Evidence for Competitive Displacement of *Ceratitis cosyra* by the Invasive Fruit Fly *Bactrocera invadens* (Diptera: Tephritidae) on Mango and Mechanisms Contributing to the Displacement

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ABSTRACT  *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae) invaded Kenya in 2003. Before the arrival of *B. invadens*, the indigenous fruit fly species *Ceratitis cosyra* (Walker) was the predominant fruit fly pest of mango (*Mangifera indica* L.). Within 4 yr of invasion, *B. invadens* has displaced *C. cosyra* and has become the predominant fruit fly pest of mango, constituting 98 and 88% of the total population in traps and mango fruit at Nguruman, respectively. We tested two possible mechanisms responsible for the displacement namely: resource competition by larvae within mango fruit and aggression between adult flies. Under interspecific competition, larval duration in *B. invadens* was significantly shorter (6.2 ± 0.6–7.3 ± 0.3 d) compared with *C. cosyra* (8.0 ± 1.2–9.4 ± 0.4 d). Pupal mass in *C. cosyra* was affected by competition and was significantly reduced (7.4 ± 0.3–9.6 ± 0.6 mg) under competitive interaction compared with the controls (12.1 ± 1.5–12.8 ± 1.1 mg). Interspecific competition also had a significant adverse effect on *C. cosyra* eclosion, with fewer adults emerging under co-infestation compared with the controls. Interference competition through aggressive behavior showed that fewer *C. cosyra* (3.1 ± 0.8) landed on mango dome compared with the controls (14.2 ± 1.5) when adults were mixed with *B. invadens* adults in Plexiglas cages. Similarly the number of times *C. cosyra* was observed ovipositing was significantly lower (0.2 ± 0.2) under competitive interaction compared with the controls (6.1 ± 1.8). Aggressive encounters in the form of lunging/head-buttting and chasing off other species from the mango dome was higher for *B. invadens* compared with *C. cosyra*. Our results suggest that exploitative competition through larval scrambling for resources and interference competition through aggressive behaviors of the invader are important mechanisms contributing to the displacement of *C. cosyra* by *B. invadens* in mango agroecosystems.

KEY WORDS invasive species, *Bactrocera invadens*, native species, *Ceratitis cosyra*, competitive displacement

The fruit fly *Ceratitis cosyra* (Walker) has long been recognized as the most damaging tephritid fruit fly pest of mango (*Mangifera indica* L.) in Africa, including Kenya (Lux et al. 2003a). Few other tephritid fruit flies, such as *Ceratitis fusciventris* (Bezzi), *Ceratitis rosa* (Karsch), *Ceratitis anonae* (Graham), and to a limited extent *Ceratitis capitata* (Weidemann), also coexist with *C. cosyra* on mango in different parts of Africa, but *C. cosyra* has generally been regarded as the primary pest of mango. Losses are because of direct feeding damage and loss of export market opportunities through quarantine restrictions imposed by importing countries to avoid entry and establishment of unwanted fruit flies. For example, because of the threat posed by invasive fruit flies, Mauritius and South Africa have recently banned the importation of mango and avocado from Kenya. Direct damage caused by the fruit flies usually ranged from 20 to 80% (Lux et al. 2003a; S.E. et al., unpublished data). In 2004, a shift in dominance between *C. cosyra* and an invasive species *Bactrocera invadens* Drew, Tsuruta & White was observed in mango orchards at Nguruman in the Rift Valley Province of Kenya, just 1 yr after its detection in the country (Lux et al. 2003b). Ekesi et al. (2006) in assessing the level of damage of the new invasive species on mango speculated that competitive displacement appeared to be in progress.

