

Mechanisms contributing to the competitive success of the invasive fruit fly *Bactrocera invadens* over the indigenous mango fruit fly, *Ceratitis cosyra*: the role of temperature and resource pre-emption

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Abstract

We investigated the influence of temperature and infestation sequence on interspecific competition between two fruit flies: an invasive (*Bactrocera invadens* Drew, Tsuruta & White, (B) and a native (*Ceratitis cosyra* Walker, C) (both Diptera: Tephritidae) species. Mango fruits [*Mangifera indica* L. (Anacardiaceae)] were co-infested with larvae at different constant temperatures (15, 20, 25, and 30 °C) and relative humidity of 50 ± 8%, using different infestation sequences at each temperature (BC together; BC/CB 1, 2, and 3 days apart). There were significant effects of competition in most experimental treatments, resulting in reduced larval survival, pupal mass, and adult emergence for both species. At most of the infestation/temperature combinations, *C. cosyra* was clearly the inferior competitor. The only exception was at 20 °C when the outcome depended on the sequence of infestation: no *C. cosyra* survived when the sequence was BC, but more *C. cosyra* than *B. invadens* survived when it was CB. At 15 °C, all *C. cosyra* larvae died, while the development of *B. invadens* was prolonged and adult emergence reduced. We conclude that resource pre-emption and fluctuations in temperature in mango agroecosystems help to explain observed shifts in dominance between *B. invadens* and *C. cosyra* on mango in many parts of Africa. The small window of competitive superiority for *C. cosyra* at 20 °C and CB infestation sequence, together with other factors such as fecundity and alternative hosts, may allow for co-existence in some environments.

Introduction

Globalization of trade in fresh fruits and vegetables and increased travel have intensified the risk of inadvertent spread of alien invasive species, with far-reaching implications (Sandlund et al., 1999). Invasive species are notorious for altering successional patterns, mutualistic relationships, community dynamics, ecosystem function, and resource distribution (Mooney & Cleland, 2001), and invasive species that cause extinction of native species will ultimately reduce local and global species diversity (Vitousek et al., 1996; Collins et al., 2002). Among arthropods,

alien invasives have also been reported to negatively impact native species through ecological interactions such as exploitative and interference competition (Begon et al., 1986; Denno et al., 1995; Duyck et al., 2006). In exploitative competition, individuals of one species acquire resources to a greater extent than individuals of another species, whereas in interference competition, members of one species limit or deny individuals of another species access to resources (Reitz & Trumble, 2002).

Among the Tephritidae (Diptera), dactine fruit flies are well documented invaders and rank high on quarantine lists worldwide (Clarke et al., 2005). Through the fruit trade, many of these fruit flies have been introduced into various countries with the resultant direct and indirect cost of their introduction running into hundreds of millions of dollars (Duyck et al., 2004; Follett & Neven, 2006). In

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Africa, one such invader was detected in 2003 at the Kenyan coast (Lux et al., 2003a) and later described as *Bactrocera invadens* Drew, Tsuruta & White (Drew et al., 2005). The pest is probably native to Sri Lanka (Drew et al., 2008) and has rapidly expanded its geographical range, now reported from 24 African countries including the Comoros Island (Drew et al., 2005; French, 2005; Vayssières et al., 2005; Ekesi et al., 2006; Mwatawala et al., 2006a; Francois-Xavier et al., 2008; Rwomushana et al., 2008a,b). Before the arrival of *B. invadens*, the mango fruit fly, *Ceratitis cosyra* (Walker) (Diptera: Tephritidae), indigenous to Africa (White & Elson-Harris, 1992; Mukiyama & Muraya, 1994; Lux et al., 2003b), was the most important pest of mango, *Mangifera indica* L. (Anacardiaceae), in Kenya. In 2004, however, a shift in dominance between *C. cosyra* and *B. invadens* was observed in mango orchards at Nguruman, Rift Valley Province of Kenya just 1 year after detection of the invasive species. Moreover, *B. invadens* has a wider host range (Mwatawala et al., 2006a; Rwomushana et al., 2008a,b) than *C. cosyra* (Copeland et al., 2006), although both insects infest *Annona* spec., guava (*Psidium guajava* L.), *Citrus* spec., and the marula plum [*Sclerocarya birrea* (A. Rich.) Hochst].

