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Contribution of natural food sources to reproductive behaviour, fecundity and longevity of *Ceratitis cosyra*, *C. fasciventris* and *C. capitata* (Diptera: Tephritidae)

A. Manrakhan[1,2]* and S.A. Lux[1]

[1]International Centre of Insect Physiology and Ecology, PO Box 30772,
Nairobi, Kenya: [2]Agricultural Research and Extension Unit,
Réduit, Mauritius

Abstract

The influence of food sources comprising the natural diet on the reproductive behaviour, fecundity and longevity of three African fruit flies *Ceratitis cosyra* (Walker), *C. fasciventris* (Bezzi) and *C. capitata* (Wiedemann) was investigated. Three natural food sources, varying in protein and sugar content, were evaluated. These included bird droppings (farm chicken), aphid honeydew and guava (*Psidium guajava* L.) juice. For *C. fasciventris* and *C. capitata*, flies fed on a protein-rich diet displayed higher frequency of calling, mating and oviposition than flies fed on a protein-poor diet, whilst for *C. cosyra*, quality of diet significantly influenced the mating behaviour of the flies, but not the calling and oviposition behaviour. Net fecundity rates were lowest for *C. fasciventris* and *C. capitata* when fed only on guava juice (0.1, 2.6 eggs per female, respectively), and higher for those on a diet of honeydew only (9.5, 33.8 eggs per female, respectively) and a combined diet of guava, honeydew and chicken faeces (11.8, 25.8 eggs per female, respectively). For *C. cosyra*, due to low numbers of eggs collected, no significant differences in fecundity between diets could be detected. All species fed only on a diet of chicken faeces since emergence died within the first three days of adult life without laying eggs, but when carbohydrates were provided by addition of guava juice and honeydew, the longevity of the flies was sustained for more than four weeks after adult emergence. The practical implications of these findings for control purposes are discussed.

Keywords: *Ceratitis cosyra*, *Ceratitis fasciventris*, *Ceratitis capitata*, Tephritidae, nutritional ecology, reproductive behaviour, insect demography

Introduction

Africa is the aboriginal home of several economically important tephritid fruit flies including *Ceratitis capitata* (Weidemann), *C. cosyra* (Walker), *C. fasciventris* (Bezzi), *C. rosa* Karsh and *C. anonae* Graham among others (White & Elson-Harris, 1994; De Meyer, 2001; Lux *et al.*, 2003). Most of these flies traverse national boundaries and pose a serious threat to fruit production. For example, assessment by the African Fruit Fly Initiative revealed that of the 1.9 million tons of mangoes produced annually in Africa, about 40% is lost to fruit fly infestation (Lux *et al.*, 2003).

Ceratitis cosyra has been reported to be the dominant species among the other *Ceratitis* fruit fly species in attacking

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*Address for correspondence: Agricultural Research and Extension Unit, Réduit, Mauritius
Fax: +230 4660056
E-mail: aruna@intnet.mu

mango fruits in sub-Saharan Africa (Malio, 1979; Javaid, 1986; Mukiama & Muraya, 1994; Labuschagne *et al*., 1996; Lux *et al*., 2003). The next important pest species of mango are *C. rosa* and its close relative *C. fasciventris* (Lux *et al*., 2003). According to the same authors, *C. capitata*, although being a highly destructive pest in other parts of the world, is a rather minor pest of mango in Africa. Despite the economic importance of *C. cosyra*, little has been published so far on its biology. Malio (1979) described aspects of the life table of this pest. As for *C. rosa*, Orian & Moutia (1960), Quilici & Franck (1999) and Quilici *et al*. (2002) worked on its biology and behaviour, whilst for *C. fasciventris*, a newly described species (De Meyer, 2001), its biology is totally unknown.

Adult feeding plays a key role in the life of a tephritid as it enables the fly to survive and realize its reproductive potential (Tsitsipis, 1989; Drew & Yuval, 2001). The food sources encountered by adult flies in nature include fruit juices, extrafloral glandular secretions, nectar from flowers, pollen grains, honeydew, bird faeces and bacteria (Christenson & Foote, 1960; Neilson & Wood, 1966; Prokopy, 1976; Smith & Prokopy, 1981; Malavasi *et al*., 1983; Hendrichs & Hendrichs, 1990; Aluja & Birke, 1993; Warburg & Yuval, 1997). The nutritional value of some of these natural food sources on the fecundity and survival of several fruit fly species, such as *Bactrocera oleae* (Gmelin), *B. cucurbitae* (Coquillett), *B. dorsalis* (Hendel), *C. capitata* and *Rhagoletis pomonella* (Walsh) has been reported (Tsiropoulos, 1977; Hendrichs *et al*., 1991, 1993; McQuate *et al*., 2003). But apart from studies on *C. capitata* (Hendrichs *et al*., 1991), there has been no research on the contribution of natural food sources to adult longevity and fecundity of the other African tephritid fruit flies listed above.

Studies conducted in semi-field conditions (greenhouses and field cages containing host and non-host plants) and also in the field (mango orchards) have revealed that *C. cosyra*, *C. fasciventris* and *C. capitata* feed on fruit juices, bird faeces and honeydew, among others (Manrakhan, 2005). The main objective of the present study was to determine the relative contribution of these natural food sources to adult reproduction and survival of these flies, in particular to calling, mating, oviposition, and longevity.