*B. invadens* is believed to have invaded Africa from the Indian subcontinent and was discovered in Sri Lanka after it was first reported from Africa, where it has become a significant pest of quarantine and economic importance (Mwatawala et al. 2004, Drew et al. 2005). The insect is rapidly spreading across tropical Africa and in addition to Kenya, it is now reported from 28 other African countries, including the Comoros Island (Drew et al. 2005; French 2005; Ekesi and Billah 2006; S.E. et al., unpublished data). Although it has now been reported from >30 plant species, its...
primary host is currently mango (Mwatawala et al. 2004, Drew et al. 2005, Ekesi et al. 2006, Ekesi and Billah 2006, Rwomushana et al. 2008). The introduction of species into a new area can alter successional patterns, mutualistic relationships, community dynamics, ecosystem function, and resource distribution (Mooney and Cleland 2001). Invasive species can also negatively impact resident populations through ecological interactions such as competition leading to displacement. Reitz and Trumble (2002) defined competitive displacement as “the removal of a formerly established species from a habitat through superior use, acquisition or defense of resources by another species.” This can occur through many different facets that are often broadly categorized as exploitative or interference in nature. Competitive displacement is frequently difficult to document under natural conditions, but it is occasionally conspicuous when organisms invade a new continent or islands (Mooney and Drake 1986). In general, opportunities to study the invasion process have usually been missed because such community revolutions are generally very swift and most research efforts are concentrated on controlling the invading pest (Brown et al. 1995). Several studies have however tried to identify attributes of invasive species, determine factors that govern their establishment and subsequent rate of spread (Williamson 1996, Reitz and Trumble 2002; Bruno et al. 2005). In spite of the progress in these areas, predicting the outcome of a particular invasion remains a daunting task (Lodge 1993).

Among fruit flies, competitive displacements of indigenous species by introduced species have also been reported (Duyck et al. 2004, 2006). However, like in other species of insects, they are often too rapid for systematic studies of the casual factors. Since 2001, we had been investigating seasonal population fluctuation of C. cosyra at Nguruman, Rift Valley Province, Kenya. By October 2003, we recorded B. invadens in McPhail traps baited with NuLure at the start of our routine seasonal population studies of C. cosyra in the orchards. We continued to monitor population of both species in this area, and in the present article we document evidence of competitive displacement of the indigenous species C. cosyra by the invader B. invadens on mango agroecosystem and provide some laboratory data on possible mechanisms of the displacement.

Materials and Methods

Field Experiments

Description of Experimental Site. The study was carried out from October/November to January 2000–2007 at Nguruman, Kajiado District in the Rift Valley Province of Kenya. Nguruman is an irrigation scheme located at 01° 54’ 44 S, 36° 17’ 15 E and altitude of 700 m. The mango growing area is supplied, in addition to rains, with furrow irrigation water from three rivers (Oloiborto, Entasopia, and Sampus), which cut across the area and eventually discharge into Lake Natron of Tanzania. This rich and productive area is surrounded by a dry savannah belt and thus could be described as an “ecological island.”

The average maximum and minimum temperature during the experimental period was 21 and 35°C, whereas minimum and maximum relative humidity was 33 and 76%, respectively.

Trapping System and Collection of Insects. A smallholder mango farm (Mololo farm) measuring ~ 0.5 ha was used for the experiments. Interviews with the farmer before monitoring and fruit sampling revealed that no pesticide treatments had previously been employed against fruit flies or any other insect pests in the farm. Early harvesting as a means to evade fruit fly infestation was the only fruit fly management strategy used by the farmer.

McPhail traps were the only traps used to monitor fly densities during the experiments. Traps were baited with liquid protein bait consisting of 300 ml of aqueous solution of 9% NuLure and 3% borax. Five traps were distributed randomly in the orchard at a distance of 30 m between traps. Traps were rotated sequentially after each sampling. The traps were placed on trees at between 1.5 and 2.0 m above ground and were checked once a week. NuLure was renewed every 7 d. At each check, the number of fruit flies captured was taken to the laboratory where they were counted and their identity determined.

Fruit Sampling and Handling of Insects. Ripe and occasionally, unripe mango fruit were sampled from the tree and the ground (as “windfalls”). Fruit were transported to the laboratory in screened 3-liter plastic buckets, weighed, and counted. Fruit from separate collections were placed individually in 2-liter rectangular plastic containers that had ~0.5- and 2.5-cm ellipsoidal holes cut at the bottom (Copeland et al. 2002). The container was then nested inside a 4-liter rectangular plastic container with heat sterilized moistened sand at the bottom for pupation. The holes in the smaller container allowed mature pupariating larvae to fall into the larger container below to pupariate after leaving the mango fruit.

