Patterns of resource distribution among conspecific larvae in two fruit fly species: *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae)

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Abstract
1 *Anastrepha fraterculus* (Diptera: Tephritidae) and *Ceratitis capitata* (Diptera: Tephritidae) are fruit fly pests whose larvae are frequently found sharing the same fruit with conspecifics. Because larvae are incapable of leaving the fruit in search of non-infested fruit, they are forced to share nutritional resources and eventually compete with other larvae for these.

2 In the present study, we investigated the effect of intraspecific competition on the development of *A. fraterculus* and *C. capitata* larvae, and compared the strategies adopted by these species.

3 To this end, newly-hatched larvae were transferred into a container with a fixed amount of larval diet at increasing larval densities and several developmental parameters were measured.

4 The two species showed similarities and differences in the way in which they responded to an increasing density. In *A. fraterculus*, pupal weight and the duration of the larval stage decreased as the competition levels increased. Larvae of *C. capitata* showed a consistent reduction in pupal weight and larval survival as the larval density increased. In *A. fraterculus*, the reduction in pupal weight was heterogeneous, with most pupae showing a marked decrease in weight and only few pupae showing slight negative effects or no effect at all, whereas, in *C. capitata*, the reduction was similar for all pupae.

5 The differences in the way in which these species responded to competition suggest that there are different patterns of resource distribution among conspecific larvae. The implications of these findings for oviposition behaviour and the life history of the two species are discussed.

Keywords *Anastrepha fraterculus*, *Ceratitis capitata*, contest competition, invasive species, larval competition, oviposition behaviour, scramble competition.

Introduction

Nutrients incorporated by holometabolous insects during larval development affect their life expectancy and potential fecundity during the adult stage (Sokolowski, 1985; Zucoloto, 1991; Fernandes-da-Silva & Zucoloto, 1993; Agnew *et al.*, 2002). In many insect species, females lay their eggs in confined

environments (wood, mushrooms, fruit and other plant tissues, other insects, etc.) in which larvae develop until they are ready to pupate (Fitt, 1989). In these systems, the probability of larvae engaging in a competitive interaction is high because they cannot escape and search for better quality patches.

The strength of the competition and its effects on individuals are determined, at least partially, by the size of the patch, its nutritional quality and the number of competitors (Lack, 1947; Fitt, 1989; Craig *et al.*, 2000; Aluja *et al.*, 2001; Dukas *et al.*, 2001; Díaz-Fleischer & Aluja, 2003). Several studies report

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that larval competition can negatively affect the probability of molting to the next developmental stage or the time taken to reach the pupal or adult stage (Taylor, 1988; Fitt, 1989; Agnew *et al.*, 2000; Harvey *et al.*, 2013). Simiarly, a shortage of food during the larval stage might affect the size or weight of the individuals in subsequent stages, and such parameters are positively correlated with the reproductive success of the adults (Quiring & McNeil, 1984; Averill & Prokopy, 1987; Honěk, 1993; Allen & Hunt, 2001; Navarro-Campos *et al.*, 2011).

Intraspecific competition may take on a variety of forms, which are characterized at their extremes as either scramble or contest competition, depending on the utilization of resources by competing larvae (Nicholson, 1954). Under scramble competition, the resource is equally distributed among individuals, which leads to a homogeneous reduction in the amount of available resources for each individual. Under contest competition, the resource is unequally distributed among competitors and a few individuals gather a significantly larger amount of the available resources at the expense of their competitors (Allen & Hunt, 2001). Under this scenario, the number of surviving larvae remains constant as the larval density increases (Hassell, 1975). Conversely, in scramble competition, when larval density increases, the number of surviving larvae does not decline and individuals experience a reduction in body size and a prolongation of the developmental time (Peters & Barbosa, 1977) until a threshold density at which the number of surviving larvae decreases abruptly (Hassell, 1975; Fitt, 1989).

