitt	41	34	7	23.705±1.93D	19.920 - 27.491
	Apple	41	32	9	23.609±2.07D	19.553 - 27.666
	Tommy	41	27	14	23.580±2.18D	19.313 - 27.848



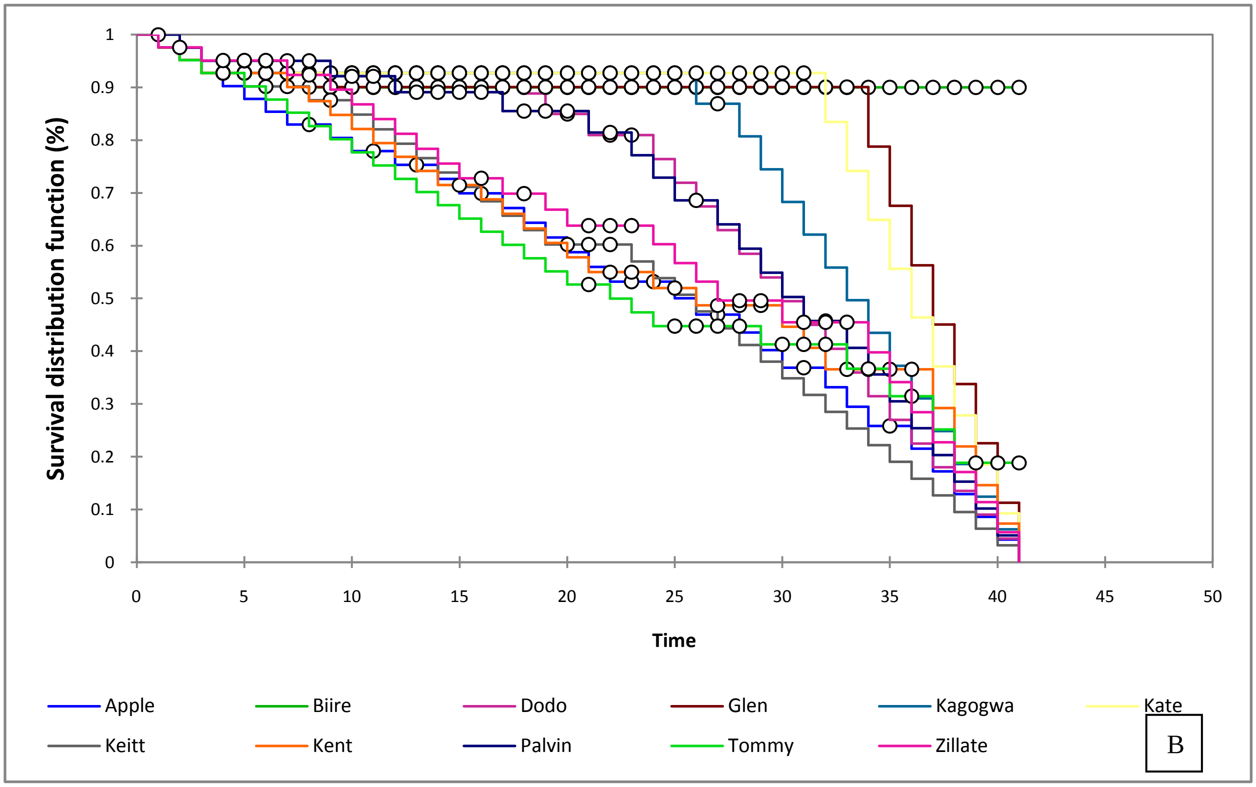


Figure 4. Survival distribution function curves of B. invadens adults on five host plants (A) and variety-specific survival on eleven mango varieties (B).

Table 3. Effect of five host species on B. invadens adult weight and sex ratio. Means within the groups with similar letters are not significantly different

Host plants	**Adult weight**			**Sex ratio**
	mg/ fly ± SD			
	Female	**Male**	**Overall**	**(Female:Male)**
Tropical almonds	2.135±0.89a	2.118±0.91a	2.127±0.89a	1.0882a
Guava	1.682±0.57ab	1.872±0.74ab	1.812±0.69ab	0.4681b
Mango	1.458±0.39b	1.833±0.48ab	1.703±0.48b	0.5333b
Avocado	1.500±0.71ab	1.636±0.67ab	1.615±0.65b	0.1818c
Citrus	1.500±0.71ab	1.364±0.50b	1.385±0.51b	0.1818c
F. value	$F_{4,82} = 3.951$	$F_{4,143} = 2.844$	$F_{4,230} = 5.402$	$X^2_4 = 13.085$
P-value	0.006	0.026	0.000	0.011