Sample containers were checked every 3-4 d for puparia and adults flies. Puparia were sieved from the sand and held for adult emergence in transparent Plexiglas cages (25 by 25 by 25 cm). Adult flies were fed on a diet consisting of 3 parts sugar and 1 part enzymatic yeast hydrolysate ultrapure (USB Corporation, Cleveland, OH). Water also was provided on pumice granules. After 5 d when adult body color had fully developed, flies were allowed to die within the cages or were killed by freezing. Fruit samples were discarded after ~4 wk. Fruit infestation index was calculated as the ratio of number of adults per kilogram of fruit collected (Cowley et al. (1992)).

Laboratory Studies on Mechanisms of Displacement

Resource Competition between Larvae. Adult female B. invadens and C. cosyra were obtained from a culture maintained on mango (‘Apple’) for six generations. The flies were exposed separately to a mango dome (a whole fruit in which the pulp and seed had...
been removed leaving just the skin) in a 50- by 50- by 50-cm Plexiglas cage to obtain eggs of each species. After 24 h of oviposition, eggs were collected from the dome by using a fine brush and placed on a wet filter paper in petri dishes for hatching. After hatching, 20 or 40 newly emerged larvae of each species of fruit fly were collected from the dishes and gently introduced with a fine brush into each of 60 or 80 holes (20–40 holes per each fruit fly species) perforated with an entomological pin on the surface of a single large ripe mango. Controls with single species treatment (one fruit for each species) had 20 or 40 holes for the larvae. Each hole was ≈ 1 mm in diameter and 1 cm in depth. The experiments therefore consisted of the following five treatments: 1) 40 larvae of *B. invadens* versus 20 larvae of *C. cosyra*, 2) 20 larvae of *B. invadens* versus 40 larvae of *C. cosyra*, 3) 40 larvae of *B. invadens* versus 40 larvae of *C. cosyra*, 4) Control (40 larvae each), and 5) control (20 larvae each). Prospects for interspecific competitions depend both on the frequency of co-infection and the density of larvae within the fruit. Daily oviposition rates of *B. invadens* at peak period of egg laying can vary from 15 to 75 eggs per female per d, whereas *C. cosyra* can lay between 10 and 40 eggs per female per d (Ekesi et al. 2006; S.E. et al., unpublished data). The larval densities and combinations for the treatments described above were therefore chosen on the basis of the level of fecundity of each species and these densities are within the range used by several other authors studying larval development and interspecific competition of Tephritidae (Keiser et al. 1974, Fitt, 1986, Kainacker et al. 1987, Duyck et al. 2006). After larval introduction, each mango was transferred into 2-liter rectangular, plastic containers as described above, and fruit handling and rearing of insects were similar to the procedures described for the field experiment. At pupation, puparia were held individually in 95- by 30-mm vials with a screen glued to one cut end of the cage until adult emergence and species determination. Developmental duration, total pupal harvest, pupal weight, and percentage of eclosion were determined. Each fruit containing both fruit fly species served as a replicate, and there were four replications per treatment and the experiment was repeated twice. The experiments were carried out in a room maintained at 28 ± 1°C, 50 ± 5% RH, and a photoperiod of 12:12 (L:D) h.

**Aggression.** Aggressive interaction was quantified by transferring five pairs of *B. invadens* and five pairs of *C. cosyra* (mixed together) to a 50- by 50- by 50-cm Plexiglas cage containing a mango dome. Flies were 10–14 d old. Several droplets of 2% NuLure were applied on the surface of the dome. The dome served as a source of egg laying and the NuLure as food. In the control cages, each species (five pairs) was held separately without observation. One to three observers collected data for between 10 and 12 h (2 h) and recorded the number of landings and egg laying on the mango dome.

A second independent assay assessed aggressive behavior in the form of lunging, head-butting, or pushing between the species. In this assay, the following treatment combinations were used: 1) *B. invadens* females versus *C. cosyra* females, 2) *B. invadens* males versus *C. cosyra* female, 3) *B. invadens* female versus *C. cosyra* male, 4) *B. invadens* male versus *C. cosyra* female, 5) *B. invadens* females only, 6) *B. invadens* males only, 7) *C. cosyra* females only, and 8) *C. cosyra* males only. In treatments 1–4, five insects of each species was used, whereas in treatments 5–8, 10 insects were used. Mango dome with droplets of NuLure also was provided as in the landing and egg-laying assay, and insect age was also the same. Four observers collected data between 10 and 12 h (2 h) and recorded the number and outcome of aggressive interactions in the form of lunging, head-butting, and pushing between species when on the dome. Departure from the mango by either species was classified as either unprovoked (without apparent cause) or as a result of aggression. Four replications were maintained per each treatment and the experiment was repeated twice. The laboratory experimental conditions were similar to the resource competition experiments.

