Host use and Resource Sharing by Fruit/Seed-Infesting Insects on *Schoepfia schreberi* (Olacaceae)

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ABSTRACT   The interactions between the fruit fly *Anastrepha spatulata* Stone (Diptera: Tephritidae) and two species of moths, the gelechiid *Coleotechnites* sp. and an unidentified tortricid species, were examined on their effects on seed production in terms of their exploitation within fruits of *Schoepfia schreberi* J.F. Gmel (Santalales: Olacaceae). The study was carried out in three experimental sites during 3 yr. Under conditions of abundant fruit, *A. spatulata* was the dominant exploiter at the population level, as shown by its ability to infest the largest number of fruits of the three herbivores and substantially displace its moth competitors. In a separate experiment, when resource-partitioning species were excluded, *A. spatulata* infested twice as many fruits as the two moth species (44.3%). Field observations examined the ability of *A. spatulata* to locate suitable fruits. We found that, the variation in fruit characters influenced fruit suitability in relation to its size (4.1261 ± 0.0272 mm [mean ± SE]) and weight (0.0618 ± 0.0005 mg [mean ± SE]). Uninfested fruits produce viable seed but the interaction of all species (exploiting for the fruits) led to limited seed formation.

KEY WORDS   *Anastrepha spatulata*, fruit-seed predator, *Coleotechnites* sp., exploitation, species coexistence

Ecological communities are groups of species with different spatial and temporal strategies for resource exploitation. One of the most common and potentially most important outcomes of the interaction of a guild of species exploiting a common resource is coexistence with varying degrees of mutual influence. This coexistence occurs in many guilds of herbivorous insects, which interact both directly through competition and indirectly through the effects of the upper trophic level organisms affecting the interacting herbivores (Strong et al. 1984, Price 2003, Craig 2007, Ohgushi et al. 2007).

Herbivorous insects not only tend toward specialization on particular plants or plant groups, but also on particular plant parts (e.g., fruits, foliage, stems, roots) (Schoonhoven et al. 2005). However, it is common for guilds of several unrelated insects to exploit the same plant part in any particular species. The effects of insects are particularly important with respect to plant reproduction, and insect damage is frequently the most important cause of fruit abortion and seed mortality (Herrera 1989, Sallabanks and Courtney 1992). Given that seed exploitation can be an important influence on growth and spread of plant populations, understanding the interactions among the various vertebrates or invertebrates that consume fruits or seeds of a particular plant is necessary to fully appreciate the influence of each species on the population dynamics of the host plant (Trasevet et al. 1995, Wenny 2000, Silvius and Fragoso 2002, Maron and Crone 2006, Rodríguez-Pérez et al. 2011). For instance, fruiting strategies to minimize or compensate for fruit or seed predation include synchronous or asynchronous fruiting in plant populations (Korine et al. 2000, Bourchier and Crowe 2011), fruit or seed abortion (Grimm 1999, Ostergard et al. 2007), masting (Lázaro et al. 2006), and changes in plant appearance (Juenger et al. 2005).

Many species of insects are specialized to exploit one or a small group of related plants (Bernays and Chapman 1994). This specialization creates communities dominated by species that are superior competitors in securing resources from a given host plant, although species may be displaced from ecological dominance by competitive exclusion if a superior competitor enters the system (Hardin 1960). When resources are abundant and rich in nutrients, individuals of several species may coexist, using the same resource and forming an ecological guild. Such guilds are excellent models to observe the complex interactions stemming from intra- and interspecific competition (Denno et al. 1995, Munday et al. 2001), and

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potentially leading to resource partitioning among the multiples species interacting (Behmer and Joern 2008).