In assessing the level of damage of the new invasive species on mango, Ekesi et al. (2006) speculated that competitive displacement appeared to be in progress. Similar overturns in abundance have been noted in Tanzania and Benin between these two species (Vayssières et al., 2005; Mwatawala et al., 2006b). The mechanisms that trigger competitive displacement are usually very difficult to establish and may be specific to each pair of competing species. *Bactrocera invadens* and *C. cosyra* are ecological homologues that compete for the same ecological niche. In conventional niche theory, the primary determinant of competition is overlap in resources (or niche overlap), presenting opportunities for competitive responses (the ability of a species to withstand competition exerted by other species) and competitive effects (the negative effects of a species on other species) (Goldberg & Barton, 1992).

Factors such as superior competitive abilities, resource pre-emption, release from natural enemies, and abiotic factors including temperature and anthropogenic disturbances, may permit an invasive species to become dominant. Understanding the interspecific interactions between an invader and a resident should lead to better predictive ability and a more effective way of managing the invasive species (Williamson, 1996). The specific effect of temperature on competition between *B. invadens* and *C. cosyra* has not been evaluated before. Therefore, our study was designed to assess whether competitive superiority through resource exploitation at different temperatures could represent one mechanism involved in the docu-

mented dominance of *B. invadens* over *C. cosyra* in the field. We report results in which manipulative experiments were conducted at four constant temperatures and different infestation sequences to detect asymmetrical competition between the larvae of the invasive species *B. invadens* and the native species *C. cosyra* on mango fruits.

Materials and methods

Insect material

The initial stock culture of *B. invadens* originated from a natural population of infested mango fruits collected at a local market in Nairobi, Kenya, in 2003 and the larvae were subsequently reared on a yeast-carrot-based artificial diet in the laboratory for about 54 generations following the methodology described in Ekesi et al. (2007). Prior to being used in the experiments for interspecific competition studies, the insects were transferred back to mango (apple variety) and reared for a minimum of five generations. Adult female *C. cosyra* were obtained from a laboratory culture which had been maintained on mango (apple variety) for 108 generations following the methodology of Lux et al. (2005). Both fruit fly cultures are rejuvenated every 6–12 months by incorporation of wild flies to ensure that the cultures are genetically similar to wild populations. The cultures were maintained in rearing rooms at 28 ± 1 °C, $50 \pm 8\%$ r.h., and L12: D12 photoperiod.

Egg collection

Eggs of *B. invadens* and *C. cosyra* were collected from the stock colonies by offering ripe mango dome (mango fruit skin that has the seed and pulp scooped out) to the mature female flies. Each dome was pierced with an entomological pin (38 mm long, 0.3 mm diameter) to facilitate oviposition. The domes were placed over a 9 cm diameter Petri dish lined with moistened filter paper and placed in a $30 \times 30 \times 30$ cm Perspex cage having adult flies of either species of fruit fly. Eggs were collected from the underside of the domes within 6 h of oviposition using a moistened fine camel's hair brush, placed on a wet filter paper in a Petri dish, and held at ambient temperature to allow larvae to hatch.

Larval competition experiments

The opportunity for interspecific competition largely depends on the frequency of co-infestations and density of larvae within fruits (Barker, 1983). The larval competition experiments were, therefore, conducted in the laboratory through pairwise combinations of newly hatched *B. invadens* and *C. cosyra* larvae. Shortly after eclosion, 20 newly emerged larvae of each species of fruit fly were collected from the dish and gently introduced with a moistened fine

camel's hair brush into each of 20 holes for control fruit, or 40 holes (20 holes per fruit fly species) for co-infested fruit perforated with an entomological pin on the surface of a single large ripe mango (220–250 g) with the aid of a binocular microscope. This density of larval infestation has previously been used in interspecific interaction studies of Tephritidae (Keiser et al., 1974; Fitt, 1986; Krainacker et al., 1987; Qureshi et al., 1987; Duyck et al., 2006) and is comparable to observed larval densities from field collected mango samples (I. Rwomushana, unpubl.). Each hole was ca. 1 mm in diameter and 1 cm in depth and randomly distributed on the fruit surface. Infestation procedure was either done on the same day or in asynchrony of 1-, 2-, or 3-day intervals. The treatments were as follows: (1) fruit infested same day with larvae of both species, (2) fruit infested with *B. invadens* larvae 1 day before introduction of *C. cosyra* larvae, (3) fruit infested with *B. invadens* 2 days before *C. cosyra* larvae, (4) fruit infested with *B. invadens* larvae 3 days before *C. cosyra* larvae, (5) fruit infested with *C. cosyra* 1 day before introduction of *B. invadens*, (6) fruit infested with *C. cosyra* larvae 2 days before *B. invadens* larvae, (7) fruit infested with *C. cosyra* larvae 3 days before *B. invadens* larvae, and (8) controls (larvae of one species only, i.e., no co-infestation).

