Host Plants and Host Plant Preference Studies for *Bactrocera invadens* (Diptera: Tephritidae) in Kenya, a New Invasive Fruit Fly Species in Africa

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ABSTRACT *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae), an invasive fruit fly species of Asian origin, was detected in Kenya in 2003, and is now well established in several parts of the country. We assessed the host range of this major quarantine pest in Kenya by collecting a wide range of cultivated and wild host plants from December 2004 to April 2006. Fruit were collected from 90 plant species representing 40 families from the Coast, Eastern, and Rift Valley provinces of the country where the fly population had been observed to occur in large numbers and where fruit and vegetable production is predominant. Fourteen plant species, among them cultivated and wild fruiting species, were found to be hosts of *B. invadens*. Fruit of mango, *Mangifera indica* L. (Anacardiaceae); banana *Musa* sp. *AAA* (Musaceae); and citrus [*Citrus limon* (L.) Burm.f. (lemon), *Citrus reticulata* Blanco (tangerine), and *Citrus sinensis* (sweet orange) (all Rutaceae)], were among the cultivated species heavily infested by *B. invadens*. Marula *Sclerocarya birrea* (A.Rich) Hochst. (Anacardiaceae) and *Terminalia catappa* L. (Combretaceae) were found to be the most infested noncultivated plants. These wild plants evidently ensure that sufficient reproductive bases exist for *B. invadens* during the off-season when the cultivated hosts are not in fruiting. In laboratory host preference studies, mango and banana were found to be the most preferred host plants among the nine cultivated plant species tested.

KEY WORDS *Bactrocera invadens*, fruit fly, host plants, host preference, infestation index

In March 2003, an invasive species of fruit fly from the genus *Bactrocera* Macquart was detected in Kenya (Lux et al. 2003) and most recently described as *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae) (Drew et al. 2005). Since the first report, the insect has rapidly spread across the African continent and in addition to Kenya it is now known from 20 other countries, including Angola, Benin, Burkina Faso, Cameroon, Comoros Island, Congo, DR Congo, Equatorial Guinea, Ghana, Guinea, Ivory Coast, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan, Tanzania, Togo, and Uganda (Drew et al. 2005, French 2005, Vayssières et al. 2005, Ekesi et al. 2006). *B. invadens* is thought to have invaded Africa from the Indian subcontinent, and it was discovered in Sri Lanka after it was first reported from Africa (Drew et al. 2005), where it has become a significant pest of quarantine and economic importance (Mwatawala et al. 2004; Vayssières et al. 2005; Ekesi et al. 2006; Ekesi 2006). *B. invadens* belongs to the *Bactrocera dorsalis* Hendel complex of tropical fruit flies (French 2005), which comprises >75 species largely endemic to South East

Asia (Drew and Hancock 1994; Tsuruta and White 2001; Clarke et al. 2004, 2005), with undescribed species remaining in collections (Lawson et al. 2003). The group is arguably regarded as one of the most destructive to fruits and vegetables worldwide (White and Elson-Harris 1992; Clarke et al. 2005; Drew et al. 2005). Most recently, *B. dorsalis* was accidentally introduced into French Polynesia where it has displaced two other tephritid species, spread to five different Society Islands, and it infests 29 different host fruit so far (Vargas et al. 2007). In Kenya, trap catches using methyl eugenol (ME) as attractant revealed that *B. invadens* is now widely distributed and prevalent in several cultivated and forested areas, particularly in the warm humid lowland areas (S.E. et al., unpublished data). Previously documented species of *Bactrocera* in Kenya include melon fly *Bactrocera cucurbitae* Coquillett; olive fruit fly, *Bactrocera oleae* (Gmelin), *Bactrocera biguttula* (Bezzi); and *Bactrocera munroi* White (White and Elson-Harris 1992, Copeland et al. 2004). Among the four species, *B. cucurbitae* was the most prevalent and destructive, attacking both cultivated and wild cucurbit plants (Ekesi 2006). Other *Bactrocera* species within the *B. dorsalis* complex in Africa include *Bactrocera zonata* (Saunders), which is also an invasive species now established in Egypt (Anonymous 2005) and known to

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be highly destructive attacking 13 plant species in Mauritius and Réunion (Quilici and Jeuffrault 2001). The arrival of *B. invadens* adds to the list of *Bactrocera* species on the continent and neighboring Islands and compounds the fruit fly problems in the region.

Most frugivorous tephritids within the *B. dorsalis* group are known to attack a wide range of fruit, vegetable, and wild plant species. For example, three species within the *B. dorsalis* complex: *Bactrocera papayae* (Drew & Hancock) has 209 recorded hosts across 51 plant families, *B. dorsalis* has 124 host species across 42 families in tropical Asia, and *Bactrocera carambolae* (Drew & Hancock) has 77 host species across 27 families (Drew 1989; Hollingsworth et al. 2003; Clarke et al. 2005). Of the *Bactrocera* species reported in Kenya, the host range of *B. cucurbitae* are primarily cucurbits, but it has been recorded from a few non-cucurbit hosts (White and Elson-Harris 1992). The olive fly exclusively infests fruit of *Olea europaea* L., *B. munroi* infests *Olea europaea* and *Olea welwitschii* Gilg & Schnellenberg, and *B. biguttula* the coastal olive, *Olea woodiana* Knobl. (Copeland et al. 2004). In Benin, Vayssières et al. (2005) reported 10 plant species as host of *B. invadens.* In Tanzania, Mwatawala et al. (2006) identified 15 fruit species as host to *B. invadens.* The only published host record from Kenya is its attack on *Strychnos mellodora* S. Moore and mango, *Mangifera indica* L. (Lux et al. 2003, Drew et al. 2005, Ekesi et al. 2006). Host status is a dynamic phenomenon and this list is by no means exhaustive, and given that the *B. dorsalis* complex to which *B. invadens* belongs attack several host plant species, it is envisaged that this list is likely to increase.