Fruits of *Schoepfia schreberi* J.F. Gmel (Olacaceae) are used by a guild of insects from several orders (Aluja et al. 2000, López and Cervantes 2010, López-Ortega and Khalaim 2012). One of these, *Anastrepha spatulata* Stone (Diptera: Tephritidae), is a specialist exploiter of its fruits. Also, its fruits support the larvae of two species of microlepidoptera and their associated guild of parasitoids (unpublished data, M.L.-O.) Preliminary observations of this guild of fruit or seed-feeding insects suggest that community membership is affected by a complex set of interactions at various trophic levels.

Our main goal was to identify the types of interactions among the principal members of the fruit and seed-feeding guild of insects on *S. schreberi.* In particular, 1) the interactions among *A. spatulata* and two species of Lepidoptera *Coleotechnites* sp. (Lepidoptera: Gelechiidae) and an unidentified tortricid; and 2) understand resource partitioning, if any, that may occur, and measure their impact on seed production. Field observations were used to estimate resource-partitioning values (for fruits) for each of the three herbivores and to estimate the number of fruits producing viable seed. Subsequently, exclusion experiments were performed to estimate maximum attack rates on fruits by individual species and the ability of each species to reduce the fitness of the plant, (estimated as changes in numbers of viable seeds).

We also analyzed if variation in fruit characters influenced selection of fruits for oviposition on *A. spatulata.* In particular, we examined whether there was a relationship between abundance of fruits and coexistence of members of the fruit-feeding guild, and whether life history traits allow a herbivore to dominate the guild by exploiting fruits and seeds of this plant?

Materials and Methods

Experimental Sites. The study was carried out in three sites in the state of Veracruz, Mexico: 1) "La Camelia" (CM) (Alamo, 20° 85′ N, 97° 83′ W; altitude 245 m). The site is dominated by oak and semievergreen tropical forest of medium height, surrounded by extensive citrus plantations; 2) "Osto" (OT) (Tlaltetela, 19° 18′ N, 96° 50′ W; altitude 838 m). The vegetation is a fragmented oak forest mixed with tropical dry forest and pastures; and 3) "Tejeria"(TJ) (Teocelo, 19° 21′ N, 96° 54′ W; altitude 924 m). The vegetation consists of a fragmented oak forest intermixed with coffee plantations and orchards [orange, *Citrus x sinensis* (L.) Osbeck, and guava, *Psidium* spp.].

Schoepfia schreberi is a hemiparasitic plant (Werth et al. 1979). It can be found in various vegetation types ranging from deciduous tropical forests to dry oak forests, and has a wide geographical distribution (Tropicos.org 2013). Flowering and fruit set in the study sites occurred from December through February. Each tree had two cycles of flowering, one of

which was dominant in terms of fruit formation, as determined by biotic (bud and flower predators) and abiotic factors (principally high temperatures and lack of rain).

The Arthropods. Adults of *A. spatulata* and of the two fruit-feeding moth species were present in December and January. A larvae of *A. spatulata* can complete development in a single fruit, whereas larvae of the two lepidopterans require several fruits to complete their development. Larvae of the unidentified tortricid complete their development and pupate outside the fruit, whereas those of *Coleotechnites* sp. pupate within the fruit (before pupation they bore an exit hole and then seal it with a thin cap of material to facilitate the subsequent emergence of the adult). All three herbivores have the potential to significantly reduce plant fitness through seed destruction, and may destroy all seeds in affected fruits.