After larval introduction, the holes were sealed with tape to prevent larvae from boring out of the fruit through the infestation holes. Each mango was then transferred into a 3-l rectangular, plastic container (20 × 12.5 × 15 cm) (Kenpoly, Nairobi, Kenya) containing a moistened sand layer (3–5 mm deep). The sand held the exudate dripping from the rotting fruits and served as pupation medium for the mature larvae that left the fruits (Woods et al., 2005). Fruit samples were then transferred to thermostatically-controlled environmental chambers (MLR-153; Sanyo, Osaka, Japan) set at constant temperature of 15, 20, 25, or 30 °C (± 1 °C) and $50 \pm 8\%$ r.h. From the 6th day after fruit infestation, the sand was sifted daily to recover puparia. Each puparium from the controls and co-infested fruits was weighed and then held individually at ambient temperature in a transparent 30-ml glass vial plugged with cotton wool. By holding each puparium individually it was possible to relate the pupal mass of each vial to the identity of the fly at eclosion. The vials were observed daily for a period of 30 days after pupariation and the number of emerged adults was recorded. The range of variation of pupal development of both species (i.e., the lapse of time from the first to the last adult emergence) is known to vary between 1–10 days depending on the temperature (Ekesi et al., 2006; Rwomushana et al., 2008a,b; S Ekesi, unpubl.; I Rwomushana, unpubl.) and as diapause has not been reported for these species, puparia failing to eclose at the end of 30 days were considered unviable. Each co-infested

fruit and the control served as a replicate and there were five replications per treatment.

Data analysis

All parameters recorded (duration of larval development in days, pupal mass, and adult emergence) at each temperature were $\ln(x + 1)$ -transformed to reduce heteroscedasticity and then subjected to one-factor analysis of variance (ANOVA). Student–Newman–Keuls test ($\alpha = 0.05$) was used to identify significant main effects for each temperature. At each temperature, a two-sample t-test was used to determine the effect of interspecific competition on the life history parameters between the two fruit species. A factorial analysis was applied on the data to assess the interaction between temperature, infestation sequence and species on larval development, pupal weight, and number of adults that emerged from the treatments. All statistical tests were performed using SAS software (SAS Institute, 2001).

Results

Larval development

Interspecific competition had significant direct effects on larval development rates, pupal weight, and survival (number of adults produced; Table 1). There were also some significant F-values for two-way interactions (especially for temperature and species), and for three-way interactions on number of adults.

Table 2 shows the effect of temperature and infestation sequence on mean larval development rates. *Bactrocera invadens* developed faster than *C. cosyra* in all the control treatments in which there was no interspecific competition, although the differences were only significant at 25 °C. In 11 out of 17 pairwise comparisons when interspecific competition took place and both species produced pupae, *C. cosyra* developed faster than *B. invadens*, and vice versa in four of them, but in no case were the differences significant. Infestation sequence effects were significant for *C. cosyra* in three out of three experimental temperatures (20, 25, and 30 °C) but only at 20 °C for *B. invadens*.

Table 3 shows effect of temperature and infestation sequence on pupal weights. *Bactrocera invadens* had heavier pupae than *C. cosyra* in all the control treatments, although the differences were only significant at 15 and 25 °C. *Bactrocera invadens* pupae were also heavier in 15 of the 17 possible pairwise comparisons, although only significantly so in two of them. At 20 °C, the pupal weights were identical when *C. cosyra* was introduced 3 days ahead of *B. invadens*, and the former were non-significantly heavier than the latter at 30 °C when

Table 1 Analysis of variance for larval development, pupal mass, and number of adults resulting from interspecific competition between *Bactrocera invadens* and *Ceratitidis cosyra*