Materials and methods

Insect material

Adult flies used originated from puparia of *C. cosyra*, *C. fasciventris* and *C. capitata* obtained from the colonies maintained at the International Centre of Insect Physiology and Ecology in Nairobi, Kenya. Laboratory-reared flies were used instead of wild flies since this allowed the studies on the three fruit fly species to run concurrently. Moreover, it would have been impossible when rearing flies from wild fruits to differentiate, using morphological characters, females of *C. fasciventris* from those of *C. rosa*, which can be reared from the same wild fruits (De Meyer, 2001).

Experimental set up

For each species, groups of 5 males and 10 females were established upon emergence and each group was maintained in cylindrical cage made of a metal frame (24 cm in diameter and 22 cm high) covered with a netting material (1 mm mesh size). Within each species, each group of flies was kept on a different diet (one of five diets described below) and was observed daily for 8 weeks. All the flies were kept under laboratory conditions at ambient temperatures (23–30°C) and 45–57% relative humidity under a photoperiod of L:D 13:11 h. For *C. capitata* and *C. fasciventris*, the experiment was replicated five times, while for *C. cosyra* three times due to low availability of flies from the colony.

Food sources and diets

All flies were provided with water *ad libitum* and one of the diets composed of the following natural food sources: guava juice, honeydew and bird (chicken) faeces, or artificial components such as yeast hydrolysate (Enzymatic, United States Biochemical Corporation, Cleveland, Ohio) and sucrose. The following five diets were used:

1. Juice from guava (*Psidium guajava* L.) which was freshly prepared from fruits collected as mature directly from the trees.
2. Honeydew collected on a 9 cm diameter Petri dish placed under an aphid-infested citrus (*Citrus* spp.) tree within two days preceding the experiment.
3. Fresh chicken faeces obtained from caged chicken fed on a ground maize diet. Ideally we would have used faeces from a group of wild birds, known to be present in fruit orchards, and kept in captivity for this experiment. But for practical reasons, we used chicken faeces collected from a local farm which would conveniently meet our daily material requirements.
4. A combination of three natural food sources; guava juice, honeydew and chicken faeces placed in separate containers.
5. A mixture of enzymatic yeast hydrolysate and sucrose (1:4).

Guava juice and chicken faeces were each mixed 3:1 with water. Each mixture was half-filled into a 9 cm diameter Petri dish and then absorbed into cotton wool to prevent flies from drowning. Honeydew was offered on a Petri dish as collected. All natural food sources were changed daily in the morning at 0800 h. The artificial diet, a mixture of yeast hydrolysate and sucrose, was changed on a weekly basis.

Reproductive behaviour

The following reproductive activities were measured by recording frequencies of their occurrence:

1. 'Calling' – a pre-mount courtship behaviour by males involving bursts of rapid wing vibration and eversion of a balloon-like structure formed by a membranous portion of the rectal epithelium for release of pheromone. The function of this behaviour is to attract females and also other males (Burk, 1981).
2. 'Mating' – actual copulation.
3. 'Ovipositing' – ovipositor insertion by a female into an oviposition dome to deposit eggs.

The oviposition dome consisted of a plastic cup containing a small piece (approximately 1 cm × 1 cm × 0.5 cm) of host fruit: mango (*Mangifera indica* L.) for *C. cosyra*, guava (*P. guajava*) for *C. fasciventris* and citrus (*Citrus* spp.) for *C. capitata*. Each host fruit was covered with humid black cloth and parafilm membrane (Parafilm 'M', American National Can, Greenwich, Connecticut) to simulate the waxy

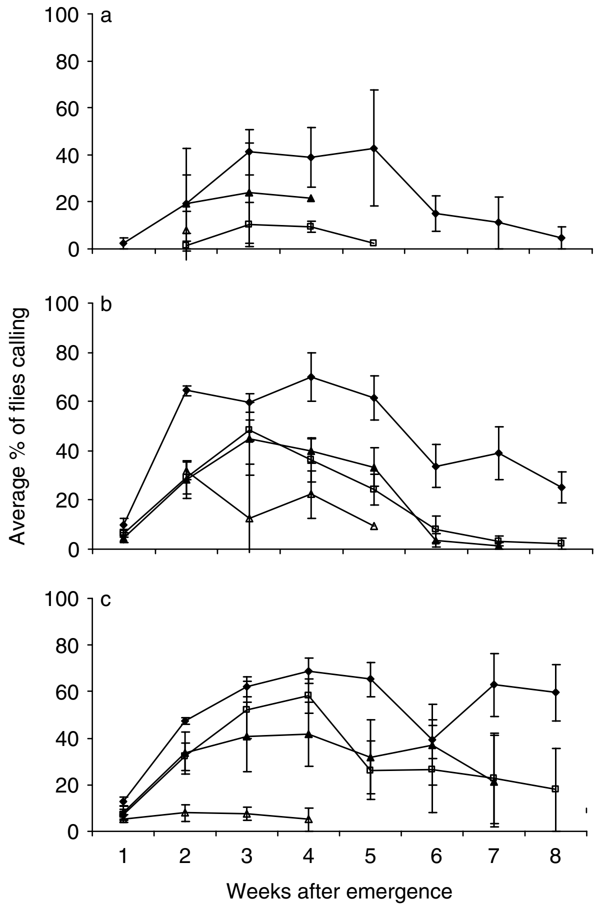

Fig. 1. Effect of adult diet on percentage of males observed calling in three species of *Ceratitis*: (a) *C. cosyra*, (b) *C. fasciventris* and (c) C. *capitata* (mean ± SE). △, Guava; □, guava, honeydew and chicken faeces; ▲, honeydew; ◆, yeast and sucrose.

layer of the fruit skin. Artificial egg-laying devices were used to prevent any contact of the flies with the fruit, which would have been used by them as another food source in addition to the diet tested.