Study No. 1: Evaluation of the insect community and rates of seed production. Observations were made in CM and OT on the insect community of fruits of *S. schreberi* during the flowering and fruiting periods of 2009, 2010, and 2011. At each site we placed per experimental tree one funnel trap (0.60 by 0.08 m, upper and lower diameters, and 0.5 m in height) to catch fruits. Traps were distributed along transects covering 100 h in CM (trees were in shaded areas surrounded by continuous vegetation of different heights and ages), and 62 h in OT (trees were in more open areas surrounded by isolated fragments of vegetation). Traps were checked every 10–15 d, to avoid losing insects to emergence. For each year we sampled 22 trees per site, and recorded the temperature and rainfall at each site (December to May). During the fruiting period of *Schoepfia schreberi* (December through May) for 2009 through 2011, the average temperature in CM was 22.44°C, minimum 12.1°C and maximum 35.08°C, whereas in OT the average was 23.64°C, minimum 8.00°C and maximum 45.00°C, and precipitation mean at CM was 34.69 mm and OT 20.74 mm. Fruits were collected continuously from fruit set until no fruit remained on the tree. Fruits collected in traps were taken to a laboratory at Instituto de Biotecnologia y Ecologia Aplicada in Xalapa, Veracruz. They were weighed and placed in plastic buckets whose tops were covered with organdy fabric and held outdoors in the shade until all insects had emerged (3–4 wk). All emerging adult insects were counted and identified to species level. The number of viable seeds produced per kilogram of fruit in each bucket was determined by counting fruits and viable seed. Finally, specimens of the two moth species were deposited in the Mississippi Entomological Museum-Mississippi State University and in the Hasbrouck Insect Collection-Arizona State University. The gelechiid moth recovered was identified as a new species of *Coleotechnites* n. sp. (S. Lee, Arizona State University, personal communication.

Study Number 2: Levels of Infestation and Effects on Seed Production. This experiment took place in January and February of 2009 and 2010 at TJ and OT. At each site, we selected five mature *S. schreberi* trees

(3–5 m tall) dispersed over each study site. Within each study tree, we selected four branches at random; each one with 60–80 fruits, before oviposition by the insects being studied had started. Each branch was enclosed with an organdy sleeve cage to exclude insect attack on developing fruits. Sleeves were 40 by 50 cm and were supported internally by a wire frame to give sleeves a fixed shape. After 10–15 d, the number of fruits in each cage was reduced to 50 and treatments were established. In treatment 1 (T1), fruits were exposed to moths only. For this treatment, the original organdy sleeve that was enclosing the branch was removed and replaced with fine plastic mesh (≈5-mm-mesh hole size, a size that allowed adult moths to enter cages (the tortricid's body was 1.5 wide by 4 mm long and the *Coleotechnites* sp. moth's body was 3.9 wide by 7.1 mm long), but which excluded the tephritid fly. Treatment 2 (T2) consisted of fruits exposed to attack by flies only. In this treatment, two gravid *A. spatulata* females were placed inside of one of the originally caged branches. To obtain a rate of oviposition similar to that which would have occurred naturally, females were captured from the same tree, from uncaged branches when they were observed ovipositing. Flies were removed from cages after 10 d. Treatment 3 (T3) consisted of the control branches on which the organdy cages were left in place until the end of the experiment. Treatment 4 (T4) was the positive control, which consisted of an uncaged branch exposed to attack by all locally occurring insects. The fruits from treatment 4 were collected in a funnel trap as they fell from the tree. For the other three treatments (T1, T2, and T3), once fruits were mature, but before any insects they might contain (this being possible only for T1 and T2) had emerged, branches were cut and taken to the laboratory to determine the number of fruits, seeds, and larvae or pupae of moths (T1) or fruit flies (T2). Similar measurements were made of fallen fruits collected from the positive control (T4).

Study Number 3: Factors Affecting Fruit Selection by *A. spatulata*. This experiment was carried out in December and January of 2010 and 2011 at TJ and OT. We selected four branches of four trees (80–100 fruits each), and covered each branch with an organdy fabric sleeve (50 by 50 cm) to exclude all insects. During the first week of the experiment, naturally occurring oviposition by wild flies was observed frequently on fruits of nearby branches (Fig. 1a). Further on, we systematically observed oviposition of wild flies on fruits previously protected by sleeves. We selected one of the sleeved test branches, and the sleeve was removed to expose fruits between 0900 and 1700 hours. Usually one to three female flies were attracted to the fruits of the uncovered branch (Fig. 1b). Fruits considered to have been selected by flies were those on which a gravid female landed and inserted its ovipositor (Fig. 1c), and then withdrew and dragged the ovipositor on the exterior surface of the fruit, presumably depositing a marking pheromone (Fig. 1d). The fly's host marking behavior was similar to that reported for other fruit infesting tephritids (Nufio and Papaj