Parameter	Factor	F	d.f.	P
Larva development	Temperature	72.85	3,172	<0.0001
	Infestation sequence	1.40	7,172	0.0027
	Species	2.30	1,172	0.0131
	Temperature*infestation sequence	1.81	21,172	0.0227
	Temperature*species	7.15	3,172	0.0001
	Infestation sequence*species	1.47	7,172	0.1801
	Temperature*infestation sequence*species	1.14	21,172	0.3374
Pupal weight	Temperature	17.75	3,172	<0.0001
	Infestation sequence	4.53	7,172	0.0001
	Species	159.45	1,172	<0.0001
	Temperature*infestation sequence	3.19	21,172	<0.0001
	Temperature*species	2.28	3,172	0.0812
	Infestation sequence*species	1.88	7,172	0.0760
	Temperature*infestation sequence*species	0.69	21,172	0.6958
No. of adults	Temperature	51.50	3,172	<0.0001
	Infestation sequence	15.00	7,172	<0.0001
	Species	196.25	1,172	<0.0001
	Temperature*infestation sequence	4.81	21,172	<0.0001
	Temperature*species	41.47	3,172	<0.0001
	Infestation sequence*species	7.32	7,172	<0.0001
	Temperature*infestation sequence*species	2.78	21,172	0.0065

introduced 2 days earlier. Infestation sequence effects were significant for *C. cosyra* in two out of three experimental temperatures (25 and 30 °C) but at all four temperatures for *B. invadens*.

Table 4 shows effect of temperature and infestation sequence on survival. *Bactrocera invadens* survived better than *C. cosyra* in three out of four of the control treatments, the exception being at 20 °C. The difference was only significant at 30 °C. At 15 °C no *C. cosyra* survived at all, even in the controls. *Bactrocera invadens* had superior survival than *C. cosyra* in all but three of the 28 possible pairwise comparisons. The three exceptions occurred when *C. cosyra* was introduced first at 20 °C. No *C. cosyra* survived at this temperature when *B. invadens* was introduced first. Differences in survival were significant in all but one (25 °C with *C. cosyra* introduced 1 day earlier) of the 18 pairwise comparisons for which F-values could be determined.

Discussion

Interspecific competition has long been considered as one of the primary factors that influence community assembly (Elton, 1946; Schoener, 1974; Chase & Leibold, 2003) and because the mechanisms governing community assembly and biotic invasions are conceptually similar (Tilman, 2004), it is reasonable to test whether superior competitive

ability is the primary mechanism by which some invasive species become dominant and, in turn, reduce the abundance and species richness of native species (Holway, 1999; Bruno et al., 2005). In our study, interspecific competition between *B. invadens* and *C. cosyra* on mango at different temperatures was found to reduce larval survival, pupal mass, and adult emergence, and at most of the insect/temperature combinations, *C. cosyra* was clearly the inferior competitor. Differential temperature tolerance by insects is one of the critical factors that mediate interspecific competition (Denno et al., 1995) and in our study temperature indeed played a significant role in the outcome of the competitive interaction between the two species. *Ceratitidis cosyra* was more affected by temperature change under interspecific competition: it disappeared (larvae could not develop to the pupal stage) at all infestation sequences at 15 °C as well as when *B. invadens* was given a head start at 20 °C. However, it co-existed with *B. invadens* at 25 and 30 °C and particularly out-competed the invasive species in terms of adult emergence when it was given a 1–3-day head start at 20 °C. It is recognized that species tend to co-exist at intermediate temperatures and competitive extinction or dominance occurs at extreme temperatures (Park, 1954; Wilson et al., 1984; Phillips et al., 1995; Davis et al., 1998a,b). The upper temperature limit for the current study did not exceed 30 °C and as the fitness of both insects was negatively

Table 2 Effect of interspecific competition between *Bactrocera invadens* (B) and *Ceratitis cosyra* (C) at different temperatures on the duration of larval development of the two species