Each of the reproductive behaviours was measured at the peak time of its diurnal occurrence. For *C. capitata*, calling and mating were recorded every 30 min between 0900 and 1100 h and for *C. fasciventris* and *C. cosyra*, calling and mating were recorded between 1600 and 1800 h. The oviposition events for the three species were recorded every 30 min between 1600 and 1800 h. All behaviours were recorded daily in each cage period for 8 weeks.

Fecundity

Eggs were collected and counted daily from the oviposition domes and were then transferred to a wet black cloth placed on a Petri dish for hatching. The black cloth eased counting and collection of eggs. The oviposition domes were washed and later re-used whenever necessary, but host fruits within the devices were renewed daily. Egg fertility was recorded 4 days after collection of eggs and was measured as the proportion of eggs that hatched into larvae. The 8-week period of assessment of both daily egg production and fertility was divided into three time periods according to the patterns of egg laying by adult females on all diets: (i) 0–14 days after emergence; (ii) 15–35 days after emergence; and (iii) 36–56 days after emergence.

Gross and net fecundity rates for flies maintained on each diet were also determined. Gross fecundity is the lifetime egg production per female. Net fecundity is the average lifetime production of eggs per female weighted by the survival probability (Carey, 1993).

Longevity

Daily records of fly mortality (male and female) were taken from each cage for 8 weeks. Mean longevity refers to the average duration of life of flies in each treatment. Maximum longevity refers to the one individual with the longest lifespan in each treatment.

Statistical analyses

The effect of diet on reproductive behaviour of flies was analysed by repeated measures analysis of variance (Proc Mixed). For the three fruit fly species, only data from the first week to the fourth week were considered in the analysis. The effect of diet on latency to reproductive behaviours (calling and mating) was analysed by Wilcoxon scores rank-sum non-parametric tests (Proc Npar1way). Fecundity, daily egg production, egg fertility and longevity data were analysed by the General Linear Model (Proc GLM) (SAS, 2001). Daily survival data were analysed using the Kaplan-Meier model (Proc Lifetest) (SAS, 2001). Proportion of egg fertility was arcsine square root transformed while fecundity, daily egg production and longevity data were log $(x+1)$ transformed, to stabilize variances. To compare female vs. male longevity for each treatment, t-tests were performed (SAS, 2001).

Results

Reproductive behaviour

The influence of different diets on the reproductive behaviour of each of the three fruit fly species is presented in figs 1–3. Results for the diet consisting only of chicken faeces were not presented since it failed to sustain longevity of the flies until the start of their reproductive activities. Generally, *C. fasciventris* and *C. capitata* displayed calling and oviposited more frequently as compared to *C. cosyra* (calling: $F = 13.56$, $df = 2, 191$, $P < 0.01$; oviposition: $F = 15.63$, $df = 2, 190$, $P < 0.01$). There was no significant difference in frequency of mating among the three fruit fly species.

Calling

For two of the fruit fly species, *C. fasciventris* and *C. capitata*, the frequency of calling was significantly affected by the type of diet (table 1). Interestingly, *C. fasciventris* and *C. capitata* males, when fed with yeast and sucrose, exhibited higher levels of calling activity (by about 50%) than males kept on any of the natural diets (fig. 1). In the case of the natural diets, for two of the species, *C. fasciventris* and *C. capitata*, the frequency of calling was high when males had access to proteins or amino acids, thus either when fed on honeydew only, or on a combined diet of guava juice,

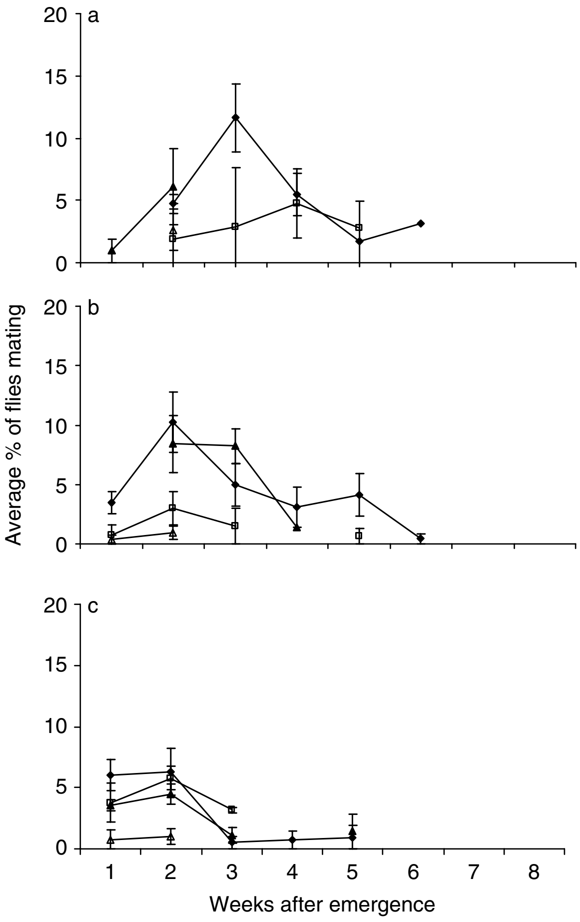

Fig. 2. Effect of adult diet on percentage of flies observed mating in three species of *Ceratitis*: (a) *C. cosyra*, (b) *C. fasciventris* and (c) *C. capitata* (mean ± SE). △, Guava; □, guava, honeydew and chicken faeces; ▲, honeydew; ◆, yeast and sucrose.

honeydew and chicken faeces. But when kept on guava juice only, calling frequency was reduced to about 20% as compared to the earlier mentioned protein or amino acid containing diets. Although similar trends were observed for *C. cosyra*, differences in calling were not significant between males fed artificial, protein rich and protein poor natural diets (table 1).