3.2.3. Effect of host plants on adult fly weight and sex ratio

Bactrocera invadens adult weights differed significantly depending on the host species on which the larvae were reared ($F_{9,225} = 3.052$; $P = 0.002$) (Table 3). The female flies on tropical almonds were heaviest (2.135±0.89mg), followed by those on guava, and lightest on mango (1.458±0.39mg). Female flies on guava, avocado and citrus were not significantly different in weight, but differed with tropical almonds and mango (Table 3). Male flies on tropical almonds were heaviest (2.118±0.91mg), followed by those on guava and mango, and lightest on citrus (1.364±0.50mg). Female flies on guava, mango and avocado were not significantly different in weight, but differed with tropical almonds and citrus, the latter two being significantly different too ($P < 0.05$) (Table 3). With the exception of tropical almonds and citrus, female flies were generally heavier than their male counterparts. Overall, B. invadens adult flies reared on tropical almonds were significantly heavier than those on mango, avocado and citrus, but did not differ significantly with guava flies (Table 4). The level of bias in sex ratios varied significantly across the fruits (P = 0.011). More male adults emerged than female adults when their larvae were reared from all host plants, except tropical almonds that registered relatively more females than males (Table 4). The level of sex ratio bias among adults varied significantly, in mango and guavas, approximately one female emerged for every two males (1/2), while in avocado and citrus the ratio was 1 female: 4 males (1/4).

3.3. Relationship between Fruit fly host preference and offspring performance

Host preference (oviposition) and offspring performance (larval development rates, longevity, adult weights, and gender ratio) were nearly perfectly and significantly correlated (Table 4). Host preferences always resulted into strong and significant linear relationships with offspring performance, the former explaining between 73 (female weight) and 87 % (development rates) variability in the latter. Adult longevity significantly correlated as well to host preference, but the higher intercept (22.8) recorded might imply that there are other various factors for survival other than host preference (Table 4). The relationship between host choice and chances of female offspring (female:male ratio) was also strongly correlated (R2 = 79.9%, P = 0.000). MANOVA of the relationship between host preference and the offspring performance measures showed strong support for the preference-performance hypothesis (PPH) with overall coefficient of determination of 75.4% (P = 0.000). In terms of varieties, the results also corroborated the predictions of the PPH. Results of MANOVA of the relationship between host preference and offspring performance measures showed an overall coefficient of determination of 65% (P = 0.003). However, these results indicate that the performance prediction of the PPH was partially supported as development rates of B. invadens reared on various mango varieties showed a weaker and insignificant relationship with offspring preference (R^2 = 19%, P = 0.186).

Table 4: Linear regression and Multivariate Analysis of variance (MANOVA) between B. invadens host preference and offspring performance indicators of five host species and 11 mango fruit varieties

Performance indicator	Slope	Intercept	R^2	d f	F-value	P (0.05)	Regression equation
Fruit Species							
Development rate	0.03	0.38	0.867	8	84.608	0.000	Y = 0.026X + 0.384
Survival/ Longevity	0.89	22.84	0.745	8	38.037	0.000	Y = 0.890X + 22.84
Female weight	0.04	1.31	0.730	8	35.140	0.000	Y = 0.037X + 1.308
Male weight	0.04	1.41	0.762	8	41.513	0.000	Y = 0.038X + 1.410
Overall weight	0.04	1.42	0.732	8	35.552	0.000	Y = 0.036X + 1.422
Sex ratio (female:male)	0.05	0.01	0.799	8	51.664	0.000	Y = 0.052X + 0.001
MANOVA			0.754	6,8	17680	0.000	
Mango Varieties							
Development rate	0.00	0.01	0.19	8	02.060	0.186^{ns}	Y = 0.000X + 0.001
Survival/ Longevity	0.27	21.08	0.65	8	16.700	0.003	Y = 0.268X + 21.08
MANOVA			0.65	2,8	13.110	0.003	

n.s = not significant

4. Discussions

The study tested the hypothesis that because of its polyphagous nature, B. invadens can obscure the expected positive correlation between adult oviposition preference and offspring performance. We specifically aimed to establish patterns of oviposition in relation to resource type and to compare offspring performance among the resource types. The results however contracted the null hypothesis as the relationship between host preference and the offspring performance measures showed strong support for the preference-performance hypothesis (PPH), with overall coefficients of determination of 75.4% and 65% for fruit species and mango varieties, respectively (Table 4). The preference–performance hypothesis predicts that females should distribute their offspring among habitats to maximize fitness (Schriber, 1983; Thompson 1988; Valladares et al., 1991; Nufio et al., 2004). It is clear from the results in our study that PPH shapes host preference of B. invadens, particularly among fruit species. This finding is supported by several previous studies (Craig et al., 1989; Anderson et al., 1989; Price et al., 1990; Rossi & Strong, 1991; Horner & Abrahamson, 1992; Hanks et al., 1993) that showed significant influences of host-plant preference on offspring performance. The perfect correlation between oviposition preference and performance indicate that females maximize offspring fitness by selecting high quality hosts for feeding in order to optimize performance of their offspring.