Temperature (°C)	Infestation sequence	Larva development time (days)			
		<i>B. invadens</i>	<i>C. cosyra</i>	t	P
15	Infested same day	24.8 ± 1.8	nd	–	–
	B 1 day before C	29.4 ± 1.4	nd	–	–
	B 2 days before C	27.6 ± 1.7	nd	–	–
	B 3 days before C	27.2 ± 0.8	nd	–	–
	C 1 day before B	27.3 ± 0.4	nd	–	–
	C 2 days before B	26.8 ± 0.9	nd	–	–
	C 3 days before B	27.2 ± 1.8	nd	–	–
	Controls	27.6 ± 2.3	30.8 ± 2.1	2.28	0.0625
		F _{7,32} = 0.96	–		
		P = 0.47	–		
20	Infested same day	17.1 ± 0.5ab	21.7 ± 0.6a	1.03	0.0984
	B 1 day before C	16.8 ± 0.9ab	nd	–	–
	B 2 days before C	14.6 ± 1.1b	nd	–	–
	B 3 days before C	15.0 ± 1.2ab	nd	–	–
	C 1 day before B	14.4 ± 0.7b	11.2 ± 0.9b	1.93	0.0531
	C 2 days before B	15.1 ± 1.0ab	11.8 ± 0.5b	2.33	0.0528
	C 3 days before B	16.8 ± 0.3ab	13.1 ± 0.5b	1.66	0.1356
	Controls	18.4 ± 0.3a	20.3 ± 0.4a	2.56	0.0936
		F _{7,32} = 3.43	F _{4,20} = 1.07		
		P = 0.0078	P = 0.0394		
25	Infested same day	9.2 ± 0.9	10.9 ± 0.8a	0.96	0.3637
	B 1 day before C	9.2 ± 0.6	8.1 ± 0.1b	2.02	0.1141
	B 2 days before C	9.5 ± 1.3	8.8 ± 0.5b	0.68	0.5221
	B 3 days before C	9.2 ± 1.1	8.9 ± 0.1b	0.67	0.5371
	C 1 day before B	9.9 ± 0.3	8.1 ± 0.4b	1.83	0.1172
	C 2 days before B	9.8 ± 0.5	8.0 ± 0.4b	1.35	0.2243
	C 3 days before B	9.3 ± 0.4	8.4 ± 0.5b	0.62	0.5703
	Controls	9.2 ± 0.2	11.3 ± 0.1a	5.31	0.0007
		F _{7,32} = 0.90	F _{7,32} = 5.92		
		P = 0.52	P = 0.0024		
30	Infested same day	7.1 ± 0.9	6.6 ± 0.3b	0.49	0.6383
	B 1 day before C	6.3 ± 0.8	6.8 ± 0.4b	2.19	0.0713
	B 2 days before C	8.5 ± 0.7	6.9 ± 0.2b	2.92	0.0781
	B 3 days before C	8.5 ± 1.5	nd	–	–
	C 1 day before B	7.0 ± 0.1	7.4 ± 0.3b	0.54	0.6125
	C 2 days before B	6.5 ± 0.4	7.3 ± 0.5b	0.80	0.9372
	C 3 days before B	8.4 ± 0.1	6.8 ± 0.5b	1.88	0.1335
	Controls	6.7 ± 0.6	10.7 ± 0.4a	2.21	0.0583
		F _{7,32} = 0.66	F _{6,28} = 1.31		
		P = 0.70	P = 0.0312		

Means (± SE) within a column and within one temperature followed by different letters are significantly different (Student–Newman–Keuls test: P<0.05).

nd = not determined.

correlated with temperature and perhaps negatively impacted *C. cosyra* more than *B. invadens*, the relative abundance of *C. cosyra* would be expected to decrease with increasing levels of the unfavourable temperature extreme, to a point where its reduced fitness would result in

competitive displacement by *B. invadens* especially at temperatures below 15 °C and above 30 °C.

Interspecific competition may also be more likely to affect species responses to environmental change in communities characterized by diffuse competition, i.e.,

Table 3 Mean weight of puparium following interspecific competition between larvae of *Bactrocera invadens* (B) and *Ceratitis cosyra* (C) at different temperatures on mango