**Statistical Analysis**

A nonlinear regression based on Gauss–Newton method was applied to field data by using the Proc NLIN procedure. In this analysis, the function y is observed fruit fly response, x is time, and exp is the exponential function; a, b and c are parameters estimated by the nonlinear least squares estimation (Draper and Smith 1981, Kfir 1997). In the resource competition and aggression studies, we protected against type I error by including global comparison by using analysis of variance (ANOVA) for a complete randomized design (Scheiner and Gurevitch 1993) for comparisons within a species among treatments and were appropriate post-ANOVA mean separation was done using Tukey’s honestly significant difference (HSD) test (P = 0.05). Wilcoxon paired test (Siegel and Castellan 1988) was applied to test for interspecific differences within a treatment. Data for larval developmental time, pupal harvest, and pupal weight were transformed to natural logarithms, whereas the proportion of adult emergence data were arcsine transformed before analyses. All analyses were performed using the SAS (SAS Institute 1989) software.

**Results**

**Field Data**

In the 2000–2002 season, the indigenous fruit fly *C. cosyra* was the principal pest detected in monitoring traps and reared from mango fruit apparently because *B. invadens* had not invaded the study area (Fig. 1). During the October 2003 to January 2004 growing season, of 2,916 fruit flies collected from monitoring traps, 72% of the population was *C. cosyra*, 27% was *B. invadens*, and other flies consisting mainly of *C. rosa*, *C. fasciventris*, *C. capitata*, and *Dacus* spp. made up 1% of the population (Fig. 1A). In the same year, fruit infestation data showed that 52% were *C. cosyra*, whereas 18% were *B. invadens* (Fig. 1B). By Novem-
November 2004, *B. invadens* rapidly increased its percentage of the fly population reaching 75% in monitoring traps (Fig. 1A). On mango fruit, the invader had occupied 80% of the population (Fig. 1B). By October 2007 to January 2008, a complete reversal of the 2003 figure was observed, with 98 and 88% of the fly population consisting of *B. invadens* in traps and fruit, respectively (Fig. 1A and B).
In the estimated regression parameters the high values of coefficient of determination indicate a good fit to the data generated. The mean number of C. cosyra per trap per d was high from the beginning but started to decrease rapidly after the invasion of B. invadens (Fig. 1C). A similar case was also observed in fruit. By the 2003–2004 season, the density of C. cosyra on mango fruit was 4.5 flies per kg fruit but decreased to 0.7 flies per kg fruit in the 2007–2008 season. In contrast, the level of infestation by B. invadens has showed an increase from 4.1 flies per kg fruit in the 2004–2005 season to 5.6 flies per kg fruit in the 2007–2008 season (Fig. 1D).

Mechanisms of Displacement

Resource Competition by Larvae. Larval duration was affected by interspecific competition among the different infestation combinations and was shorter under competitive interactions between both species compared with the controls: B. invadens (F = 24.43, df = 4, 25; P = 0.0001), C. cosyra (F = 18.56; df = 4, 35; P = 0.0001) (Fig. 2A). Under co-inestation, larval duration of B. invadens was found to be shorter (6.8–7.3 d) compared with C. cosyra (8.0–9.4 d). Wilcoxon paired test revealed significant differences in larval duration among the two species when 40 larvae of B. invadens was co-infested with 20 larvae of C. cosyra (Z = –3.3706, df = 7, P = 0.0008) and when 40 larvae of B. invadens was co-infested with 40 larvae of C. cosyra (Z = –3.3731, df = 7, P = 0.0007) but no significant difference in the treatment fruit with 20 larvae of B. invadens versus 40 larvae of C. cosyra (Z = –2.7674, df = 7, P = 0.0057).