Except in the case of *C. fasciventris*, latency of calling (time until the start of calling activities) was not affected by diet. Males of *C. fasciventris* fed on guava started calling only in the second week after emergence whilst males of the same species fed on the other diets (honeydew, combined diet of guava juice, honeydew and chicken faeces and the artificial diet of yeast and sucrose) started calling in the first week after emergence (*C. fasciventris*: $\chi^2 = 15.38$, df = 3, $P < 0.01$) (fig. 1).

For *C. fasciventris* and *C. capitata*, there was a significant interaction between effects of diet and age indicating that, in addition to the diet, age also plays an important role in influencing calling behaviour of males. Whilst for *C. cosyra*, there was no significant interaction between diet and age.

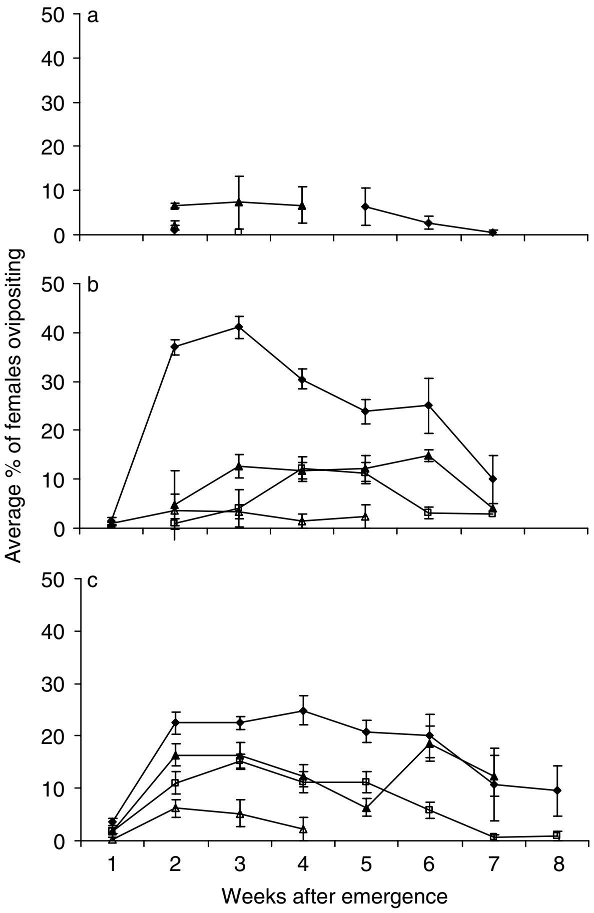

Fig. 3. Effect of adult diet on percentage of females observed ovipositing in three species of *Ceratitis*: (a) *C. cosyra*, (b) *C. fasciventris* and (c) *C. capitata* (mean ± SE). △, Guava; □, guava, honeydew and chicken faeces; ▲, honeydew; ◆, yeast and sucrose.

Mating

For all fly species, there was a significant effect of diet on the frequency of mating (table 1). Flies kept on a protein rich diet (e.g. yeast and sucrose or a combination of guava, honeydew and chicken faeces) copulated more frequently than flies on a protein poor diet, such as guava only. Diet influenced latency of copulation in only *C. fasciventris* and *C. capitata* and not *C. cosyra*. For *C. fasciventris*, flies fed on artificial diet yeast and sucrose started mating at an earlier age compared to flies fed on natural diets ($\chi^2 = 10.07$, df = 3, $P = 0.02$). For *C. capitata*, flies fed on honeydew or yeast and sucrose started mating at an earlier age compared to flies fed on the two other diets, that is guava and a combined diet of guava, honeydew and chicken faeces ($\chi^2 = 10.85$, df = 3, $P = 0.01$).

The effects of diet on mating frequency varied significantly with age for the three fruit fly species, indicating strong effect of diet during the first 2–3 weeks of their life, after which the effect of diet became not significant (fig. 2).

Table 1. Results of repeated measures ANOVA on effect of diet on weekly percentages (between 1–4 weeks) of calling, mating, oviposition of *Ceratitis cosyra*, *C. fasciventris* and *C. capitata*.

Species	Effect	Behaviour	F	df	*P*
C. cosyra	Diet	Calling*	1.75	3, 10	0.22
		Mating**	8.49	3, 8	< 0.01
		Oviposition*	3.56	3, 11	0.05
	Diet × Age	Calling*	1.07	3, 24	0.42
		Mating**	8.21	9, 8	< 0.01
		Oviposition*	1.19	9, 24	0.35
C. fasciventris	Diet	Calling*	10.30	3, 21	< 0.01
		Mating**	9.42	3, 16	< 0.01
		Oviposition**	91.19	3, 17	< 0.01
	Diet × Age	Calling*	2.98	3, 44	< 0.01
		Mating**	2.63	9, 16	0.04
		Oviposition**	35.94	9, 12	< 0.01
C. capitata	Diet	Calling*	13.17	3, 21	< 0.01
		Mating**	8.81	3, 16	< 0.01
		Oviposition**	24.70	3, 16	< 0.01
	Diet × Age	Calling*	2.54	9, 47	0.02
		Mating**	5.12	9, 16	< 0.01
		Oviposition**	5.47	9, 16	< 0.01

*A first order autoregressive covariance structure was found to best fit the model for the dependent variable.
**An unstructured covariance structure was found to fit the model for the dependent variable.