Temperature (°C)	Infestation sequence	Pupa weight (mg)			
		<i>B. invadens</i>	<i>C. cosyra</i>	t	P
15	Infested same day	15.1 ± 0.4a	nd	–	–
	B 1 day before C	13.2 ± 0.6ab	nd	–	–
	B 2 days before C	13.7 ± 0.9ab	nd	–	–
	B 3 days before C	13.6 ± 0.7ab	nd	–	–
	C 1 day before B	12.4 ± 0.1b	nd	–	–
	C 2 days before B	12.7 ± 0.3ab	nd	–	–
	C 3 days before B	12.1 ± 0.2b	nd	–	–
	Controls	14.2 ± 0.3a	10.2 ± 0.3	6.40	0.0007
		$F_{7,32} = 1.37$	–		
20	Infested same day	14.9 ± 0.4a	13.3 ± 3.3	1.51	0.2198
	B 1 day before C	12.9 ± 0.4c	nd	–	–
	B 2 days before C	14.4 ± 0.3ab	nd	–	–
	B 3 days before C	14.0 ± 0.4b	nd	–	–
	C 1 day before B	12.6 ± 0.4c	11.3 ± 0.2	2.35	0.2381
	C 2 days before B	13.2 ± 0.4bc	12.6 ± 0.2	5.62	0.1500
	C 3 days before B	12.9 ± 0.1c	12.9 ± 0.1	6.88	0.3900
	Controls	13.5 ± 0.2bc	12.2 ± 0.1	5.96	0.1000
		$F_{7,32} = 6.78$	$F_{4,20} = 1.68$		
25	Infested same day	15.0 ± 0.5ab	12.9 ± 0.8a	2.29	0.0513
	B 1 day before C	15.3 ± 0.7a	12.1 ± 0.1ab	1.80	0.1463
	B 2 days before C	13.2 ± 0.2c	11.8 ± 0.5ab	3.23	0.1780
	B 3 days before C	13.0 ± 0.3c	11.8 ± 0.1ab	3.82	0.0880
	C 1 day before B	14.0 ± 0.3bc	10.6 ± 0.1b	2.68	0.0367
	C 2 days before B	14.0 ± 0.3bc	11.1 ± 0.1ab	2.52	0.0355
	C 3 days before B	14.1 ± 0.1bc	9.9 ± 0.1b	12.72	0.0002
	Controls	15.8 ± 0.6a	12.3 ± 0.1ab	6.23	0.0033
		$F_{7,32} = 5.62$	$F_{7,32} = 1.57$		
30	Infested same day	12.5 ± 0.4ab	9.6 ± 0.3bc	4.86	0.0038
	B 1 day before C	12.3 ± 0.6ab	10.8 ± 0.4b	1.83	0.1164
	B 2 days before C	13.4 ± 0.4ab	13.9 ± 0.2a	2.09	0.0821
	B 3 days before C	11.2 ± 1.4b	nd	–	–
	C 1 day before B	13.7 ± 0.3ab	9.0 ± 0.1c	5.98	0.0019
	C 2 days before B	14.0 ± 0.6a	12.4 ± 0.4a	4.84	0.2230
	C 3 days before B	14.1 ± 0.4a	12.2 ± 0.2a	3.21	0.3240
	Controls	12.6 ± 0.4ab	11.5 ± 0.4ab	1.83	0.1043
		$F_{7,32} = 3.24$	$F_{6,28} = 6.10$		
		P = 0.0103	P = 0.0026		

Means (± SE) within a column and within one temperature followed by different letters are significantly different (Student–Newman–Keuls test; $P < 0.05$).

nd = not determined.

competitive interactions in which species are affected more or less equally in the face of environment change (MacArthur, 1972). This was manifested at the temperatures of 25 and 30 °C where *C. cosyra* was not excluded through competitive interactions with *B. invadens*. We observed

that at the various co-infestation treatments, temperature also altered the intensity of competitive interactions between the species in that a significant number of *C. cosyra* emerged despite the competitive dominance of *B. invadens* and particularly when it was given a head start. Higher

Table 4 Mean adult emergence following interspecific competition between larvae of *Bactrocera invadens* (B) and *Ceratitis cosyra* (C) at different temperatures on mango