Optimum B. invadens hosts for adult performance such as tropical almonds, guava and Biire mangoes are also good for offspring performance, which indicates that there exists no large trade-off between host suitability for adult and offspring performance. However, hosts good for off-spring performance are not always good for adult performance. Offspring performance is excellent on mango varieties as indicated by the high coefficients of determination of 65% and adult mean survival time (R^2 = 65%, P = 0.003), while adult development rates did not show significant relationship with oviposition preference. Similarly, although citrus host species showed relatively higher oviposition preference than avocado, the latter had better performance indicators than the former, which was also the case with many mango varieties. Most mango orchards are either mixed with citrus, or the latter is available in most places. In addition, some relatively less offspring performance varieties are generally abundant at stages when the suitable ones are phonologically not available. Therefore, oviposition in less suitable hosts is likely to be a common occurrence whenever these fruits are prevalent. This favors a tradeoff whereby natural selection leads to lesser quality hosts being adopted in favor of reduced intraspecific competition (Anderson et al., 1989; Anderson et al., 1989; Aluja & Mangan, 2008).

Most performance parameters of B. invadens did co-vary among the fruit hosts, suggesting that fitness components are predominantly under similar genetic control (Scheirs et al., 2003). Indeed all parameters ranged between 73.0 – 86.7%, with low variability among parameters (Table 4). We therefore predict that although there is no single unequivocal fitness parameter, a few fitness components of B. invadens could be considered when testing hypotheses related to PPH theory. This however does not seem the case for mango varieties, as only mean survival time fitness measure significantly correlated with oviposition preference. It is also possible that the lack of a positive host preference-offspring performance in terms of mango varieties reared larvae development rates could have been due to a methodological constraint in our experimental design: host preference was based on natural field infestation. Stanton (1982) and Ahman (1985), argued that preference cannot be determined in the field as not all plants will be of equal abundances and availability, but see Aluja & Mangan (2008). It is therefore possible that a positive correlation may have been obscured, and hence validation with laboratory choice experiments is recommended for the mango varieties. However, this finding among polyphagous species is not unique, as other studies have reported similar findings (Karban & Courtney, 1987; Courtney & Kibota, 1990; Horner & Abrahamson, 1992; Larsson et al., 1995; Scheirs et al., 2003).

Several other reasons have been put forward to explain the subvert occurrence of a one-to-one correspondence between preference and performance observed in mango varieties. Among these, host confusion and limited discriminatory ability of B. invadens for the several mango varieties (Larsson & Ekbom, 1995), the highly homogenous mango fruit varieties appearance (Chew & Courtney, 1991), concordance of certain less suitable varieties phenology with B. invadens oviposition (Briese, 1996), and generally overwhelming B. invadens abundance in the region (Wiklund, 1982). B. invadens has been reported as the most polyphagous species, infesting 29 hosts from 15 botanical families, and is economically the most important fruit fly in the region and continent, where it infests over 44 known cultivated and wild hosts (Isabirye et al., Unpublished data; Ekesi et al., 2006; Mwatawala et al., 2006; Rwomushana et al., 2008; Vayssières et al., 2009; Mwatawala et al., 2009). Their highly polyphagous nature and behavioral adaptation characteristics could be facilitating oviposition on varieties that are less suitable for offspring performance (Aluja & Mangan, 2008).

The observed behavior on mango varieties in this study could also suggest an optimal foraging hypothesis which ensures that adult females maximize their fitness and not necessarily that of offsprings (Scheirs et al., 2004). It is also possible that development rate among different mango varieties is an incomplete metric of local adaptation and offspring performance. Adults may not have a physiological advantage for depending on a given mango variety, but may be well suited for dealing with natural enemies associated with a particular variety (Lill et al., 2002; Forister, 2004), or that adult adaptation may be slower to evolve than adult preference, a situation which has been found in other taxa (Thompson, 1988; Forister, 2004). Based on the preference–performance hypothesis, the weak oviposition preference and offspring performance among some fruits and in particular mango varieties in this study might also an evolutionary consequence of fitness differences among varieties. This is a common occurrence when performance is not consistently higher in the preferred varieties over time, or if opposing selection pressures prevent fixation of the genes governing a particular habitat preference (Rausher, 1984).