2001). We also estimated the time between ovipositor insertion and withdrawal. We collected 10 fruits selected by wild flies for oviposition and 40 more fruits at random of the 16 marked branches. All fruits were returned to the laboratory where they were weighed (Ohaus AdventurerPro, Parsippany, NJ) and measured (length and width) with an electronic caliper (Hangzhou United Bridge Tools Co., Ltd., Hangzhou, China). Only 160 fruits were selected for oviposition by female insects.

Data Analysis: Study Number 1. We used a Wilcoxon–Mann–Whitney test to determine if there were differences among study sites in the numbers of each species in the insect guild attacking *S. schreberi* fruits, the number of fruits collected, the numbers of each insect emerged, and the number of viable seeds remaining. We used Pearson's product moment correlation coefficient (Cox and Hinkley 1974) to determine if the number of *A. spatulata* reared was correlated to the number of fruits collected.

Study Number 2 (Cage Exclusion). The data were analyzed using a hierarchical binary model with three levels (level 3 was study location [$k = 1,\ldots,2$], level 2 was tree [$j = 1,\ldots,10$], and level 1 was fruit [$i = 1,\ldots,50$]), modeling the probability that a given fruit would be attacked by insects. The response variable was thus binary, with fruits either being attacked or not attacked, given as y_{ijk} (fruit not attacked) and y_{ijk} (fruit attacked), and the overall model is given as in equation 1

$$logit\ p_{ijk} = \log \frac{p_{ijk}}{1 - p_{ijk}} = \beta_0 + \beta_1 D1_{ijk}$$
$$+ \beta_2 D2_{ijk} + \beta_3 D3_{ijk} + w_k + u_{ij} \quad [1]$$

where p_{ijk} is the probability that fruit i in three j and location k was attacked; $D1$, $D2$, and $D3$ are indicator variables used to identify treatment and which were coded according to the reference cells method (Hosmer and Lemeshow 2000); using treatment 3 as the reference class, β_1, β_2, β_3 are regression coefficients associated with treatment effects. In this model it is assumed that $w_k \sim N(0,\sigma_w^2)$ and $u_{ij} \sim N(0,\sigma_u^2)$ are random effects that induce correlation between observations at different levels of hierarchy.

Study Number 3.

On factors influencing the preference of *A. spatulata* to oviposit on fruits of a particular size or weight, another hierarchical binary model was developed with three levels (level 3: tree [$k = 1,\ldots,4$], level 2: branches [$j = 1,\ldots,4$], and level 1: fruits [$i = 1,\ldots,50$]). The response variable was denoted as y_{ijk}, which is to say the data for fruit i on branch j and tree k, which again can take on two values: 0 (fruit not attacked) or one (fruit attacked). The probability that a fruit would be attacked is then estimated as a function of the length, width, and weight of a fruit as