Oviposition

Both *C. fasciventris* and *C. capitata* females fed on yeast and sucrose oviposited most frequently, followed by those fed on any of the protein-containing natural diets, either honeydew only or a combined diet of guava, honeydew and chicken faeces (fig. 3). The oviposition of the flies fed on guava juice only was severely hampered (table 1). Females of *C. cosyra*, which is an oligophagous species, are known to be more ‘choosy’ in selecting objects for oviposition, hence did not oviposit so easily under the experimental conditions. As such, no significant difference was found in frequency of oviposition by females of *C. cosyra* that were fed on different diets.

There was a significant interaction between diet and age of flies for *C. fasciventris* and *C. capitata*, while this interaction was not significant for *C. cosyra*, possibly due to the low number of females ovipositing.

Fecundity

There were no significant differences in preoviposition periods between females fed on different diets, for all species studied. In all species, higher fecundity was noticed in flies fed on artificial diet (yeast and sucrose) compared to flies fed on natural diets (honeydew, combined diet of guava, honeydew and chicken faeces), although in the case of *C. cosyra*, this difference was not significant, possibly due to the overall low number of eggs collected for this species (a total of 1181 collected in 8 out of 12 cages for *C. cosyra* compared to 18,933 and 16,065 collected in 19 and 20 cages out of 20 respectively for *C. fasciventris* and *C. capitata*). Gross and net fecundity were highest for *C. fasciventris* and *C. capitata* flies fed on sucrose and yeast hydrolysate, and substantially lower on a combined natural diet (guava juice, honeydew and chicken faeces) or honeydew alone. The flies fed on guava juice exhibited the lowest gross and net fecundity (table 2).

Results of daily egg production per female and egg fertility for the three species for each of the three time periods are summarized in table 3. Again, due to the low number of eggs collected, no significant differences in daily egg production per female (eggs per female per day) and egg fertility were found for *C. cosyra* among the four diets. On the other hand, both *C. fasciventris* and *C. capitata* reached a peak in their daily egg production and egg fertility between 15 and 35 days after adult emergence in all four diets, but the fertility was highest when flies were fed on sucrose and yeast hydrolysate and lowest when fed on guava juice only.

Daily egg production per female and fertility significantly differed among the three species, and were the highest for *C. capitata* (eggs per female per day: F = 4.01, df 2, 49, *P* = 0.02; fertility: F = 4.63, df = 2, 49, *P* = 0.01).

Longevity

Longevity of all three fruit fly species (both males and females), was significantly influenced by diets (fig. 4). With the exception of chicken faeces, which when offered alone did not sustain the fruit flies beyond one week, on all other diets, longevity of extended for more than 2 weeks after adult emergence. Maximum longevity for both sexes of all fly species was recorded when the flies were fed on the artificial diet containing sucrose and yeast hydrolysate (table 4). For *C. fasciventris* and *C. capitata*, similar longevity was also recorded when flies were fed on either a diet of honeydew or a combination of guava, honeydew and chicken faeces. Interestingly, with the exception of chicken faeces only, on all other natural diets, minimum longevity for females and males of *C. fasciventris* and *C. capitata* was recorded when the flies were fed on guava juice only. For *C. cosyra* females and males, there was no significant difference in mean longevity between flies fed on diets of honeydew, guava and a combination of guava, honeydew and chicken faeces. No significant differences were found between sexes of the three species.

Table 2. Effect of adult diet on mean preoviposition period, gross and net fecundity in *Ceratitis cosyra*, *C. fasciventris* and *C. capitata*.

Species and food source	Preoviposition period (days)*	Gross fecundity (eggs per female)*	Net fecundity (eggs per female)*
C. cosyra			
Guava	10.50 a	4.46 a	3.13 a
Honeydew	10.50 a	24.52 a	9.97 a
Guava, honeydew and chicken faeces	22.00 a	2.05 a	1.43 a
Yeast and sucrose	15.67 a	32.13** a	24.83** a
$F_{(3,8)}$	0.68	0.91	0.69
C. fasciventris			
Guava	10.50 ab	0.14 c	0.12 c
Honeydew	14.20 a	15.70 b	9.52 b
Guava, honeydew and chicken faeces	13.20 a	20.29 b	11.76 b
Yeast and sucrose	8.40 b	342.81 a	299.70 a
$F_{(3,16)}$	2.15	37.04	40.19
C. capitata			
Guava	9.60 a	4.32 c	2.63 c
Honeydew	7.60 a	87.73 b	33.84 b
Guava, honeydew and chicken faeces	7.80 a	121.90 b	25.82 b
Yeast and sucrose	6.40 a	384.53 a	68.74 a
$F_{(3,16)}$	0.89	60.40	60.98

*Means within a column followed by the same letter are not significantly different ($P < 0.05$; Tukey HSD-test).
**Means with high variances due to low number of eggs laid by *C. cosyra* flies possibly due to lack of 'readiness' of *C. cosyra* flies to accept artificial devices for egg-laying.