Because of the "novelty status" of *B. invadens*, very little is known about the ecology of this pest, and the need to document the host plants of this important quarantine pest becomes crucial. Therefore, the main objective of this study was to catalog the host plants of *B. invadens* in Kenya, given its importance as a major quarantine pest, to provide necessary information that may be useful for management of the pest. We also conducted host preference studies in the laboratory in a choice and no-choice tests that included nine of the major export fruits and vegetables that were either infested or not infested in the field survey to ascertain the most preferred host plant of the insect.

Materials and Methods

Field Surveys. *Sampling Sites.* Host fruit survey was carried out from December 2004 to April 2006 in three provinces in Kenya where *B. invadens* had been previously confirmed with ME-baited traps to be in high abundance (Lux et al. 2003; S.E. et al., unpublished data). Priority was particularly given to locations with large diversity of fruit, spread across the Coast, Eastern, and Rift Valley provinces of the country (Fig. 1). At the Rift Valley Province, surveys were concentrated at Nguruman division. At the Coast Province, sampling locations included forested areas on the fringes of the Indian Ocean and high altitude areas in the Taita hills. In the Eastern Province (representing the highland region of the country), sampling locations were varied up to the fringes of Mt. Kenya forest. At each location, approximate latitude, longitude and altitude were taken using a global positioning system device (Table 1).

Fruit Collection, Handling, and Processing. Fruit were collected from cultivated fields, backyard gardens, woodlands, roadside shrubs, forested areas, and protected reserves. Often, a few fruit not encountered from sampling sites were purchased from roadside markets, and whenever possible attempts were made to establish the place of origin. Fruit samples collected included ripe to overripe fruit, including those with visible symptoms of fruit fly damage both from the tree and from the ground as "windfalls." Attempts were made to sample large quantity of fruit with a minimum of 15 fruit per fruiting species although in some cases this sample size could not be maintained due to unavailability of fruit. Fruit collections of the different plant species were separately placed in perforated polyethylene bags in the field for transport to the rearing facility. The rearing facilities were located in each ecozone where fruit were collected and included the International Centre of Insect Physiology and Ecology (*icipe*)-Muhaka field station for Coast, *icipe* field station at Nguruman for Rift Valley, and *icipe* headquarters in Nairobi for Eastern Province samples.

At the rearing facility, fruit were counted, weighed, and secured in well-aerated rectangular plastic containers. Small fruit (<5 cm in diameter) were held together in 1.5-liter rectangular transparent plastic containers (20 by 12.5 by 8 cm) (Kenpoly, Nairobi, Kenya). Larger fruit (>5 cm in diameter) were held in groups of two or three in 3-liter rectangular plastic containers (20 by 12.5 by 15 cm) (Kenpoly). Fruit >10 cm diameter in were held in cylindrical plastic buckets (25 by 30 cm) (no. 20, Nairobi Plastics Limited, Nairobi, Kenya). The rim of the containers was covered with a fine netting material held in place by the perforated cover of the containers that was capable of retaining adult tephritids. The fruit were placed on 40–60 mm of moistened sterilized sand at the bottom of the rearing containers. The sand served both as the pupation medium for the larvae that exited the fruit in addition to soaking up fruit juices (Woods et al. 2005). Fruit were held at ambient conditions for 4–6 wk, depending on the fruit species.