Pupal weight did not differ significant among co-infested treatments in B. invadens when compared with the controls (F = 8.32; df = 4, 35; P = 0.1215) (Fig. 2B). However, in C. cosyra pupal weight was signifi-
significantly reduced (7.4–9.6 mg) under competitive interaction with *B. invadens* compared with the controls (12.1–12.8 mg) (*F* = 22.56; df = 4, 35; *P* = 0.0001) (Fig. 2B). Wilcoxon test for the following treatments were significant among the two species: 40 larvae of *B. invadens* versus 20 larvae of *C. cosyra* (*Z* = 3.3706, df = 7, *P* = 0.0008), 20 larvae of *B. invadens* versus 40 larvae of *C. cosyra* (*Z* = 3.3861, df = 7, *P* = 0.0008), and 40 larvae of *B. invadens* versus 40 larvae of *C. cosyra* (*Z* = 3.3756, df = 7, *P* = 0.0007).

The total puparia (*B. invadens* and *C. cosyra*) harvested under co-infection was 39.1 ± 2.6, 34.2 ± 1.8, and 42.2 ± 3.2 in the respective treatments: 40 *B. invadens* larvae versus 20 larvae of *C. cosyra*, 40 *B. invadens* larvae versus 40 *C. cosyra* larvae, and 40 *B. invadens* larvae versus 40 *C. cosyra* larvae. The proportion of initial larvae of *B. invadens* that emerged as adults was not significantly different across treatments (*F* = 1.36; df = 4, 35; *P* = 0.2876), but there was a significant difference in adult emergence across treatment for *C. cosyra* (*F* = 12.78; df = 4, 35; *P* = 0.0001). When mango fruit was infested at the level of 40 *B. invadens* larvae versus 20 *C. cosyra*, the proportion of adult *C. cosyra* that emerged was 0.21 compared with 0.79 *B. invadens* adults (*Z* = 3.4164, df = 7, *P* = 0.0006) (Fig. 2C). Infestation of 40 *B. invadens* larvae versus 40 *C. cosyra* larvae resulted in 0.23 *C. cosyra* compared with 0.77 *B. invadens* adults (Fig. 2C) (*Z* = 3.3731, df = 7, *P* = 0.0007). Competitive interaction therefore had a significant adverse effect on *C. cosyra* survivorship.

Aggression. Under interspecific competition, fewer *C. cosyra* landed on the mango dome compared with the controls (*F* = 11.13; df = 1, 14, *P* = 0.0001) (Fig. 3A). Between species, more *B. invadens* were recorded on the dome compared with *C. cosyra* (*Z* = 3.8706, df = 7, *P* = 0.0008). Similarly, the number of times *C. cosyra* was observed ovipositing was significantly lower under competitive interaction compared

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**Fig. 3.** Behavioral responses (mean ± SE) of *B. invadens* and *C. cosyra* under competitive interaction in the laboratory: (A) Number of landings. (B) Number of times observed laying eggs. (C) Number of aggressions. Bi, *B. invadens*; Cc, *C. Cosyra*; ♀♂, females; ♂♂, males.
with the controls \((F = 21.30; \text{df} = 1, 14; P = 0.0001)\) (Fig. 3B). Aggressive encounters recorded as the number of times each insect was observed lunging and chasing off the other species from the mango dome was higher for \(B. \text{ invadens}\) compared with \(C. \text{ cosyra}\) (Fig. 3C). In general, both females and males of \(B. \text{ invadens}\) were highly aggressive to either sex of \(C. \text{ cosyra}\) in the various encounters and rarely was the reverse observed: For example, \(B. \text{ invadens}\) male versus \(C. \text{ cosyra}\) male \((Z = 3.3933, \text{df} = 7, P = 0.0007)\) and \(B. \text{ invadens}\) female versus \(C. \text{ cosyra}\) male \((Z = 3.3400, \text{df} = 7, P = 0.0007)\) (Fig. 3C).

**Discussion**

Increased levels of travel and trade have led to a heightened spread of invasive species, a leading anthropogenic disturbance with far-reaching implications (Naeem et al. 1995). About one fifth of invasive species may cause extensive economic and ecological damage with unpredictable negative effects on native populations that are second only to habitat destruction (D’Antonio and Vitousek 1992; Jenkins 1996). The results of the current study clearly indicate rapid displacement of \(C. \text{ cosyra}\) by \(B. \text{ invadens}\) at Nguruman, Kenya, 4 yr after its detection in the African continent. Several \(Bactrocera\) species are notorious and well-documented invaders and rank high on quarantine lists worldwide (Clarke et al. 2005). In 2003 when \(B. \text{ invadens}\) was introduced, it caused 18% of fruit infestation on mangoes at Nguruman. However, 4 yr later, the invader has become the predominant species, constituting > 80% of fruit fly population infesting mango fruit.