Temperature (°C)	Infestation sequence	Total puparia	No. of adults			
			<i>B. invadens</i>	<i>C. cosyra</i>	t	P
15	Infested same day	22.0	3.8 ± 0.4b	No emergence	—	—
	B 1 day before C	16.0	8.4 ± 0.7a	No emergence	—	—
	B 2 days before C	18.3	6.2 ± 0.6ab	No emergence	—	—
	B 3 days before C	15.0	9.2 ± 1.2a	No emergence	—	—
	C 1 day before B	16.0	2.2 ± 0.6b	No emergence	—	—
	C 2 days before B	17.6	3.4 ± 1.2b	No emergence	—	—
	C 3 days before B	8.0	2.2 ± 0.8b	No emergence	—	—
	Controls	14.0/6.4 ¹	9.0 ± 0.3a	No emergence	—	—
			$F_{7,32} = 8.11$ P = 0.0001			
20	Infested same day	26.0	8.0 ± 1.4b	1.3 ± 0.3c	5.73	0.0023
	B 1 day before C	16.5	7.8 ± 1.2b	No emergence	—	—
	B 2 days before C	19.8	13.0 ± 1.7a	No emergence	—	—
	B 3 days before C	16.4	11.4 ± 1.0a	No emergence	—	—
	C 1 day before B	25.3	8.2 ± 1.7b	15.0 ± 1.6a	6.95	0.0010
	C 2 days before B	24.6	9.8 ± 1.2b	12.6 ± 2.4b	11.14	<0.0001
	C 3 days before B	16.4	2.5 ± 0.7c	13.0 ± 1.0b	4.34	0.0025
	Controls	14.2/16.6	13.3 ± 1.1a	15.5 ± 0.7a	0.38	0.7122
			$F_{7,32} = 6.41$ P = 0.0001			
25	Infested same day	27.0	12.6 ± 0.9c	2.8 ± 0.8c	5.75	0.0004
	B 1 day before C	19.3	11.2 ± 0.4c	1.0 ± 0.1c	23.74	<0.0001
	B 2 days before C	27.3	14.2 ± 1.3b	1.0 ± 0.1c	16.51	<0.0001
	B 3 days before C	20.0	12.2 ± 1.3c	1.0 ± 0.1c	7.85	0.0014
	C 1 day before B	30.6	15.0 ± 0.7ab	14.2 ± 1.6a	4.45	0.0735
	C 2 days before B	25.0	15.6 ± 0.2ab	7.4 ± 1.2b	6.63	0.0006
	C 3 days before B	26.5	16.6 ± 1.0a	8.6 ± 1.1b	6.04	0.0038
	Controls	18.5/17.2	16.2 ± 0.7a	15.2 ± 0.6a	1.02	0.3362
			$F_{7,32} = 2.91$ P = 0.0180			
30	Infested same day	16.3	6.8 ± 0.5c	1.3 ± 0.3b	9.49	<0.0001
	B 1 day before C	21.6	10.2 ± 2.1b	2.7 ± 1.2b	3.62	<0.0001
	B 2 days before C	17.2	11.0 ± 1.3b	1.5 ± 0.3b	3.16	0.0203
	B 3 days before C	16.6	10.6 ± 1.2b	1.0 ± 0.1b	9.51	0.0002
	C 1 day before B	18.6	7.6 ± 1.5c	2.0 ± 1.2b	2.98	0.0023
	C 2 days before B	19.4	10.2 ± 1.0b	3.4 ± 0.1b	7.26	<0.0001
	C 3 days before B	17.8	10.4 ± 0.7b	3.8 ± 0.6b	11.19	0.0004
	Controls	14.0/12.3	13.8 ± 1.9a	6.0 ± 0.3a	2.90	<0.0001
			$F_{7,32} = 1.54$ P = 0.0190			
			$F_{7,32} = 13.95$ P = 0.0001			

Means (± SE) within a column and within one temperature followed by different alphabets are significantly different (Student–Newman–Keuls test: P<0.05).

¹Values denote *B. invadens* control/*C. cosyra* control.

temperature means individuals of each species must take up more resources to meet their higher metabolic needs exerting higher per capita competitive intensity upon each other. Although *B. invadens* exerted a higher competitive dominance over *C. cosyra* at higher temperatures, the lack

of extinction indicates a slightly higher per capita competitive strength of *C. cosyra* at higher temperature compared with the lower temperatures.

Our results also showed that when competition takes place between *B. invadens* and *C. cosyra*, an asynchrony of

1–3 days was sufficient to change the relative competitive ability of either species and this was particularly noticeable at 20 °C. An earlier head start by *B. invadens* drives *C. cosyra* to extinction at 20 °C, but with the reverse, many *C. cosyra* are recovered from mango. Thus, temporal variation in laying high numbers of eggs and egg laying tactics at a given temperature regime and a consequent relatively high number of offspring of *B. invadens* (Ekesi et al., 2006) may give competitive advantage to *B. invadens* at the cost of *C. cosyra* under field conditions. Similar results were reported in *Rhagoletis pomonella* (Walsh), albeit intraspecifically (Averill & Prokopy, 1987). On few infestation sequences, the outcome of the competitive interaction was rather difficult to understand. For example, at 25 °C, *B. invadens* puparia were significantly heavier when the invader was given a 1-day head start, compared with when it was given 2 or 3 days head start. The explanation for this outcome is elusive but we can only speculate that under a shorter infestation sequence, individuals consume more food and develop at a higher pace as a result of competitive interaction resulting in heavier puparia. When the insects have longer infestation sequence, larvae perhaps develop at much slower pace oblivious of any eventual competition with another species resulting in smaller puparia.