Rearing cages were checked daily, and puparia were picked from the sand with a pair of soft forceps, counted and placed in petri dishes with moistened filter paper. In some large juicy fruit, pupation occurred inside the fruit, and in this case rotting fruit also were dissected to completely recover all remaining puparia. The petri dishes with puparia were then held in small, ventilated, transparent cylindrical plastic cages (5.5 by 12.5 cm) (no. J-12, GP Plastics, Nairobi, Kenya) until eclosion. Emerging tephritids were provided with an artificial diet that consisted of a volumetric mixture of 1:3 enzymatic yeast hydrolysate and sugar, and water was provided in pumice granules. Flies were allowed to feed for 4 d until full adult development and body colorations were attained.
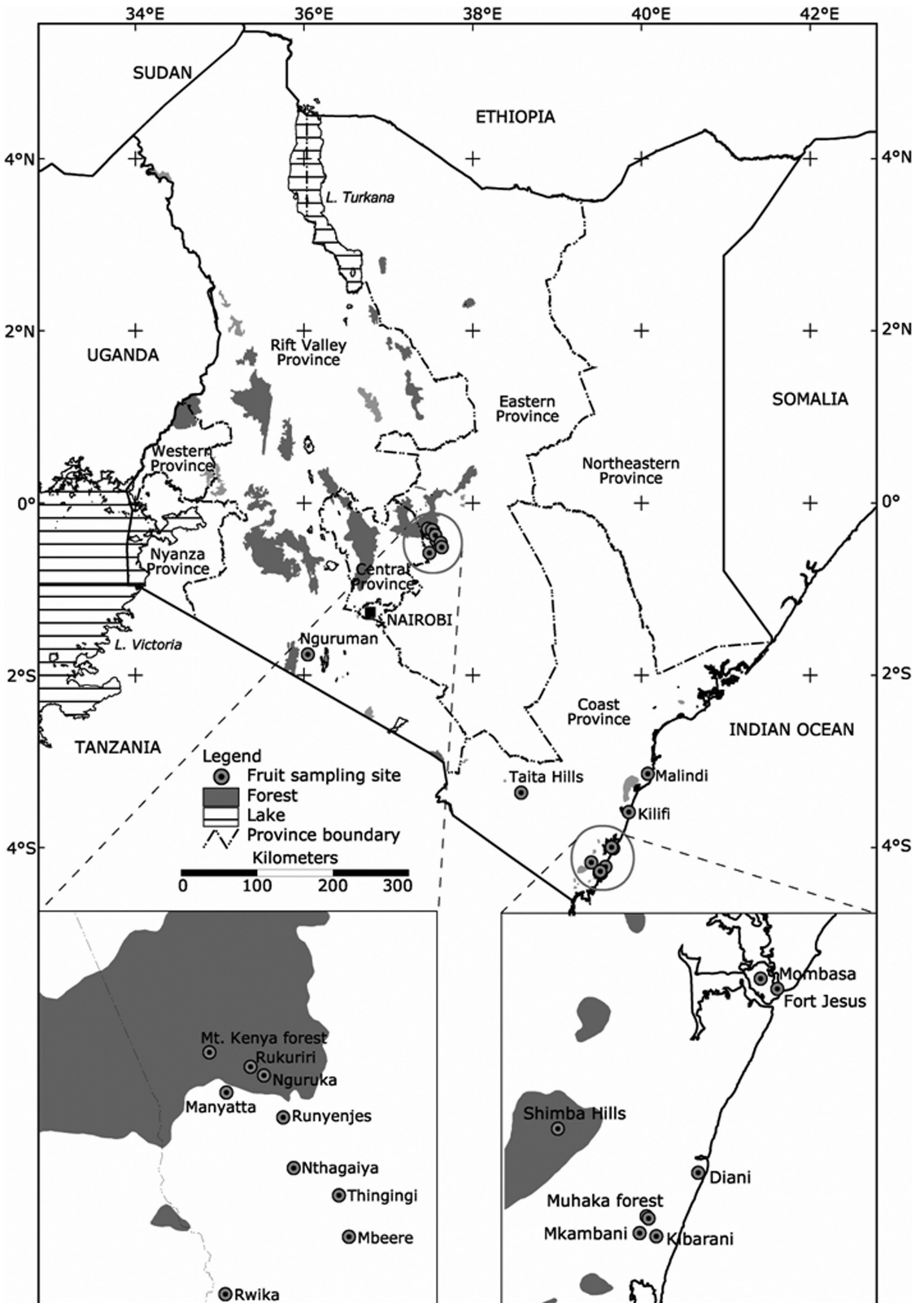
Fig. 1.   Map of Kenya showing fruit collection sites.

Table 1. Fruit sampling sites with approximate georeferenced positions and altitude

Province	Locality	Approximate longitude	Approximate latitude	Approximate altitude (m)
Coast	Diani Forest	04° 20′ 03 S	39° 34′ 10 E	30
	Kibarani	04° 19′ 47 S	39° 31′ 03 E	350
	Malindi	03° 11′ 40 S	40° 05′ 20 E	32
	Kilifi	03° 47′ 15 S	39° 51′ 56 E	167
	Mkambani	04° 12′ 35 S	39° 37′ 03 E	44
	Muhaka area	04° 16′ 35 S	39° 33′ 36 E	44
	Muhaka forest	04° 19′ 27 S	39° 32′ 27 E	46
	Shimba Hills	04° 13′ 21 S	39° 22′ 09 E	380
	Fort Jesus	04° 02′ 36 S	39° 35′ 37 E	20
	Mombasa	04° 03′ 25 S	39° 39′ 32 E	40
	Taita hills	03° 24′ 51 S	39° 35′ 20 E	1,405
Eastern	Rwika	00° 37′ 43 S	37° 30′ 03 E	1,213
	Manyatta	00° 23′ 39 S	37° 30′ 07 E	1,600
	Nthagaiya	00° 29′ 24 S	37° 35′ 31 E	1,328
	Mt. Kenya forest	00° 20′ 51 S	37° 28′ 55 E	2,004
	Nguruka	00° 22′ 28 S	37° 32′ 46 E	1,183
	Rukuriri	00° 21′ 52 S	37° 31′ 49 E	1,732
	Runyenjes	00° 25′ 23 S	37° 34′ 09 E	1,532
	Thingingi	00° 30′ 49 S	37° 38′ 07 E	1,850
	Mbeere	00° 33′ 42 S	37° 38′ 49 E	1,200
Rift Valley	Nguruman	01° 48′ 31 S	36° 03′ 34 E	760

They were then killed by placing them in a freezer and later preserved in 70% alcohol. All specimens were shipped to the *icipe* Biosystematics unit for identification where a reference collection is kept. Samples of flower, fruit (for small fruit), leaf, twig (or both) from unknown plant species also were collected, pressed, and bagged. The collected plant samples were identified using the keys of Kenya trees, shrubs, and lianas (Beentje 1994). Photographs also were taken of each plant or fruit sampled to aid in plant identification, most of which was provided by Dr. R. S. Copeland (*icipe*). Voucher specimens of all collections of the plant species are maintained at *icipe.* Plant nomenclature used conforms to the International Plant Names Index database (IPNI 2004) and the Missouri Botanical Garden database W³ TROPICOS (MBOT 2006).