Although fruit flies commonly invade new zones (Fletcher 1986), relatively few cases of competitive displacement are documented. Perhaps, the most notable examples include displacement of \(C. \text{ capitata}\) by the Queensland fruit fly, \(Bactrocera\) \(tryoni\) (Froggatt), around the Sydney area in Australia (Debach 1966) and displacement of the same species by \(Bactrocera\) \(dorsalis\) (Hendel) from the coastal areas in Hawaii in 1945 (Duyck and Quilici 2002). In the latter case, the displacement is to some extent mediated by host fruit in that \(C. \text{ capitata}\) persists in lowlands on coffee (\(Cofe\text{ea arabica}\) L.), their presumed ancestral host in Africa to which it is better adapted (Vargas et al. 1995). In the Mascarene Islands, the indigenous \(Ceratitis\) \(catoirii\) Guerin-Menelle seems to have been displaced by \(C. \text{ capitata}\) and \(C. \text{ rosa}\) in La Réunion occurring in small numbers on the east and south coast of the island (Duyck et al. 2004, 2006), whereas in Mauritius it seems to have disappeared (White et al. 2000). Presumably, the invasion of \(Bactrocera\) \(zonata\) (Saunders) in Mauritius in 1987 and La Réunion in 1991 may have compounded the displacement of the indigenous species (Duyck et al. 2004, 2006). In our study, the speed with which \(B. \text{ invadens}\) displaced \(C. \text{ cosyra}\) and its efficient utilization of mango fruit suggests that there has been a prolonged adaptation by \(B. \text{ invadens}\) to using mango as host fruit. In its aboriginal home of Sri Lanka, the pest has been reared from mango at low elevation regions of the country but the magnitude of damage to mango is not well known (M.K.B. et al., unpublished data).

The mechanisms that trigger competitive displacement are usually very difficult to establish and may be specific to each pair of competing species. In the conventional niche theory, the primary determinant of competition is overlap in resources (or niche overlap). \(B. \text{ invadens}\) and \(C. \text{ cosyra}\) are ecological homologs that, in spite of substantial difference in the range of host plants and the level of polyphagy, largely compete for the same ecological niche—mango fruit. Results from larval competition for food resources revealed that co-infestation of mango by larvae of both species adversely affected \(C. \text{ cosyra}\). Most notable is that few adults of \(C. \text{ cosyra}\) eclosed when \(B. \text{ invadens}\) larvae infest mango at a higher density (40 larvae of \(B. \text{ invadens}\) and 20 larvae of \(C. \text{ cosyra}\)). In growing populations, larval duration may be the most important parameter, but it may be less critical compared with pupal mass in stable populations (Yoshimura and Clark 1991), and we did observe that pupal weight was adversely affected in \(C. \text{ cosyra}\) under competitive interaction where it was significantly lower compared with the control. One significant and interesting observation was that under competitive interaction, the duration of larval development was shortened in both species. This may be explained in part by the fact that under interspecific interaction, individuals of each species exert a higher per capita competitive intensity upon each other by taking up more resources to meet their higher metabolic needs resulting in faster development and shorter duration. Another explanation could be that the larvae were responding to competitive stress by developing sooner because of less food availability reaching the next developmental stage in small sizes. This was clearly observed in \(C. \text{ cosyra}\) with lower pupal weights when exposed to competition with \(B. \text{ invadens}\).