Discussion

To survive and reproduce, fruit flies need sugars as energy source and proteins to attain reproductive maturity and produce eggs (Webster & Stoffolano, 1978; Tsitsipis, 1989). Based on earlier observations of fruit fly feeding, both in the laboratory and in the field, three natural food sources, varying in content of sugars and proteins, were chosen for this study: (i) guava juice, which contains mainly sugars, and very little proteins (about 1%) (Simonne *et al.*, 2005); (ii) honeydew, which constitutes over 80% of sugars (Downes & Dahlem, 1987) as well as substantial amounts of essential amino acids and a few amides (Boush *et al.*, 1969), and in addition, in the field also serves as a substrate for growth of bacteria, some of which might also be used as food by fruit flies; and (iii) bird faeces, which contain very few sugars if

Table 3. Mean daily egg production and egg fertility of laboratory-reared *Ceratitis cosyra*, *C. fasciventris* and *C. capitata* fed on water and natural food sources or enzymatic yeast hydrolysate and sucrose (1 : 4) for a period of 8 weeks from adult emergence.

Species and food source	0–14 days after emergence*		15–35 days after emergence*		36–56 days after emergence*	
	Eggs per female per day	Egg fertility (%)	Eggs per female per day	Egg fertility (%)	Eggs per female per day	Egg fertility (%)
C. cosyra						
Guava	0.29 a	4.67 a	0.02 a	2.82 a	0.00 a	0.00 a
Honeydew	0.70 a	8.37 a	0.83 a	23.64 a	0.00 a	0.00 a
Guava, honeydew and chicken faeces	0.00 a	0.00 a	0.10 a	2.76 a	0.00 a	0.00 a
Yeast and sucrose	0.01 a	0.00 a	1.06 a	21.44 a	0.47 a	7.11 a
$F_{(3,8)}$	2.57	1.75	1.12	1.20	1.43	2.95
C. fasciventris						
Guava	0.01 b	0.00 c	0.00 b	1.11 b	0.00 b	0.00 c
Honeydew	0.01 b	0.00 c	0.57 b	39.24 a	0.18 b	11.57 ab
Guava, honeydew and chicken faeces	0.07 b	4.05 b	0.86 b	22.44 a	0.06 b	3.67 bc
Yeast and sucrose	5.46 a	17.76 a	11.08 a	45.62 a	1.46 a	17.55 a
$F_{(3,16)}$	125.05	27.52	64.71	11.82	18.18	8.45
C. capitata						
Guava	0.11 c	4.83 b	0.24 c	20.43 b	0.00 a	0.00 b
Honeydew	1.25 b	34.59 a	2.89 b	64.60 a	0.64 a	18.81 a
Guava, honeydew and chicken faeces	1.03 b	35.84 a	4.59 b	80.74 a	0.63 a	20.18 a
Yeast and sucrose	8.17 a	56.21 a	12.54 a	79.91 a	0.36 a	9.25 a
$F_{(3,16)}$	52.79	24.37	58.11	17.26	2.82	13.35

*Means within a column followed by the same letter are not significantly different ($P < 0.05$; Tukey HSD-test).