Laboratory Host Preference Studies. *Choice Test.* The experiments were conducted in 90- by 90- by 90-cm Plexiglas cages in a laboratory maintained at ambient conditions. Nine fruit and vegetable species, including mango, papaya (*Carica papaya.* L.), banana (*Musa* sp. AAA), guava (*Psidium guajava* L.), sweet orange [*Citrus sinensis* (L.) Osbeck], custard apple (*Annona squamosa* L.), cucumber (*Cucumis sativus* L.), avocado (*Persea americana* Miller) and tomato (*Lycopersicon esculentum* Miller), which were hosts and nonhosts records from the field surveys, were tested. Each experimental cage was divided equally into nine subunits, and each unit held one fruit species supported by a string from the roof of the cage. Distance between each fruit species was 30 cm. All fruit and vegetable species were tested when they were either fully ripe (mango, papaya, banana, orange, guava, tomato, and custard apple) or at mature green stage (avocado and cucumber). It is generally well established that host plants are most susceptible to fruit flies at these stages. One hundred adult *B. invadens* (consisting of 50 females and 50 males) at 2–3 wk old were then released inside the cages for a period of 24 h. Flies were fed on 1:3 volumetric mixture of enzymatic yeast hydrolysate and sugar. Water also was provided on pumice granules. After 24 h, all fruit species were removed and incubated individually as described for field surveys. Records were kept for pupal recovery and percentage of adult emergence from the total puparia recovered. Four replicated cages were maintained and the experiment was repeated twice.

No-Choice Test. Two sets of experiments were conducted under the no-choice test. In the first experiment, we measured female fecundity on fruit domes of the nine plant species for a period of 10 d. Fruit domes were made by scooping the pulp and seeds out of the fruit. Fruit peel thickness varied slightly among the fruit species and ranged from 2.2 to 2.5 mm in diameter. Each fruit dome was then transferred into a 20- by 20- by 20-cm Plexiglas cage, and a pair of adult *B. invadens* was released inside the cage. Records were kept of the number of eggs laid daily on the dome by washing the eggs off the underside of the domes. Flies were fed as described previously. To record hatch rate, the eggs were transferred onto strips of moist blotting paper and hatch rate was determined by observing for eclosion under a binocular microscope after 2 d. The cages were arranged in a complete randomized design with three replications.

In the second experiment, whole fruit were exposed to flies in 25- by 25- by 25-cm Plexiglas cages. A single fruit sample from each of the nine plant species listed above was transferred into each cage. Forty 2–3-wk-old adult flies (20 females and 20 males) were released in each cage for a period of 24 h. Flies were fed as in previous experiment. At the end of the exposure period, the fruit was removed and processed as described previously. Five replicates were maintained and the experiment was repeated twice.

Statistical Analysis. Data for field surveys are presented according to plant species, family, location,

Table 2. Host fruit infestation indices for *B. invadens* in three provinces of Kenya from December 2004 to April 2006

Province/locality	Plant species	Plant family	No. fruit	Fruit wt. (kg)	% fruit infested	No. *B. invadens* adults	*B. invadens*/kg fruits
Coast province							
Malindi	*Mangifera indica* L.	Anacardiaceae	206	65.9	64.4	6012	91.2
	Citrus sinensis (L.) Osbeck	Rutaceae	114	10.4	28.5	23	2.2
	Psidium guajava L.	Myrtaceae	84	9.8	31.3	41	4.2
Kilifi	*Musa* sp. AAA	Musaceae	262	5.2	36.4	66	12.7
	Mangifera indica L.	Anacardiaceae	43	13.2	50.8	1204	91.2
	Citrus sinensis (L.) Osbeck	Rutaceae	31	2.6	12.3	12	4.6
	Terminalia catappa L.	Combretaceae	121	3.6	35.2	443	123.1
Muhaka	*Annona cherimola* Mill.	Annonaceae	35	0.7	31.4	21	30.1
	Citrus limon (L.) Burm.f	Rutaceae	32	2.6	0.0	0	0.0
	Citrus reticulata Blanco	Rutaceae	40	4.3	12.5	24	5.6
	Citrus sinensis (L.) Osbeck	Rutaceae	15	1.9	12.5	7	3.7
	Cordia sp. cf *myxa*	Boraginaceae	33	0.6	6.1	10	17.1
	Mangifera indica L.	Anacardiaceae	119	38.4	59.7	5004	130.3
	Musa sp. AAA	Musaceae	24	0.2	0.0	0	0.0
	Psidium guajava L.	Myrtaceae	32	3.6	34.4	61	17.0
	Sclerocarya birrea (A, R.) H.	Anacardiaceae	127	2.5	36.2	597	238.8
	Sorindeia madagascariensis B.	Anacardiaceae	108	0.1	1	1	10.0
Mombasa	*Annona muricata* L.	Annonaceae	16	6.5	6.3	9	1.4
	Terminalia catappa L.	Combretaceae	16	0.4	18.8	7	17.5
Eastern province							
Mbeere	*Annona cherimola* Mill.	Annonaceae	40	1.1	15.0	59	53.6
	Mangifera indica L.	Anacardiaceae	112	29.5	40.2	296	10.0
	Musa sp. AAA	Musaceae	52	3.3	0.0	0	0.0
	Citrus sinensis (L.) Osbeck	Rutaceae	101	9.8	12.6	11	1.1
Nthagaiya	*Annona cherimola* Mill.	Annonaceae	6	0.6	50.0	51	85.0
	Mangifera indica L.	Anacardiaceae	145	40.0	31.2	257	6.4
	Musa sp. AAA	Musaceae	145	9.3	12.1	55	5.9
	Psidium guajava L.	Myrtaceae	31	3.1	12.0	36	11.6
	Citrus limon (L.) Burm.f	Rutaceae	30	2.7	0.0	0	0.0
Rwika	*Annona cherimola* Mill.	Annonaceae	86	2.2	23.5	62	28.2
	Citrus reticulata Blanco	Rutaceae	46	4.8	10.3	18	3.8
	Citrus sinensis (L.) Osbeck	Rutaceae	224	25.6	12.7	49	2.0
	Mangifera indica L.	Anacardiaceae	204	72.9	40.2	2141	29.4
	Musa sp. AAA	Musaceae	132	2.8	10.2	21	7.5
Rukuriri	*Annona muricata* L.	Annonaceae	5	0.5	20.0	0	0.0
	Lycopersicon esculentum Mill.	Solanaceae	48	4.7	0.0	0	0.0
	Mangifera indica L.	Anacardiaceae	158	19.4	1.3	0	0.0
	Psidium guajava L.	Myrtaceae	65	2.4	17.5	0	0.0
Rift Valley Province							
Nguruman	*Annona squamosa* L.	Annonaceae	58	13.2	54.1	33	2.5
	Citrus limon (L.) Burm.f	Rutaceae	21	3.0	28.6	97	32.3
	Citrus sinensis (L.) Osbeck	Rutaceae	14	1.5	0.0	0	0.0
	Lycopersicon esculentum Mill.	Solanaceae	23	1.2	8.7	2	1.7
	Mangifera indica L.	Anacardiaceae	454	148.6	57.5	5830	39.2
	Musa sp. AAA	Musaceae	9	0.9	33.3	123	129.9
	Sclerocarya birrea (A, R.) H.	Anacardiaceae	154	3.1	41.3	123	39.7
	Terminalia catappa L.	Combretaceae	92	3.2	83.9	2089	652.8