Overall, our laboratory study demonstrates that \(B. \text{ invadens}\) was a superior competitor to \(C. \text{ cosyra}\). Indeed, the success of many invasive species is believed to result primarily from their superior competitive abilities relative to native species (Williamson 1996, Bruno et al. 2005). In a series of tephritid invasions on La Réunion, Duyck et al. (2006) demonstrated that the invasive species \(B. \text{ zonata}\), tended to have higher ranks than the previously established invasive \((C. \text{ rosa}\) and \(C. \text{ capitata}\)) and native \((C. \text{ catoirii}\)) species in the hierarchy. In their study, \(B. \text{ zonata}\), which was the most recently established species was dominant in both forms of competition (scramble and interference), which the authors attributed to its large body size and shorter developmental period. In a similar laboratory scrambled competition experiment, \(B. \text{ dorsalis}\) was observed to out compete \(C. \text{ capitata}\) and inhibit its development (Keiser et al. 1974). Although not many studies have addressed competitive interaction between tephritids of different genera, our results agree with those of Duyck et al. (2006) and Keiser et al. (1974) that \(Bactrocera\) species tend to be competitively superior to \(Ceratitis\) species.
The precise interactions that take place inside the fruit is not obvious and this was not quantified. All insects were infested on the same day and initial age differences among the cohort cannot be responsible for the pronounced asymmetry. However, asymmetric competition may also arise within a cohort of equally aged individuals of the different species if there is variation in growth rate so that individuals become larger than the others (Begon 1984). Indeed, the largest individuals may be fitter than the rest and, because of large size, gain asymmetric advantage in competition. Larval development of *B. invadens* was shorter compared with *C. cosyra*, both in the controls and under competitive interaction. Duyck et al. (2006) noted that shorter larval developmental time of *B. zonata* compared with *C. catoirii*, *C. capitata*, and *C. rosa* conferred superior competitive ability on *B. zonata* than the Ceratitis species. Because *B. invadens* develop faster, the cohorts in the fruit were probably larger and older than *C. cosyra* even when they were infested on the same day. When two groups of differently sized and aged juvenile insects are reared together, the smaller and younger cohort suffers from increased mortality and reduced size (Averill and Prokopy 1987, Edgerly and Livedahl 1992, Cameron et al. 2007). Another crucial factor in the case of fruit flies may be resource degradation arising from variation in nutritional quality inside the mango fruit and it is likely that more of the lower quality resources are consumed by the inferior competitor.

Interference competition through behavioral aggression of *B. invadens* to *C. cosyra* may also have given the invader a competitive advantage over the resident. In our experiments, both male and female *B. invadens* responded aggressively to the presence of *C. cosyra* by lunging at the opponent interrupting the process of landing on a protein food source or ovipositing on the mango dome, and the level of female aggression in *B. invadens* was even more pronounced than in males. In female Bactrocera species, host marking pheromones are apparently absent (Fletcher and Prokopy 1991), as a result, female aggression especially in defense of oviposition sites is frequently intense even among conspecifics. Shelly (1999) reported that females of *B. dorsalis* defended oviposition sites on mango against conspecific females by lunging at opponents and chasing them off. If such aggression can occur among conspecifics, then it is perhaps not surprising that both sexes of *B. invadens* launched several aggressive behaviors against *C. cosyra* in our study. According to Shelly (1999), territoriality in female Bactrocera is presumably related to effect on larval competition. By defending oviposition sites (even temporarily), Shelly argued that females may provide their larvae with a “head start” in growth over related larvae and hence a competitive advantage for host fruit resources. Ostensibly, a similar thing occurs in *B. invadens* in defense of its offspring against other species of fruit flies, but this warrants further studies. In few a cases, we did observe that female *B. invadens* even interrupted egg laying to drive off *C. cosyra* from the mango dome. In his study on *B. tryoni*, Pritchard (1969) noted that nearly 20% of females observed ovipositing in the wild interrupted egg laying to drive off conspecific females through threat displays that occasionally escalated to head-buttting and pushing. Male *B. invadens* were also highly aggressive toward both sexes of *C. cosyra*. In Bactrocera species, male flies have been reported to respond aggressively in defense of sites containing resources vital to female flies, thus increasing their mating opportunities (Fletcher 1987).