$$logit\ p_{ijk} = \log \frac{p_{ijk}}{1 - p_{ijk}} = \beta_0 + \beta_1 Weight_{ijk}$$
$$+ \beta_2 Length_{ijk} + \beta_2 Wide_{ijk} + w_k + u_{ij}, \quad [2]$$
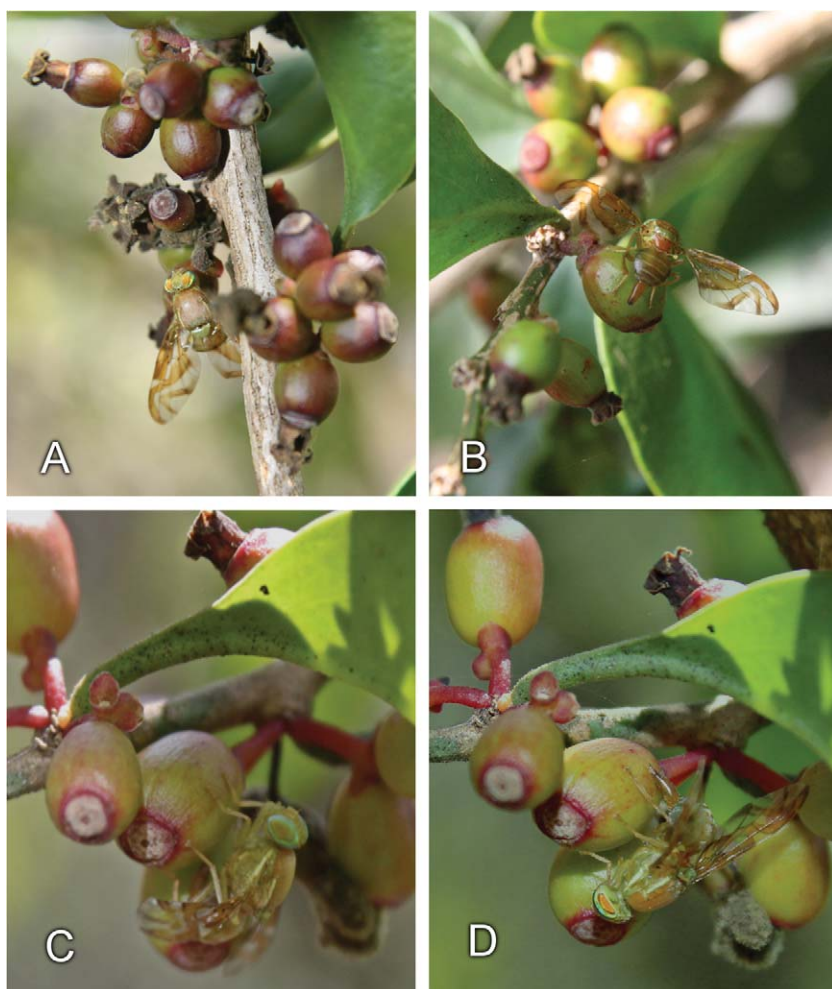
Fig. 1. Females of *A. spatulata* on fruits of *S. schreberi*: arriving at the beginning of the season (A), searching (B), ovipositing (C), and marking attacked fruit (D). (Online figure in color.)

where $w_k \sim N(0,\sigma_w^2)$ and $u_{ij} \sim N(0,\sigma_u^2)$ are random effects that induce correlation between observations at different levels of hierarchy. These models were fitted using the GLIMMIX procedure in the program SAS 9.1 for Windows (SAS Institute 2004).

Results

Study Number 1. We collected 51,909 fruits in the three study years (2009–2011). More fruits were collected at OT (63%), as compared with CM (37%). At CM fruit production occurred from January to May (Fig. 2a), whereas at OT fruits only were produced from January to March (Fig. 2c).

The level of fruit predation was high (few fruits formed seeds) (Fig. 2a and c). Infestation levels for each insect varied significantly between months: moth species sp. number 1 (tortricid) ($\chi^2 = 7.2742$, df = 1, $P = 0.0070$), the gelechiid *Coleotechnites* sp. ($\chi^2 = 9.4818$, df = 1, $P = 0.0021$), and the tephritid fly *A. spatulata* ($\chi^2 = 4.2141$, df = 1, $P = 0.0401$). In contrast,

there were no significant differences among dates or locations in the proportion of fruits producing seeds ($\chi^2 = 0.0014$, df = 1, $P = 0.9697$); of all fruits examined, only 2.44 and 1.61% produced seeds at CM and OT, respectively. Trees only produced fruits once per year during the sampling period for both sites. Temperatures during the fruiting period were less variable at CM than at OT, whereas monthly precipitation was higher at CM than at OT.