Within the Diptera, the family Tephritidae comprises 4600 species, distributed in tropical, subtropical and temperate regions worldwide (Christenson & Foote, 1960; Norrbom *et al.*, 1999). Many of these species lay their eggs in fruit, where the larval stage takes place. Because of their economic importance, tephritid fruit flies have been the focus of several studies on larval competition. An increasing larval density has been shown to affect different parameters, such as pupal weight, larval developmental time and larval mortality, in species of the genera *Bactrocera* (Duyck *et al.*, 2006, 2008; Burrack *et al.*, 2009), *Ceratitis* (Dukas *et al.*, 2001; Duyck *et al.*, 2006, 2008) and *Ragholetis* (Averill & Prokopy, 1987). Similar to *Drosophila*, tephritid flies do not adopt a single competitive strategy and evidence for both contest (Dukas *et al.*, 2001; Duyck *et al.*, 2006) and scramble (Burrack *et al.*, 2009) competition can be found.

According to Aikio *et al.* (2008), the stability of a population is linked, at least in part, to the type of intraspecific competition that it exhibits. A population exhibiting a scramble-like strategy could collapse if the resource becomes too scarce, whereas a population exhibiting a contest-like strategy would allow a fixed number to survive in case of a severe reduction of resources. Therefore, a contest-like strategy would be more stable at the population level. Under a biological invasion scenario, coexistence would be promoted when the resident population is intrinsically stable (contest-like) and the invasive population displays a scramble strategy and a higher maximum growth rate (Aikio *et al.*, 2008). Therefore, a native population with a scramble competitive strategy would be more susceptible to replacement after an invasion than a population with a contest-like strategy.

In Argentina, two fruit fly species considered to be major fruit pests overlap their distribution ranges: *Ceratitis capitata* Wiedemann and *Anastrepha fraterculus* Wiedemann (Diptera:

Tephritidae). *Ceratitis capitata* is a highly invasive African species that was first detected in Argentina in 1900 (Vergani, 1956), whereas *A. fraterculus* is endemic to the American continent. These species use fruit as a larval substrate and it is common to find more than one larva per fruit (Pavan, 1978; Malavasi *et al.*, 1980; Devescovi *et al.*, 2015). Both species are highly polyphagous, with more than 200 hosts reported for *C. capitata* (Liquido *et al.*, 1991; FAO/IAEA, 2013) and more than 80 for *A. fraterculus* (Norrbom & Kim, 1988; Norrbom, 2003). Their host range overlaps widely, setting up the conditions for competitive interactions. Yet the two species coexist and the ecological processes that allow for this are far from understood (Segura *et al.*, 2006; Devescovi *et al.*, 2015).

In the present study, we analyzed the way in which larvae of *A. fraterculus* and *C. capitata* respond to an increase in the density of conspecifics and compared the possible strategies that both species adopt under such a situation. As a result of the highly invasive potential of *C. capitata* and the fact that females lay their eggs in clutches (McDonald & McInnis, 1985; Dukas *et al.*, 2001), we hypothesized that this species would tend to exhibit a competitive strategy more similar to scramble competition. Conversely, *A. fraterculus* females generally lay only one egg per oviposition bout (Nascimento & de Oliveira, 1996) and there are no records of invasions by this species. Therefore, a contest-like strategy could be expected for *A. fraterculus*. To assess the pattern of intraspecific competition in these species, newly-hatched larvae were transferred into a container with a fixed amount of larval diet at increasing larval densities. Several biological parameters linked to the fitness of the individuals were then recorded.

Materials and methods

Insects

All the experiments were conducted with insects from laboratory colonies. The *A. fraterculus* colony was derived from an experimental colony kept at the Estación Experimental Agroindustrial Obispo Colombres (EEAOC), Tucumán, Argentina, which was originally established with pupae recovered from infested guavas (*Psidium guajava* L.) at the vicinity of Tafí Viejo (Tucumán) in 1997 (Jaldo *et al.*, 2001). Pupae from Tucumán were shipped to the Instituto de Genética 'E. A. Favret' (IGEAF-INTA), Castelar, Buenos Aires, Argentina, in 2007, and were used to establish an experimental rearing scenario in accordance with the same procedures as in the EEAOC (Jaldo *et al.*, 2001; Vera *et al.*, 2007). The *C. capitata* colony was established at IGEAF in 1994, with pupae from an experimental rearing scenario kept at the Instituto de Sanidad y Calidad Agroalimentaria de Mendoza (ISCA-MEN), Mendoza, Argentina. This colony was originally established with wild flies recovered from infested peaches [*Prunus persica* L. (Batsch)]. The rearing methods for *C. capitata* followed those described in Terán (1977).