Biological invasions are increasingly being viewed as one of the components of global change and several ecological factors interact that favor introduced species (Vitousek et al. 1996, Shea and Chesson 2002). In addition to the evidence provided above, there are possibly several other reasons why *B. invadens* has been able to adapt so quickly in the introduced range and to displace *C. cosyra*, and this warrants appraisal. First, the high reproductive capability of *B. invadens* allows it to achieve enormous population size. When one arthropod has greater realized fecundity than a competitor, that competitor will be displaced (Reitz and Trumble 2002), and this mechanism is especially enhanced when more females are recruited into the population. A female *B. invadens* has a fecundity rate of 1056.8 eggs as against 356 eggs in *C. cosyra* (Ekesi et al. 2006; S.E. et al., unpublished data). Over time, the numerical advantage of *B. invadens* may reduce the probability of *C. cosyra* individuals having access to available resources. Differences in reproductive capability alone have been attributed to rapid displacement in many insects (Brown et al. 1995, Reitz and Trumble 2002). Second, *B. invadens* is a very mobile insect and arriving at a resource first through their high mobility and dispersive power (S.E., unpublished data) probably confers competitive superiority over *C. cosyra*. In fruit flies and other insect species, early arrival can result either from early seasonal emergence or rapid colonization (Denno et al. 1995; Vargas et al. 1995). *B. invadens* has an earlier seasonal phenology than *C. cosyra* based on trap catches in McPhail traps baited with NuLure (S.E. et al., unpublished data). When coupled with the rapid population growth and/or the preemption of resources, this factor can dictate competitive outcome in fruit flies (Fitt 1984). Third, like many invading organisms in novel environments, *B. invadens* is released from the harmful effects of their coevolved natural enemies. For example, there is evidence that host specific parasitoids may influence competitive outcomes between fruit fly species (Clarke et al. 2005). So far, no parasitoids have been observed attacking *B. invadens* in Kenya from host fruit samples collected from March 2003 to date (Rwomushana et al. 2008; S.E. et al., unpublished data). Because the parasitoids that beset *B. invadens* in their aboriginal home are absent in Kenya, their population may have attained higher levels than they do in their native home. These factors—rapid growth rate, male and female territoriality/aggressive interaction, greater reproductive po-
tential, early arrival and lack of natural enemies—probably combine with one another allowing competitive displacement of *C. cosyra* at Nguruman.

*C. cosyra* however has not been completely displaced in mango orchards at Nguruman, and the reason for this also warrants assessment. There are probably some advantages that the insect has that allows for some level of coexistence with *B. invadens*. One advantage may be its more specialized host-searching abilities on mangoes having been linked more closely to this host plant over a long period in Africa. Second, *C. cosyra* has been recorded from just nine plants species in Kenya (Lux et al. 2003a, Copeland et al. 2006) compared with the increasing host range of *B. invadens* that currently stands at >14 in Kenya (Ebenhoh and Billah 2006, Rwomushana et al. 2008). It is therefore likely that *B. invadens* can switch to other suitable hosts when there is a bottleneck in carrying capacity, providing some niche on mango for *C. cosyra* to survive. For example, Nguruman is a lowland ecology with an altitude of 700 m above sea level. Generally, most *Bactrocera* species, including *B. invadens* are believed to be lowland residents (Vargas et al. 1983, Wong et al. 1985, Harris et al. 1986; Ekei et al. 2006), enabling *B. invadens* to displace *C. cosyra* in lowland ecologies. At the higher elevation areas of Kenya, such as Embu in the Eastern Province, *C. cosyra* remains the dominant species, probably because of poor tolerance of *B. invadens* to low temperatures (Ekei et al. 2006; I. Rwomushana, unpublished data). It is therefore probable that *B. invadens* may be restricting populations of *C. cosyra* to the highlands. Indeed such phenomena have been reported from Hawaii, where *B. dorsalis* largely displaced *C. capitata* from the low-elevation coastal zones and restricted *C. capitata* populations to cooler climates at high altitudes where *B. dorsalis* does not occur (Vargas et al. 1995).

The results of this study have shown that competitive displacement of *C. cosyra* by *B. invadens* has occurred at Nguruman, a low-elevation region of Kenya. Generally, the species composition of a habitat is dynamic with species appearing and going extinct over time (Southwood 1977), making competitive displacement difficult to prove. Changes are often very rapid occurring unnoticed or if noticed, it is after the changes have occurred making it difficult to examine the causes. Several factors may be involved in the displacement of *C. cosyra* by *B. invadens* on mango. But our results suggest that the most probable mechanisms of displacement include exploitative competition through larval scrambling for resources within mango fruit and interference competition through aggressive behaviors of the invader. Whatever the mechanisms involved, these findings demonstrate that the role of *C. cosyra* as the predominant pest of mango at Nguruman has been replaced by the new invasive mango fruit fly species, *B. invadens*. However, because of the systems variability (Ebenhoh 1994), it is unlikely that the insect will be completely replaced by the invader and *C. cosyra* may remain a permanent part of the mango agroecosystem.

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