number of fruit collected and weight, number of infested fruit, and number of adults. Infestation by *B. invadens* followed the methodology of Cowley et al. (1992), and it was calculated as the ratio of number of adults per kilogram of fruit collected (infestation index). In the laboratory experiments, data were tested for normality and homogeneity of variance by transforming to natural logarithms (pupal recovery and fecundity) and angular transformation (percentage of egg hatch and adult emergence) before subjecting to analyses. Because the experimental design in the choice experiment did not support the assumption of sample independence for analysis of variance (ANOVA), the nonparametric equivalents, Kruskal–Wallis and chi-square tests, were used to analyze the data. In the no-choice experiment, data were subjected to ANOVA using the generalized linear model (Proc GLM), and means were separated by Tukey honestly significant difference (HSD) test ($P = 0.05$). All analyses were performed using the SAS package (SAS Institute 2001).

Results

Field Survey. *B. invadens* was reared from a total collection of 3,913 fruit from a range of habitats that included 14 plant species and eight families from surveys carried out at the Coast, Eastern, and Rift Valley provinces of Kenya (Tables 1 and 2). Fruit species positive for *B. invadens* included both cultivated and wild host plants (Table 2). The majority of *B. invadens*-infested samples were from commercial fruit. Ten of the host plants are new records for *B. invadens* in Kenya. During the survey, a collection of 4,630 fruit

composed of 76 other plant species from 32 families did not yield *B. invadens.* Our data indicated that *B. invadens* was capable of infesting fruit over an altitudinal range of 20–1,335 m above sea level (masl), with infestation varying from 1.1 to 652.8 flies per kg of fruit (Tables 1 and 2).

Among the plant species sampled, *B. invadens* infestation was recorded from cherimolia, soursop, custard apple (Annonaceae), *Citrus limon* (L.) Burm.f. (lemon), *Citrus reticulata* Blanco (tangerine), sweet orange (Rutaceae), *Cordia myxa* L. (Boraginaceae), tomato (Solanaceae), mango (Anacardiaceae), banana *Musa* sp. *AAA* (Musaceae), guava (Myrtaceae), *Sclerocarya birrea* (A.Rich.) Hochst. (marula), *Sorindeia madagascariensis* L. (Anacardiaceae), and *Terminalia catappa* L. (tropical almond) (Combretaceae) (Table 2). The families Anacardiaceae, Annonaceae, and Rutaceae had the highest number of species infested, with *B. invadens* reared from three species sampled in each family. The most heavily infested Anacardiaceae was *M. indica*, with infestation reaching 130.3 flies per kg fruit at Muhaka, Coast Province, whereas in the Annonaceae, the wild species, *A. cherimola* sampled at Nthagaiya, Eastern Province, recorded the highest number of *B. invadens* (85.0 flies per kg fruit) (Table 2). Among the Rutaceae, *C. limon* was the most infested at Nguruman, Rift Valley Province (32.3 flies per kg fruit). In the other provinces, members of the Rutaceae sampled were less infested, and *C. sinensis* and *C. reticulata* had the highest level of infestation at 2.0–5.6 flies per kg fruit. Of the wild host fruit sampled, the highest level of infestation was recorded on *T. catappa* (652.8 flies per kg fruit) sampled from Nguruman, Rift Valley Province and *S. birrea* (238.8 flies per kg fruit) sampled from Muhaka, Coast Province (Table 2). Generally, fruit infestations were higher at low elevations than at the highland areas (Tables 1 and 2). For example, mango fruit infestation varied from 39.2 to 130.3 flies per kg fruit at the low-elevation locales in the Coast Province and Rift Valley compared with 0–29.4 flies per kg fruit in the high elevation areas of the Eastern Province (Table 2).