Experimental procedures

To perform larval competition experiments, increasing numbers of newly-hatched larvae were transferred into containers with the same amount of artificial larval diet (Duyck *et al.*, 2006). For

each species, eggs were collected and bubbled in water for 24 h (with the aid of an aquarium air pump). After bubbling, 0.3 mL of eggs was transferred to a tray containing a thin layer of an agar solution (20%) and then kept under controlled conditions at $25 \pm 1\,°C$ and $70 \pm 10\%$ relative humidity until hatching. Agar provided appropriate humidity conditions for embryonic development and kept larvae alive for a day or so, although they had no access to nutritional resources. Newly-hatched larvae were carefully transferred into a plastic container (patch) with a fine brush under a stereoscopic microscope (×10, SZ 30; Olympus, Japan) (Duyck *et al.*, 2006). Each patch consisted of a plastic cup (diameter 2.8 cm, height 1 cm) that contained 3.65 g of an artificial diet. The larval diet was composed of brewers' yeast, wheat germ and sugar in even proportions. Citric acid, sodium benzoate and methylparaben were used as preservatives and agar was used as a gelling agent (Salles, 1992). Both species were reported to develop successfully on this diet (Jaldo *et al.*, 2001; Ricalde *et al.*, 2012). After larvae were transferred, the patches were placed inside individual plastic containers (diameter 5 cm, height 13 cm) on top of a layer of vermiculite as a pupariation substrate. After 6 days, vermiculite was sifted and pupae were collected and weighed in groups with a precision scale (0.1 mg, APX-200; Denver Instrument, Bohemia, New York). This procedure continued on a daily basis until there were no larvae in the patch. This ensured that the pupae were weighed within the first 24 h after they exited the patch. Pupae were placed in a glass container with vermiculite and kept under controlled conditions at $25 \pm 1\,°C$ and $70 \pm 10\%$ relative humidity until adult emergence.

Larval densities and variables recorded

For *A. fraterculus*, the numbers of larvae transferred were: 5 (control), 30, 40, 50, 60, 70, 80, 90, 100 and 150 with 32, 20, 20, 20, 19, 20, 20, 20, 12 and 11 replicates, respectively. For *C. capitata*, the numbers of larvae transferred to the patches were: 5 (control), 20, 30, 40, 50, 60, 70, 80, 90, 100 and 150 with 44, 16, 16, 16, 20, 20, 20, 19, 30, 10 and 10 replicates, respectively. The lower number of replicates in those treatments of high densities was the result of an experimental constraint because transferring more than 100 larvae was very time consuming with respect to running more replicates at the same time. On the other hand, the control treatment (five larvae) had a larger number of replicates because some of the estimated parameters were percentages and were therefore to sensitive to the low number of larvae being transferred. Hence, we included as many replicates as possible, aiming to minimize the methodological error. The variables recorded were: larval survival (number of pupae recovered/number of larvae transferred × 100), pupal weight (g), duration of larval stage (number of days elapsed from the day the larvae were transferred to diet until the day the pupae were collected) and pupal survival (number of adults recovered/number of pupae recovered × 100).

Statistical analysis

The effect of larval density on the variables evaluated was analyzed using a generalized linear model, with larval density as fixed factor, and larval survival, pupal weight, duration of the larval stage and pupal survival as dependent variables. To obtain the most appropriate structure of variance, the Akaike information criterion was used. Multiple comparisons were performed using Fisher's least significant difference ($\alpha = 0.05$). All the analyses were conducted using Infostat, 2014 (Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina).

The dispersion of values was studied for each of the treatments and variables via the coefficient of variation (CV = SD/mean × 100). The CV was calculated for each species under study to compare the degree of homogeneity of values.