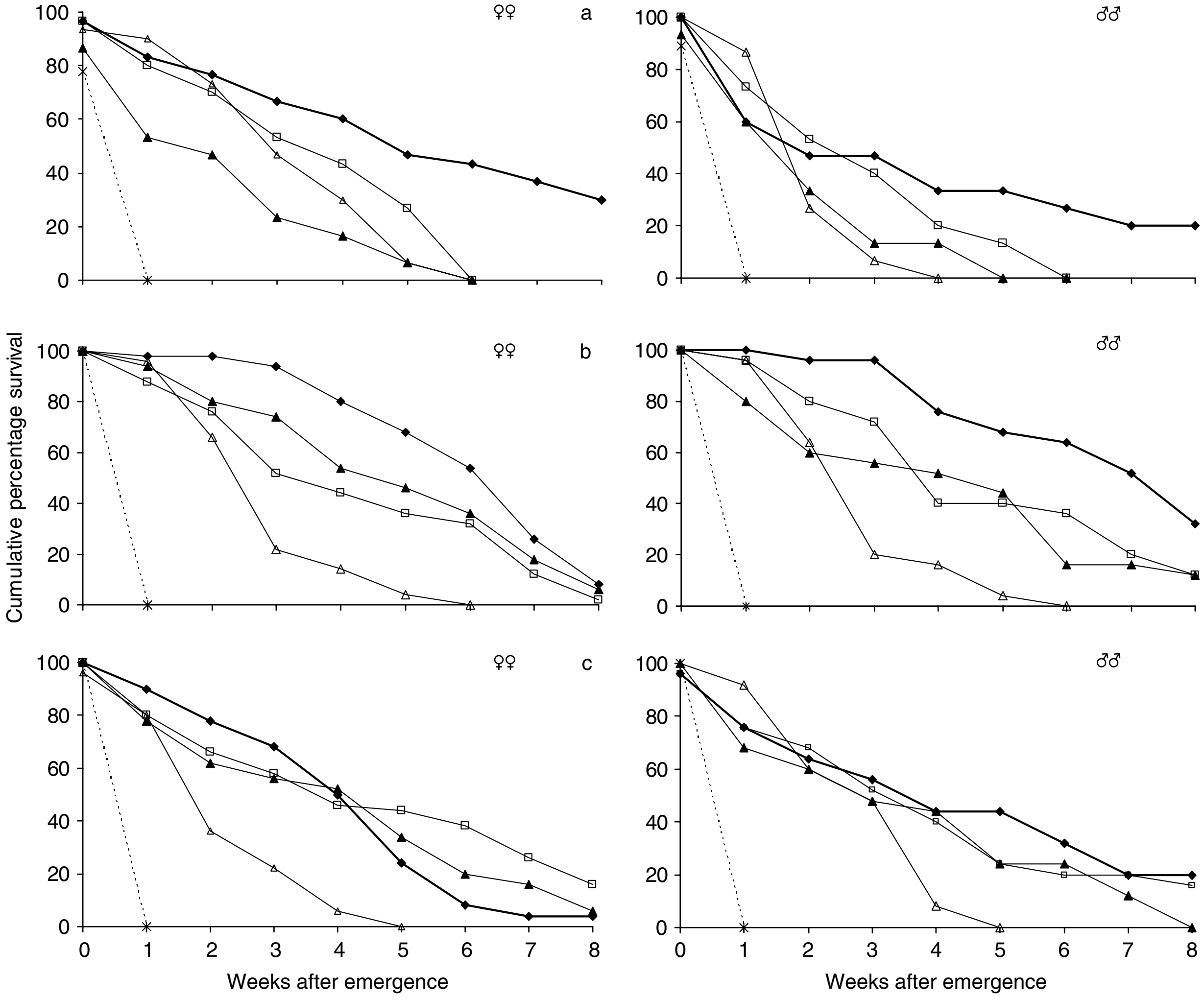

Fig. 4. Percentage survival of (a) *Coratitis cosyra*, (b) *C. fasciventris* and (c) *C. capitata* adult females and males fed on five different diets (◆, yeast and sucrose; □, guava, honeydew and chicken faeces; ▲, honeydew; △, guava; x, chicken faeces).

any, while proteins are present as both undigested and partially digested, and also in the form of microorganisms (Jacob *et al*., 1997). Certainly, not all food sources utilized by fruit flies are known, and the sources studied cannot be assumed to represent the whole spectrum of dietary components utilized by fruit flies in nature. In our studies, both guava juice alone and honeydew alone sustained life of the flies for a period of a few weeks, in contrast to chicken faeces, which, if offered alone, supported flies for a few days only. However, longevity of the flies fed on guava juice only was substantially lower compared to that of those fed on any diet containing both sugar and proteins. Similar findings were reported by Jacome *et al*. (1995), who also found that *Anastrepha serpentina* (Wiedemann) fed only on sugar showed progressive depletion of lipid reserves without replenishment, while lipid reserves of the flies kept on sugar and proteins, although depleted during the first days of adult life, were subsequently replenished. Cangussu & Zucoloto (1995, 1997), Jacome *et al*. (1999) and McQuate *et al*. (2003) also reported lower survival of flies such as *C. capitata*, *A. serpentina*, *B. dorsalis* and *B. cucurbitae* on a diet consisting of only sugar as compared to flies on a diet of sugar and protein. In contrast, studies by Carey *et al*. (1998, 2002) and Kaspi & Yuval (2000) found that medflies fed on sugar alone incurred an overall lower mortality than those fed on a diet of sugar and protein. However, Carey *et al*. (2002) also found that at the beginning, protein-deprived females died faster than protein-fed females whilst in older insects (that is after one month) the reverse occurred. Increased hazard rates for older protein-fed female flies were associated with the costly process of egg production (Carey *et al*., 2002). In the present study, male or female flies of the three species fed on guava did not survive beyond 40 days. We believe that the high mortality incurred by the flies fed on guava might have been due to the inability of the flies' low nutrient reserves to meet the high energy demands involved in (i) calling and mating activities which were ongoing, although at a low rate, and (ii) intraspecific competition during feeding and reproductive activities, since we had 15 flies in a cage initially. Interestingly, in the present study, when *C. fasciventris* and *C. capitata* were fed on guava combined with natural protein sources such

Table 4. Effect of adult diet on mean life expectancy and maximal longevity of adult female and male *Ceratitis cosyra*, *C. fasciventris* and *C. capitata*.

Species and food source	Mean longevity (days)		Maximum longevity (days)	
	Females*	Males*	Females	Males
C. cosyra				
Chicken faeces	3.00 b	2.89 b	6	5
Guava	20.50 a	12.60 a	36	28
Honeydew	13.90 a	11.13 a	36	29
Guava, honeydew and chicken faeces	22.97 a	17.53 a	41	41
Yeast and sucrose	33.33 a	22.87 a	56**	56**
Log rank (χ^2) df = 4	66.62	29.87		
C. fasciventris				
Chicken faeces	2.26 d	2.48 c	4	3
Guava	17.86 c	17.96 b	40	39
Honeydew	31.60 ab	26.96 ab	56**	56**
Guava, honeydew and chicken faeces	27.86 b	30.96 a	56**	56**
Yeast and sucrose	40.50 a	43.52 a	56**	56**
Log rank (χ^2) df = 4	317.97	169.55		
C. capitata				
Chicken faeces	3.14 c	3.00 b	4	4
Guava	14.16 b	17.36 a	29	29
Honeydew	26.44 a	23.48 a	56**	52
Guava, honeydew and chicken faeces	29.02 a	25.36 a	56**	56**
Yeast and sucrose	26.66 a	28.32 a	56**	56**
Log rank (χ^2) df = 4	245.61	96.69		

*Means within a column followed by the same letter are not significantly different ($P < 0.05$; Tukey HSD-test).
**As the study was carried out for only a period of 8 weeks, maximal longevity in these cases might be even greater than 56 days.

as honeydew and chicken faeces, longevity of some flies extended well beyond this first month, even until the end of the experiment (table 4).