Other tephritid species also were encountered during the survey period, including *B. cucurbitae, Ceratitis anonae* (Graham), *Ceratitis capitata* (Wiedemann), *Ceratitis cosyra* (Walker), *Ceratitis rosa* Karsch, *Ceratitis pedestris* (Bezzi), *Ceratitis pinax* Munro, *Dacus frontalis* Becker, *Dacus vertebratus* (Bezzi), *Trirhithrum nigerrimum* (Bezzi) and *Trirhithrum senex* Munro. The host plants data collected for these fruit flies are not presented because they were similar to previously documented information (Liquido et al. 1991; White and Elson-Harris 1992; Mukiama and Muraya 1994; Quilici and Jeuffrault 2001; Copeland et al. 2002, 2006; De Meyer et al. 2002; Ekesi 2006).

Laboratory Host Preference Studies. *Choice Test.* There was a significant difference in the number of puparia recovered (Kruskal–Wallis: H = 56.2, df = 8, $P = 0.0001$) and adult emergence (Kruskal–Wallis: H = 36.2, df = 8, $P = 0.0001$) from the nine fruit species exposed to *B. invadens* (Fig. 2A). Highest number of
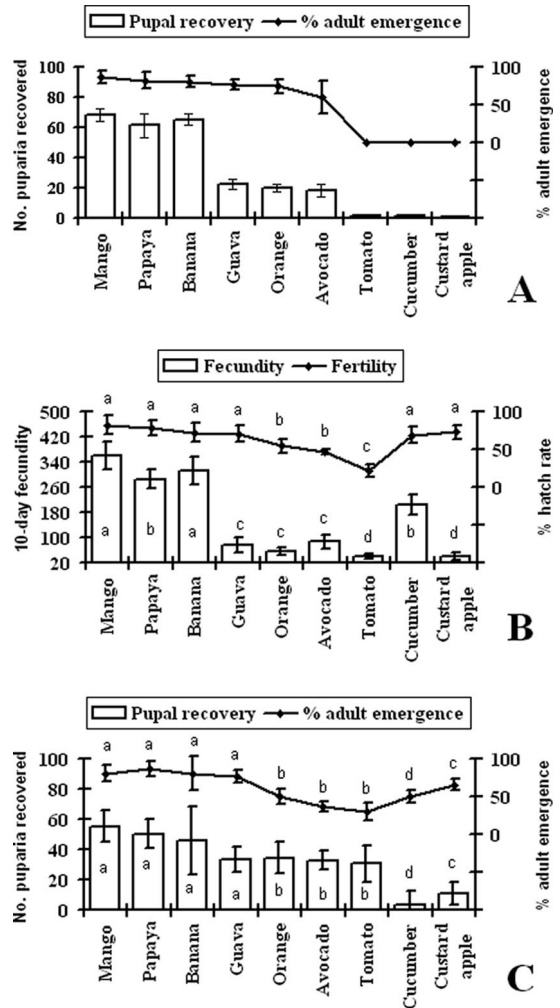

Fig. 2. Host preference and performance of *B. invadens* in terms of pupal recovery, adult emergence, fecundity, and fertility on nine cultivated plant species in a choice (A) and no-choice (B and C) tests in the laboratory. Bars and data points on line with same letter do not differ significantly by Tukey's HSD test ($P = 0.05$). Error bars denote SE.

puparia was recovered from mango, papaya, and banana, whereas the lowest recovery was observed in tomato, cucumber, and custard apple (Fig. 2A). Percentage adult emergence ranged from 60 to 86% (Fig. 2A).

No-Choice Test. There was a significant difference among the fruit species in total fecundity over 10 d ($F = 12.6$; df = 8, 18; $P = 0.0034$) and fertility ($F = 24.5$; df = 8, 18; $P = 0.0001$) (Fig. 2B). The highest number of eggs was recovered from mango, papaya, banana, and cucumber domes compared with the other five fruit species (Fig. 2B). Egg fertility ranged from as low as 21% in tomato to 82% in mango (Fig. 2B).

In the second set of experiments in the no-choice test, pupal recovery and adult emergence were also significantly different among the fruit species ($F = 33.4$; df = 8, 81; $P = 0.0001$ and $F = 24.0$; df = 8, 81; $P =$

0.0001, respectively) (Fig. 2C). Mango, papaya, and banana recorded the highest number of puparia, whereas the lowest occurred on cucumber (Fig. 2C). Percentage of adult emergence varied from 31 to 86% (Fig. 2C).