Results

In *A. fraterculus*, larval survival was not statistically different among densities ($F_{9,185} = 0,830$, $P = 0.592$) (Fig. 1A). In *C. capitata*, this parameter was affected by larval density ($F_{10,227} = 13,960$, $P < 0.001$). When the density of *C. capitata* larvae in the patch increased, larval survival decreased. The comparison among treatments showed differences between low densities (below 40 larvae/patch) and high densities (above 60 larvae/patch), with the density of 50 larvae/patch showing intermediate values (Fig. 1B).

For the two species, pupal weight decreased when the density of larvae in the patch increased (*A. fraterculus*: $F_{9,185} = 16,560$, $P < 0.001$; *C. capitata*: $F_{10,227} = 518,7$, $P < 0.001$) (Fig. 2). For *A. fraterculus*, the comparison among densities allowed the detection of four different groups: (i) 5 larvae/patch (control density); (ii) 30, 40 and 50 larvae/patch; (iii) 60, 70, 80, 90 and 100 larvae/patch; and (iv) 150 larvae/patch (Fig. 2A). For *C. capitata*, the reduction in pupal weight was more gradual and a larger number of groups was detected (Fig. 2B).

The duration of the larval stage showed significant differences among densities for both species (*A. fraterculus*: $F_{9,185} = 4,51$, $P < 0.001$; *C. capitata*: $F_{10,227} = 4,42$, $P < 0.001$) (Fig. 3). For *A. fraterculus*, two groups were identified: (i) densities below 60 larvae/patch had longer developmental times and (ii) densities ranging from 80 to 150 larvae/patch had shorter developmental times (Fig. 3A). The density of 70 larvae/patch showed intermediate values. For *C. capitata*, the comparisons did not show a clear relationship between density and developmental time. Although larval density had a significant effect on developmental time, the mean values of this variable moved within a range that was markedly shorter (approximately 0.3 days) than that found for *A. fraterculus* (approximately 1 day) (Fig. 3B).

Pupal survival was significantly affected by larval density in both species (*A. fraterculus*: $F_{9,185} = 7,39$, $P < 0.001$; *C. capitata*: $F_{10,227} = 8,41$, $P < 0.001$). In *A. fraterculus*, mean pupal survival values varied slightly at densities ranging from 5 larvae/patch to 90 larvae/patch and decreased significantly only at extremely high densities (Fig. 4A). *Ceratitis capitata* showed a similar pattern (i.e. only the highest density showed a significant reduction in pupal survival) (Fig. 4B).