From our observations it appears that proteins are less available in the flies' environment and their deficiency in the natural diet of fruit flies might limit their biological potential. Thus, it is unlikely that any combination of naturally available food sources could match the nutritional properties of the artificial diet made of concentrated sugars with a very high content of pre-digested proteins, especially designed to ensure the highest fecundity of flies, which are mass reared for the sterile insect technique. A substantial boost in fecundity of the flies fed on such enriched artificial diets was reported for *A. serpentina*, *C. capitata*, *Rhagoletis pomonella* (Walsh), and *R. indifferens* (Curran) (Hendrichs *et al*., 1991, 1993; Jacome *et al*., 1999; Lee, 2003). Also in the present studies, in all three species, gross and net fecundity was markedly higher when the flies were fed on the artificial diet and, in contrast, was severely suppressed when the flies were deprived of proteins (fed on guava juice only). Egg fertility followed the same trends. It needs to be emphasized, however, that the absolute fecundity measured for *C. cosyra* in our study is not representative of its reproductive potential. It is likely that, as opposed to the other two species, fecundity of this 'more choosy' oligophagous species might have been suppressed when it was offered only the artificial domes lacking all the necessary ovipositional cues. It is known that in such species, oocyte maturation might cease or be delayed when the flies are deprived of normally acceptable fruits, while in generalist species, oocyte maturation continues regardless of the availability of acceptable fruits (Fitt, 1986).

Despite a sub-optimal fecundity of *C. capitata*, *C. cosyra* and *C. fasciventris* on natural food sources, bird droppings (chicken faeces) and/or honeydew were found to boost fly fecundity. Hendrichs *et al*. (1993) also found that bird droppings could sustain egg production in *R. pomonella*. A diet of honeydew was also found to sustain fecundity in *R. pomonella* (Hendrichs *et al*., 1993) and the olive fly, *Bactrocera oleae* (Gmelin) (Tsiropoulos, 1977). Since natural food sources have the potential to support fruit fly population growth, the results from this study further supports the line of thought expressed by some authors (Hendrichs *et al*., 1993; Jacome *et al*., 1999) as to the inclusion in a fruit fly management programme of measures to reduce availability of natural food sources for flies, such as sanitation, treatment of aphid-infested trees and use of Scare-Eye balloons to discourage birds.

Other aspects of reproductive behaviour, such as calling and mating were also strongly affected by a deficit of proteins in the diet but this effect varied between the three congeneric species and between reproductive behaviour. Both *C. fasciventris* and *C. capitata* called and mated more frequently when fed a protein-rich diet compared to a protein-poor diet. While mating of *C. cosyra* was affected by deficit of proteins in the diet, its calling behaviour remained unaffected by quality of diet (protein rich vs. protein poor). Interestingly, Aluja *et al*. (2001) also found species differences in the effect of food quality on male reproduction in four tephritid fruit flies from the genus *Anastrepha*. The authors found that among the four species studied, calling and mating behaviour of one of them, *A. ludens* (Leow), was not influenced by male diet. The authors attributed this species difference to: (i) a different bacterial gut fauna in *A. ludens* which would provide all the nutrients required for reproduction and survival thus causing this fly to be less dependent on diet quality; or (ii) a more efficient (less energy demanding) metabolism of *A. ludens* compared to the other species; or (iii) a less energetically demanding courtship and mating behaviour of *A. ludens* compared to the other species.

In the present study, *C. cosyra* called less frequently compared to *C. fasciventris* and *C. capitata*, even on a protein rich diet. Therefore we tend to agree with Aluja *et al*. (2001) that the lack of effect of quality of diet on the calling behaviour of *C. cosyra* could be because this species does not have such an elaborate a calling pattern as the two other species. By this, we mean that *C. cosyra* might have a lower duration of calling or might call in smaller leks compared to the other two species and as such might be less influenced by supplements of protein in the diet. As shown by Yuval *et al*. (1998), lekking *C. capitata* males contained more sugars and protein than resting males, thus implying the high energetic demand of this process.

Many studies conducted on *C. capitata* that compared reproductive performance of male flies on sucrose and sucrose plus protein have similarly found that protein-fed males had a reproductive advantage over males not fed protein (Papadopoulos *et al*., 1998; Taylor & Yuval, 1999; Kaspi *et al*., 2000; Kaspi & Yuval, 2000; Shelly *et al*., 2002).

In many area-wide control programmes, *C. capitata* is the target of the control efforts with the sterile insect technique (SIT). The success of the sterile insect technique programme depends largely on competition between released males and wild males for copulation. In the present study, calling frequency for laboratory-reared flies sustained on a natural diet was 50% lower compared to flies sustained on an artificial diet (sucrose and yeast hydrolysate). Among the natural diets, when flies were fed on guava only, calling frequency was further reduced by 20%. Mating frequency was also lower on natural diets compared to the artificial diet (sucrose and yeast hydrolysate). This suggests that in the wild, sexual performance of the released flies would be lower due to the poor level of protein in natural food sources. Papadopoulos *et al*. (1998) and Kaspi & Yuval (2000) suggest that including protein in the pre-release diet could help in improving sexual performance of the released flies. In the present study, it was interesting to note that calling by males fed over an artificial diet remained the highest throughout most of their adult life. Therefore by adding protein to the pre-release diet, it might be expected that these 'well-fed' males would have higher calling and mating frequencies compared to males that are fed on only sugar before release and who have then to acquire protein from natural food sources once released. However, higher calling and mating frequencies would also entail possibly higher rates of predation. In a study conducted on the island of Chios, Greece, Hendrichs & Hendrichs (1998) found that mature signalling *C. capitata* males were the subject of the majority of attacks by vespid wasps. As such, the trade-off-between reproduction and survival would be an interesting subject of investigation in the context of the sterile insect technique and protein inclusion in pre-release diets.

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