Discussion

B. invadens was reared from 14 plant species, representing eight plant families most of which are new host plant family records in Kenya and in Africa. In the first description, Drew et al. (2005) listed four cultivated host plants, namely, guava, mango, citrus, papaya, and some unidentified wild plants as host of *B. invadens* in Africa. In Benin, West Africa, Vayssières et al. (2005) reported attacks on cashew [*Anacardium occidentale* L. (Anacardiaceae)], pepper (*Capsicum annuum* L.), *Cucurbita* spp., custard apple, guava, mango, papaya, *Diospyros montana* Roxburgh (Ebenaceae), and *Vitellaria paradoxa* C.F. Gaertner (Sapotaceae) by *B. invadens*. In Tanzania, Mwatawala et al. (2006) reported 15 host plants and identified mango, loquat [*Eriobotrya japonica* (Thunb.) Lindley], guava, and grapefruit (*Citrus* x *paradisi* Macfad.) as the favored hosts. In our study, *B. invadens* was found to infest fruit species within the families Annonaceae, Rutaceae, Boraginaceae, Solanaceae, Anacardiaceae, Musaceae, Myrtaceae, and Combretaceae, suggesting that *B. invadens* is an emerging polyphagous pest that may be capable of sustaining its population through reproduction on a range of cultivated and wild fruit.

The plant families listed above have been reported to be key host plant families of several *Bactrocera* species, including members of the *B. dorsalis* complex of fruit flies (White and Elson-Harris 1992, Tsuruta et al. 1997, Clarke et al. 2005). In Mauritius and Réunion, *B. zonata* infests *A. reticulata* and *M. indica* (Quilici and Jeuffrault 2001), and the relative importance of these plants as hosts of *B. invadens* also is confirmed by our results. *Bactrocera dorsalis* infests *Annona* spp., *Citrus* spp., *M. indica*, *Musa* spp., and *P. guajava* (Armstrong 1983, Allwood et al. 1999, Clarke et al. 2005), and this is consistent with our findings for *B. invadens.*

M. indica was the most important host of *B. invadens* among the fruit sampled within the Anacardiaceae. The data reveals mango infestation in mid- to high-elevation areas of Eastern Province of Kenya. In previous studies by Ekesi et al. (2006), no *B. invadens* was recovered from mango in this locality. The current record of *B. invadens* in this locality clearly indicates that the pest is gradually expanding its range and exploiting host fruit at higher elevation areas of the country. *S. birrea* also seems to be an important reservoir host for *B. invadens*. High infestation levels were recorded at the Coast and Rift Valley provinces (238.8 and 39.7 *B. invadens* per kg respectively). This plant generally fruit sporadically throughout the year (Jøker and Erdey 2003), and it may be an important off-season host for *B. invadens* in the absence of the primary cultivated host plants.

Among the Annonaceae, *B. invadens* was reared from *A. squamosa*, *A. muricata*, and *A. cherimola.*

Mwatawala et al. (2006) showed that *A. muricata* was a major host of *B. invadens* in Tanzania. Studies elsewhere have shown that other species of *Bactrocera*, such as *B. carambolae*, *Bactrocera correcta* (Bezzi), *B. dorsalis*, *Bactrocera kandiensis* Drew & Hancock, *Bactrocera frauenfeldi* (Schiner), and *B. papayae* are frugivorous on this family (Tsuruta et al. 1997, Hadwen et al. 1998, Hollingsworth et al. 2003, Clarke et al. 2005). *B. invadens* evidently uses these wild and planted cultivars of Annonaceae, and management activities directed at *B. invadens* should take into account the importance of these plants as hosts of the insect.

C. limon was the most infested of the Rutaceae by *B. invadens* compared with *C. reticulata* and *C. sinesis.* In Tanzania, *B. invadens* was not found to attack *C. limon*, although infestations were observed on *C. reticulata* and *C. sinensis* (Mwatawala et al. 2006). Among the *B. dorsalis* complex, *C. sinensis* seems to be a less preferred host plant. For example in Surinam, South America, Clarke et al. (2005) reported that infestation rates by *B. dorsalis* on *C. sinensis* was 1.2% compared with 16.3% for *M. indica* and 11.3% for *P. guajava*. In our study, we observed an infestation rate of up to 4.6 and 5.6 *B. invadens* per kg on *C. sinensis* and *C. reticulata*, respectively. The observed high levels of infestation in *C. limon* were indeed remarkable given the acidic nature of this plant. Vayssières et al. (2005) has reported high infestation of *B. invadens* in a similarly acidic host plant (*A. occidentale*), suggesting the pest may be adapted to a wide range of fruit characteristics.

Terminalia catappa (Combretaceae) is generally known to harbor a complex of fruit fly species of the *B. dorsalis* group, including *B. zonata*, *B. correcta*, *B. dorsalis*, *B. kandiensis*, *B. papayae*, *B. zonata*, and *Bactrocera* sp. near *nigrotibialis* (taxon A) (Tsuruta et al. 1997, Quilici and Jeuffrault 2001, Hollingsworth et al. 2003, Quilici et al. 2005, Clarke et al. 2005). The high infestation levels recorded in our study (652.8 per kg *B. invadens*) confirm the status of *T. catappa* as an important host plant of *B. invadens*. This is perhaps not surprising given that the plant species is native to Asia (Styger et al. 1999, Thomson and Evans 2006). *T. catappa* can flower up to three times a year, producing fruit almost year-round (Thomson and Evans 2006; S.E., unpublished data), and it probably harbors successive generations of this pest, which infest orchards when fruiting begins. In Kenya, *T. catappa* thrives as an ornamental tree, mostly used as shade trees around the homesteads and sometimes in proximity to mango orchards. Under such systems, management strategies for *B. invadens* also must take cognizance of the presence of this important wild host in addition to the cultivated plants.