The coefficients of variation were always higher for *A. fraterculus* than for *C. capitata*, for all variables (Table 1). For *C. capitata*, the CV was almost invariable across treatments, with some increase with density for pupal weight. For *A. fraterculus*, the CV increased with density for pupal weight, whereas the rest of the variables showed the opposite tendency.
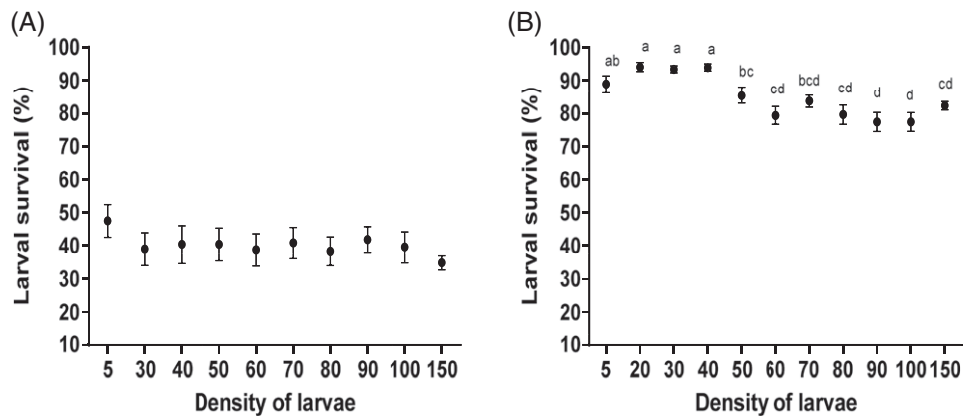
Figure 1 Percentage of pupae recovery at different densities for the two species. The density of 5 larvae/patch was considered as the control treatment. The black points indicate the mean values and the whiskers indicate the SE. Treatments with different lowercase letters indicate significant differences. (A) *Anastrepha fraterculus*. (B) *Ceratitis capitata.*
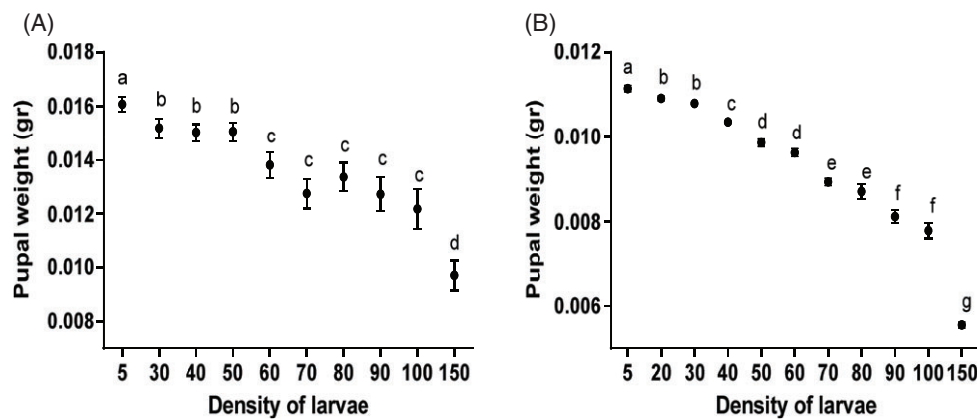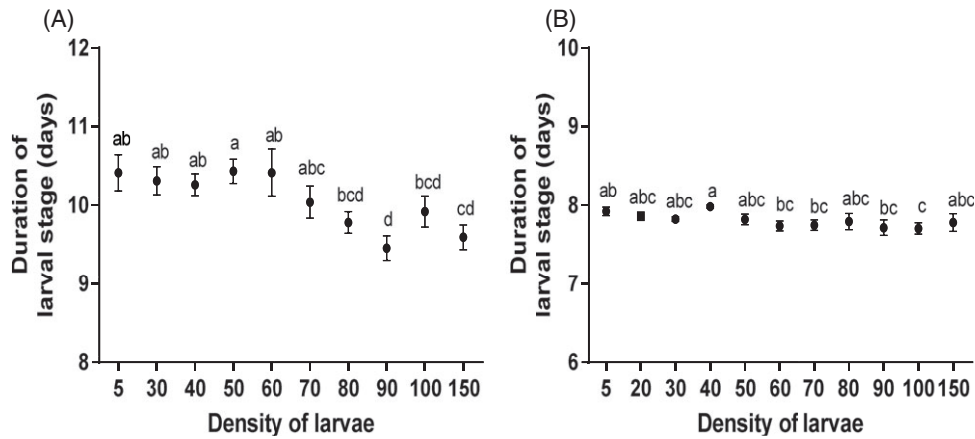

Figure 2 Pupal weight at different densities of larvae for the two species. The density of 5 larvae/patch was considered as the control treatment. The black points indicate the mean values and the whiskers indicate the SE. Treatments with different lowercase letters indicate significant differences. (A) *Anastrepha fraterculus*. (B) *Ceratitis capitata.*

Discussion

Ceratitis capitata and *A. fraterculus* are fruit fly species that are frequently found sharing the same fruit with conspecific larvae (Ratkovich & Nasca, 1953; Prokopy *et al.*, 1978; Malavasi & Morgante, 1981; Vargas *et al.*, 1984; Papaj *et al.*, 1989; Prokopy & Duan, 1998; Devescovi *et al.*, 2015). Because larvae are incapable of leaving the fruit in search of non-infested (or less infested) fruit, they are forced to share nutritional resources and eventually compete for them. In the present study, the effect of intraspecific competition during the larval stage for these two species was studied under controlled laboratory conditions. To our knowledge, the present study represents the first contribution to understanding the effects of intraspecific competition for *A. fraterculus*. The two species analyzed in the present study showed similarities as well as differences in the way they responded to an increasing larval density. This appears to illustrate the different strategies employed when these species face a food shortage and can be interpreted in relation to their oviposition behaviour and life histories.