It is difficult to say unambiguously the factors that lead to shorter developmental period of the larvae and reduced emergence under co-infestation of the two species. It has, however, been noted by Duyck et al. (2006) that shorter larval development time of *Bactrocera zonata* (Saunders) compared with *Ceratitidis catovirii* Guérin-Mèneville, *C. capitata* (Wiedemann), and *C. rosa* Karsch, conferred superior competitive ability on *B. zonata* than the *Ceratitidis* species. Krijger et al. (2001) also showed that shorter developmental times between *Drosophila* species were associated with superior competitive ability. Our results concur with the observation of these authors at 20 °C, where shorter development time of *C. cosyra*, when it was given a head start, resulted in higher adult emergence of the indigenous species under interspecific interaction. This narrow window of infestation asynchrony and competitive temperature advantage at 20 °C for *C. cosyra* may be contributing to the co-existence of small populations of *C. cosyra* with *B. invadens* on mango in the field. In this regard, our study also provides direct evidence for another mechanism: that differential temperature tolerance can lead to coexistence of fruit fly competitors. Among the different species of fruit flies, abiotic factors such as temperature have been demonstrated to promote co-existence (Duyck et al., 2006). Between *B. invadens* and *C. cosyra*, field observations also show that co-existence appears to occur at microhabitat scale with *C. cosyra* having a highly specialized host searching ability on mango (S Ekesi, unpubl.).

This, perhaps, is because it has a narrow host range (Cope-land et al., 2006) and is more closely linked to mango in its aboriginal home of Africa, compared with *B. invadens* that has a wider host range (Rwomushana et al., 2008a,b) and is still exploring the new environment. The interaction between temperature and specialized foraging abilities may therefore support co-existence between the two species.

The observed pattern in our study also suggests a competitive pre-emption of resources among species, i.e., the first larvae to develop benefit from more resources than the later ones (Qureshi et al., 1987; Blanckenhorn, 1999; Krijger et al., 2001; Duyck et al., 2006). When two groups of differently sized and aged juvenile insects are reared together, the smaller and younger cohort is more likely to suffer from increased mortality and reduced size if resources are limiting (Averill & Prokopy, 1987; Edgerly & Livdahl, 1992; Dukas et al., 2001; 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. For example, in *C. capitata* it is known that larvae are sensitive to variation in the nutritional quality of food and able to select the best among available alternatives (Zucoloto, 1987). It has also been reported that chemical changes that reduce larval growth may be accelerated with increased competition (Fitt, 1989).

The success of many invasive species in their new environment is believed to result primarily from their superior competitive abilities relative to native species (Juliano, 1998; Bruno et al., 2005). In a series of tephritid invasions on La Réunion, Duyck et al. (2006) demonstrated that the invasive species *B. zonata* tends to have higher ranks than the previously established invasive (*C. rosa* and *C. capitata*) and native (*C. catovirii*) species in the hierarchy. In their study, *B. zonata* which was the most recently established species was dominant in both forms of competition (scramble and interference), which the authors attributed to large body size and shorter developmental period. Such species hierarchy is generally attributed to differences in life history strategy (MacArthur & Wilson, 1967). Although not many studies have addressed competitive interaction between tephritids of different genera, our results agree with those of Duyck et al. (2006) that *Bactrocera* species tend to have superior competitive ability over *Ceratitidis* species over a range of temperatures and infestation asynchrony.

Understanding the factors that govern the spread and success of invasive species is a critical step towards reducing their impact (Williamson, 1996). Under natural conditions, several other mechanisms not studied here

may combine to play a role in interspecific competition between these two species. In general, these include release from natural enemies (S Ekesi, unpubl.), one species having greater realized fecundity than the competitor (which mechanism applies not just to numbers of offspring, but also to the ability to produce proportionately more females from the same resources) and interference competition through behavioural displacement of one by the more aggressive invader (S Ekesi, unpubl.). This study has shown that resource pre-emption and the capacity to tolerate a wide range of temperatures are among the factors contributing to the displacement of *C. cosyra* by *B. invadens* on mango. The results also stress the importance of interspecific competition in shaping the distribution of tephritids and explain, at least partly, the observed shift in dominance between *B. invadens* and *C. cosyra* on mango in many parts of Africa.

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