We reared *B. invadens* from banana (Musaceae), which is known to be a major host of *Bactrocera* species, the most important being *Bactrocera musae* (Tryon), and *B. papayae* (White and Elson-Harris 1992; Clarke et al. 2005). *B. invadens* can infest green banana both in the laboratory and field (S.E., unpublished data). Because this fruit is largely exported

around the world at the mature green stage, it is likely that a strategy exploiting avoidance of *B. invadens* by harvesting and shipping banana at maturity may be inappropriate for evading infestation by this pest.

The Myrtaceae, guava is known to host a variety of fruit fly species worldwide, including several species of *Bactrocera* (White and Elson-Harris 1992, De Meyer et al. 2002, Clarke et al. 2005). We were able to rear *B. invadens* from this plant confirming the status of guava as a major host plant of fruit flies. In West and Central Africa, Vayssières et al. (2005) reported this plant as a major host of *B. invadens.* Similarly in Tanzania, Mwatawala et al. (2006) showed that guava was highly favored by *B. invadens.*

Among the Solanaceae sampled in the current survey, *B. invadens* was recorded from tomato. In other regions of the world, *L. esculentum* is attacked by other *Bactrocera* species such as *B. carambolae* (Clarke et al. 2005), *B. papayae* (Hadwen et al. 1998, Clarke et al. 2005), *B. tryoni* (Froggart) (Balagawi et al. 2005), and *Bactrocera latifrons* (Hendel) (Liquido et al. 1994). However, Mwatawala et al. (2006) did not find infestation on this plant in Tanzania. In our survey, tomato samples from which *B. invadens* was reared were collected from a backyard garden. No flies have yet been detected from fruit collections at commercial scale where pesticides are regularly used for management of fruitworms and tetranychid mites.

B. invadens also was reared from Boraginaceae in *C. myxa* collected from Coast Province. Fruit fly records for *Cordia* species in Africa are scanty; nevertheless, the Boraginaceae are reported to be hosts to some *Ceratitis* species (Quilici and Jeuffrault 2001, De Meyer et al. 2002). No tephritids were reared from fruit of eight *Cordia* species collected in Kenya from 1999 to 2001 (Copeland et al. 2002). Our record from Kenya is the first with regard to infestation by *Bactrocera* species.

Among all the infested plant species, the highest infestation rates were recorded from low elevation areas of the Coast and Rift Valley provinces compared with the higher elevation areas of Eastern Province. In a recent study on mangoes in Kenya, Ekesi et al. (2006) showed a significant inverse relationship between the numbers of *B. invadens* infestation per kilogram of mango fruit and elevation from which fruit were collected, and they concluded that *B. invadens* seemed to be a lowland resident pest. Most fruit flies from the genus *Bactrocera* are considered to be lowland residents. Vargas et al.(1983) demonstrated that fruit infestation by *B. dorsalis* in native and exotic forests on Kauai Island was moderate at middle (579–800 masl) elevation and low at high (>800 masl) elevation. Generally, elevation by itself does not determine fruit fly distribution, but associated factors such as temperature, rainfall, and host plants at such elevation play a significant role (Nishida et al. 1980).

In the laboratory host preference studies, results of the choice experiment showed that mango and papaya were the most preferred host plants of *B. invadens*, followed by banana. These laboratory results agree with results obtained from the field on mango and banana, but they sharply contrast with field survey results for papaya where no infestation was recorded. The reason for lack of infestation of papaya in the field is not very clear given that large quantity of papaya (42.3 kg) was sampled from localities that were heavily infested by *B. invadens.* In Tanzania (neighboring country to Kenya), Mwatawala et al. (2006) did not record any infestation on papaya by *B. invadens* in the Morogoro region. However, in the Zanzibar region of the country, *B. invadens* infestation on papaya has been observed in field samples as low as 2 kg of fruit in a locality with a lower prevalence of *B. invadens* than Nguruman, Kenya (A. I. Ali, unpublished data). This observation largely highlights the need for continuous field survey in different localities in Kenya.

In the no-choice fecundity and fertility studies, highest numbers of eggs were laid on mango, papaya, banana, and cucumber domes compared with the other plant species tested. Pupal recovery from mango, papaya and banana were consistent with results from fecundity and fertility tests, but the level of pupal recovery from cucumber was the lowest among all the fruit tested. In general, fecundity and fertility results for papaya and mango support pupal recovery, but this was not the case with cucumber. The reason for the contrasting results is unclear and warrants further investigation.

In conclusion, within the *B. dorsalis* complex to which *B. invadens* belongs, some insects are specialist host range species, whereas others are general polyphagous species. Our result suggests that *B. invadens* may be an emerging polyphagous species. In general, the host list generated in the current study is unlikely to be exhaustive, and periodic surveys, especially for the *B. invadens* negative plant species, would be necessary. We also acknowledge that the sample size for some of the fruit species collected in the current study may be low, but results presented here may still be useful in making some phytosanitary and pest management decisions.

Host plant preference studies clearly demonstrated that mango and banana are the most preferred host plants of *B. invadens* in Kenya; thus, the pest is likely to jeopardize lucrative export of these crops from this region. Indeed, some countries have already banned the importation of these fruit from Kenya and Uganda due to the threat posed by *B. invadens* (S. Muchemi, personal communication; E. Niyibigira, personal communication). Future studies should now aim at developing effective management strategies that should include baiting techniques, use of biological control agents, sound orchard sanitation, and postharvest treatments for quarantine-sensitive markets.

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