Larvae of *C. capitata* showed a consistent reduction in pupal weight as the larval density increased. This parameter is well correlated with adult size, and small adult females were reported to be significantly less fecund than larger conspecifics (Averill & Prokopy, 1987; Nufio & Papaj, 2004). At intermediate densities, this effect was accompanied by a significant (approximately 15%) reduction in larval survival. These results agree with those obtained by Papaj *et al.* (1989), who found a decrease in *C. capitata* larval survival as the clutch size increased, as well as with those obtained by Prokopy and Duan (1998), who reported that pupal weight decreases significantly when the number of ovipositions in the fruit increases. Dukas *et al.* (2001) found that, under larval competition, pupal survival and the duration of the larval stage decreased for *C. capitata*. Conversely, in the present study, the *C. capitata* larvae that survived until the pupal stage showed no significant reduction in survival, even at the extreme density (150 larvae/patch) and the duration of the larval stage was not affected. These differences might be related to methodological differences. On the one hand, Dukas *et al.* (2001) used kumquat fruit [*Fortunella japonica* (Thunb.) Swingle] instead of an artificial medium. Artificial diets are generally more

Figure 3 Duration of larva stage at different densities of larvae for the two species. The density of 5 larvae/patch was considered as the control treatment. The black points indicate the mean values and the whiskers indicate the SE. Treatments with different lowercase letters indicate significant differences. (A) *Anastrepha fraterculus*. (B) *Ceratitis capitata.*
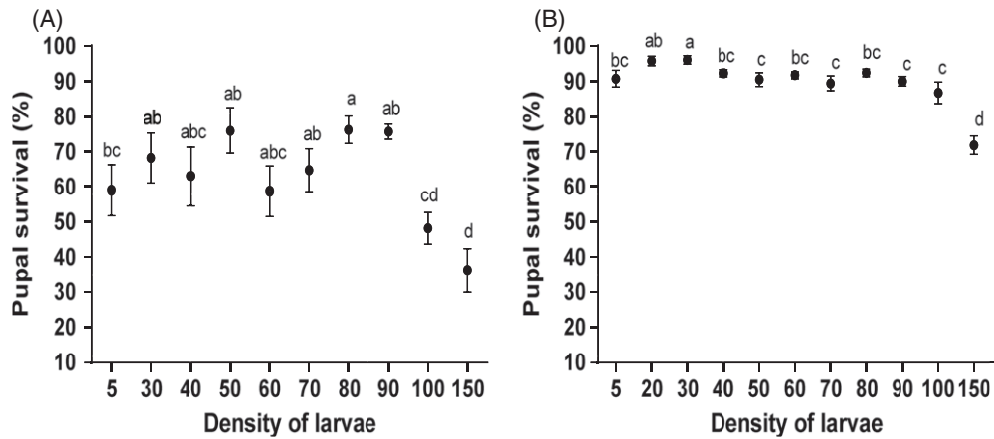
Figure 4 Percent of adult emergence at different densities of larvae for the two species. The density of 5 larvae/patch was considered as the control treatment. The black point indicates the mean value and the whiskers indicate the SE. Treatments with different lowercase letters indicate significant differences. (A) *Anastrepha fraterculus*. (B) *Ceratitis capitata.*

nutritious than fruit. In our particular case, the diet contained high levels of protein and fatty acids, and this might have affected pupal survival differentially. On the other hand, the densities used in the study by Dukas *et al.* (2001) may have been higher than the those employed in the present study. In sum, evidence for *C. capitata* suggests that the parameter most sensitive to larval competition is the weight of the pupae. Furthermore, for the variables affected by the increased density, the coefficient of variation was maintained at low values, showing a homogeneous variation around the mean.