Two possible hypotheses may explain the observed differences in B. invadens preference for ‘local’ selection varieties (Kate & Biire), and in some cases Kagogwa over the “exotics’ in this study. First, most polyphagous species adapt quickly to a new host, with larval survivorship increasing linearly over 10 generations in a new host (Hawthorne, 1999). The relatively higher preference of the flies for the local selection and Kagogwa varieties may therefore be the result of an increase in performance on these hosts. Second, studies by Szentesi & Jermy (1990); Dukas & Bernays (2000); and Egas & Sabelis (2001) have shown that experience or learning may affect host choice of phytophagous insects. B. invadens maybe probably already adapted for living on these varieties because of their predominant availability in the country over the ‘exotics’. Local selection varieties are believed to have been introduced into the country after World War II by the veterans in the 1940s, while the ‘exotics’ are a recent introduction of the 1990s (Aisu G., Personal Communication). Therefore, the country wide distribution of local selections and Kagogwa varieties has favored adaptation, which may provide an explanation for the high preference for and performance, and the high correlation between host preference and performance for the varieties.

Several studies have reported higher B. invadens preference for oviposition on Terminalia catappa (Rwomushana et al., 2008; Mwatawala et al., 2006; Mwatawala et al., 2009a; Geurts et al., 2012). The plant fitted perfectly the PPH, by recording the highest oviposition preference and offspring performance among all fruits in the study. The higher affinity for T. catappa by B. invadens males has been related to the higher plant concentration of methyl eugenol, a phenylpropanoid compound found in over 200 plant species representing 32 families (Shelly & Edu, 2007). After ingesting the compound, males sequester break-down products of methyl eugenol in the rectal gland and use these metabolites to synthesize a sex pheromone attractive to females (Nishida et al. 1988). Males fed on methyl eugenol produce a more attractive pheromonal signal and enjoy a higher mating success and advantage (Raghu, 2002; Shelly & Edu, 2007). Indeed Raghu (2002) found that sexually mature males with high nutritional reserves were most commonly collected at sites with methyl eugenol at dusk, the time of peak sexual activity, which indicated that methyl eugenol was a significant resource in the reproductive behavior of Bactrocera species. Metcalf (1990) adds that plants (like T. catappa) that contain methyl eugenol serve as mating rendezvous sites.

Results of this study provide some support for the host size models (King, 1990). According to these models, insects provide their offspring with food by ovipositing in or on hosts, and that the resource available to her offspring may affect which sex ratio a female should produce (Trivers & Willard, 1973). The host size models further suggest that females of solitary species should manipulate the sex of their offspring in response to characteristics of the hosts on which they oviposit. In our study, the order for female: male ratio was T.catappa > M. indica > P.guanjava > P.americana > C. sinensis, which is more less the order for host PPH quality and adult fly body weight (Table 3). The lower resource availability on relatively poor hosts such as citrus might be expected to increase a female's risks of starvation more than a male's, and hence ovipositing females consider chances of survivorship to be higher on better hosts like tropical almonds than citrus. Therefore, the observed higher number of male offsprings in the less suitable oviposition hosts (citrus and avocado) in our study could be a result of maternal manipulation.

From our results, B. invadens manipulate offspring sex ratio in response to host quality in the manner predicted by the host size model, and our findings are consistent with earlier findings that females manipulate offspring sex ratio in response to host size in the manner predicted by the host size model (King, 1990). However, it is still not clear whether B. invadens fits the assumptions of the host size models and thus that the sex ratio manipulation in response to host characteristics is adaptive. The proximate mechanisms of sex ratio manipulation in response to host characteristics are largely unknown. There is some evidence that external host parameters are important in oviposition decisions in some species. Our host ratio results may therefore suggest that B. invadens manipulation of offspring sex ratio in response to host species may be a response to differences among host species, rather than a response to external host dimensions. Further studies will be needed to determine more specifically what cues B. invadens females are using in their sex ratio response.

5. Conclusions

This study has added to the accumulating evidence that host preference and host-specific variation among phytophagous insects contributes significantly to offspring performance, as suggested by the PPH. On the basis of PPH, the five B. invadens hosts in this study ranked as T.catappa > P.guanjava > M. indica > P.americana > C. sinensis; and variability among mango varieties was also illustrated. The study has shown the suitability of selected host plants for the development, longevity, and survival of B. invadens. Our findings should assist to understand the biology of B. invadens and could help in its management and control, particularly on Mangoes. Further studies should consider both host-specific variations in adult and offspring performance, and focus on testing a wider range of host plant species for the development of B. invadens. An assessment of the chemical components of the host plant species would help to better understand the mechanism of host suitability, while investigation of conformity to the PPH for different agro ecological contexts and other tephritid groups would yield useful knowledge.

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