Similarly to *C. capitata*, *A. fraterculus* pupal weight decreased with larval density. However, this decrease was not accompanied by a decrease in larval survival but, instead, by a decrease in the duration of the larval stage, which may have implications for population dynamics in the field. A more rapid developmental time may result in a way of escaping competition and parasitism, thus increasing survival chances. Larval survival in *A. fraterculus* remained constant as the density increased. This resulted in an operationally lower density, and mortality only began to exhibit density-dependent effects at extreme densities. The same pattern was also reported by Jones *et al.* (1996) for *Drosophila subobscura* (Collin) (Diptera: Drosophilidae). This suggested that larval mortality is independent of the density during the first 3 days after hatching, and then becomes density-dependent as development continues. Also, larval survival in *A. fraterculus* was generally lower (overall mean of approximately 40%) than that in *C. capitata* (overall mean of approximately 80%). Therefore, it is not only possible that *A. fraterculus* exhibits the same pattern as *D. subobscura*, but also that *A. fraterculus* larvae is affected differentially by the experimental conditions (transfer of recently emerged larvae, artificial larval medium, etc.) compared with *C. capitata*. In any case, this low and sustained survival found in *A. fraterculus* does not affect our conclusions about the behaviour of this variable. The coefficient of variation took higher values compared with *C. capitata* for all the variables analyzed and, for the case of pupal weight, showed greater heterogeneity around the mean when the density increased. These results may suggest different levels of aggression when larvae face increasing levels of competition. For *A. fraterculus*, as competition levels increase, only a few individuals reach the pupa stage with high

Table 1 Coefficients of variation (%) obtained for the variables larval survival, pupal weight, duration of larval stage and pupal survival in the treatments set for *Anastrepha fraterculus* and *Ceratitis capitata*

Larval density	Larval survival		Pupal weight		Duration of larval stage		Pupal survival	
	Anastrepha fraterculus	*Ceratitis capitata*	*Anastrepha fraterculus*	*Ceratitis capitata*	*Anastrepha fraterculus*	*Ceratitis capitata*	*Anastrepha fraterculus*	*Ceratitis capitata*
5	59.31	18.3	9.56	4.6	11.95	4.51	68.93	17.5
20	—	5.89	—	2.16	—	2.25	—	5.65
30	55.74	4.52	10.31	1.25	7.82	1.61	47.21	4.93
40	63.09	4.66	8.88	1.31	6.07	1.17	58.97	4.62
50	54.01	13.46	9.78	4.59	6.68	4.28	37.51	10.67
60	55.4	15.33	15.48	4.56	12.98	3.6	47.89	5.12
70	50.61	9.92	18.52	4.43	8.86	3.82	43	10.78
80	50.01	16.74	17.92	8.6	6.32	5.97	23.02	5.14
90	41.79	16.87	22.05	8.65	7.45	5.67	12.91	6.57
100	40.36	20.18	21.07	13.21	6.79	5.16	32.85	19.37
150	20.13	4.85	19.05	4.23	5.48	4.56	56.88	11.77

pupal weights improving their fitness and the rest of the pupae reach low pupal weights. Conversely, for *C. capitata*, the number of individuals that develop to pupa is comparatively high, exhibiting a marked decrease in pupal weight, which suggests a potential negative impact on adult fitness.

The way in which *C. capitata* and *A. fraterculus* responded to competition suggests that the individuals of these two species may have different patterns of resource partitioning. The mild reduction in larval survival and the homogeneous reduction in pupal weight in *C. capitata* indicate that this species shows a strategy similar to that described as scramble competition by Nicholson (1954). Allen and Hunt (2001) proposed that these parameters are critical for demonstrating that a species adopts a scramble-like competition strategy at the intraspecific level. On the other hand, for *A. fraterculus*, larval competition could not be characterized easily by just one type of competition. For this species, pupal weight showed an overall higher heterogeneity among individuals, such that a few individuals showed a slight or no detrimental effect of sharing the resource, whereas other individuals experienced strong negative effects, suggestive of contest competition. However, larval survival was essentially not affected by density, and a significant effect was found only at the most extreme density. This pattern suggests that this species would exhibit a scramble-like competitive strategy. Allen and Hunt (2001) reported a similar pattern for flies of the family Tachinidae. It was found that the variability in the number of larvae to pupate within a clutch was evident as the clutch size increased, as expected under contest competition. However, depending on clutch size, this species exhibited different strategies: survival remained constant when the clutch size was small, as in a contest competitive strategy, and declined rapidly when the clutch size was large, suggesting scramble competition.

The competitive strategies developed by larvae of some Tephritids show good correspondence with characteristics of their life history. Fletcher (1987) found that *Bactrocera oleae* (Gmelin) larvae engage in contest competition. In this species, generally only one larva per olive fruit is capable of completing development and larval competition is frequent when more than one female lay its egg in the same host (Christenson & Foote, 1960).

By contrast, in tephritid species, females lay more than one egg per host, larvae engage in scramble competition, and the limited access to resources results in reduced larval fitness but not in direct mortality (Fletcher, 1987). *Ceratitis capitata* and *A. fraterculus* differ markedly in their clutch sizes: *C. capitata* exhibits an average clutch size that reaches seven eggs per oviposition (McDonald & McInnis, 1985; Dukas *et al.*, 2001), which implies that its larvae usually develop in groups, whereas *A. fraterculus* females lay mostly only one egg per oviposition (Nascimento & de Oliveira, 1996), with a few cases of more than one egg per clutch. In addition, females of these species use a host-marking pheromone (Prokopy *et al.*, 1982) that alerts other females to avoid ovipositing in already infested fruit. According to what has been observed in other Tephritidae, it should be expected that, in a continuum from scramble to contest competition, *C. capitata* would be closer to a scramble strategy than *A. fraterculus*. The results of the present study support this association and indicate that the relationship between clutch size and larval competition may be extended to other species. However, in the case of *A. fraterculus*, this association is not clear and may depend on the density of larvae in the patch. This is consistent with the results of a study by Burrack *et al.* (2009) for *B. oleae*, where they observed a reduction in fitness and greater mortality at densities of more than one larva per host, suggesting that this species engages in scramble rather than in contest competition.

The maximum growth rate and the density-dependence of mortality (in contest or scramble strategies) have an interacting effect on the invasive capacity and the species' ability to coexist (Aikio *et al.*, 2008). When a native and an invasive species have the same level of density dependence, the resident species could be replaced by the invasive species if it has a higher growth rate and a scramble type of intraspecific competition. A higher maximum growth rate results in a higher density-dependent equilibrium, giving an advantage under competition (Aikio *et al.*, 2008). Our results partially match these concepts. *Ceratitis capitata*, which is recognized as a highly invasive species (Duyck *et al.*, 2006), showed a strategy very similar to that described as scramble competition, whereas *A. fraterculus*, which is a native species with no record of successful invasions to new habitats, showed a more intermediate type of competition

between scramble and contest. The strategies adopted by these species could partially be responsible for the success exhibited by *C. capitata* with respect to invading and colonizing habitats that were once inhabited only by *A. fraterculus*.

Intraspecific larval competition normally leads to limited food acquisition during the developmental stage. This, in turn, affects biological parameters at this and subsequent developmental stages (in our case, pupa and adult) (Quiring & McNeil, 1984; Averill & Prokopy, 1987; Visser, 1994; Nakamura, 1995; Iwao & Ohsaki, 1996; Allen & Hunt, 2001; Andersen & McNeil, 2001; Navarro-Campos *et al.*, 2011). Our study of intraspecific larval competition allowed the identification of parameters that are sensitive to increases in larval density in both *A. fraterculus* and *C. capitata*. In light of our results, it is clear that these species use different strategies when the density increases under similar circumstances. *Ceratitis capitata* shows a strategy similar to scramble competition whereas, for *A. fraterculus*, the competitive strategy adopted depends on the competitive situation in which it is found. This information could be used to rank these species in terms of their invasive potential and to classify them in relation to the risk of invasion, depending on their competitive skills. According to Aikio *et al.* (2008) because *C. capitata* depicts a scramble-like strategy, it should be ranked above *A. fraterculus* with regard to invasive potential, showing a strategy that more closely resembles contest competition. All of our experiments were performed with insects from laboratory colonies reared on an artificial diet. It could be argued that laboratory flies may be adapted to relatively high larval densities and it is possible that our experimental design underestimates the potential for larval competition in wild populations. Further experiments with wild populations should be performed to determine to what extent the strategies demonstrated in the present study are affected by laboratory adaptation.

Acknowledgements

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