We found a positive association between the number of available fruits on each of the collection dates and the number of fruits attacked by *A. spatulata* ($r = 0.6459$, $P = 0.0021$), the tortricid moth sp. number 1 ($r = 0.5821$, $P = 0.0072$), and the *Coleotechnites* sp. (Gelechiidae) ($r = 0.7588$, $P = 0.0001$) (Fig. 2). We found a trend for peak numbers of *A. spatulata* to coincide on dates when the greatest number of fruits dropped from trees (Fig. 2b and d). However, the highest numbers for the tortricid species were early in the first fruit collections. The abundance of the gelechiid, *Coleotechnites* sp., was proportional to the
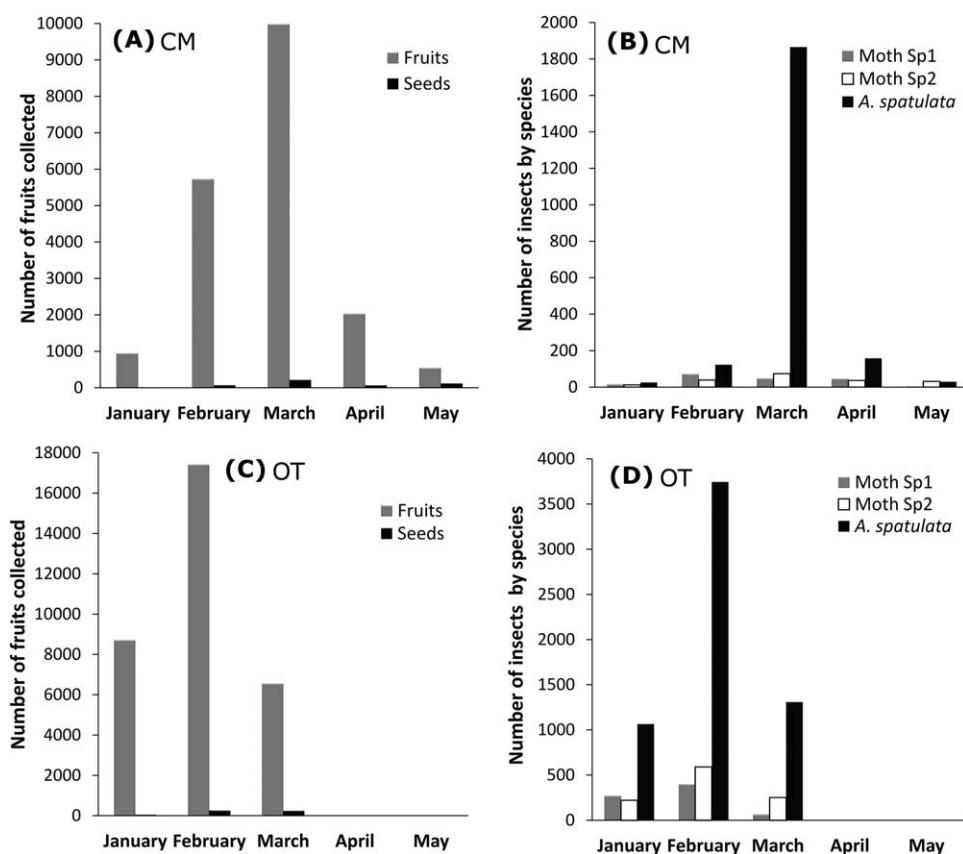
Fig. 2. Quantities of fruits per unit area dropping into fruit traps and the number of viable seeds they contain over the whole of the fruiting season at the study sites La Camelia (A) and Osto (C), and the number of insects reared from the collected fruits at the study sites La Camelia (B) and Osto (D) for 3 yr (2009–2011).

number of fallen fruit throughout the sampling period. We also found for both sites an association between the number of available fruits and the number of emerging *A. spatulata* ($r = 0.646$, $P = 0.0020$) (Fig. 3).

Study Number 2. Each exclusion treatment exhibited a distinct effect (Fig. 4a). Although in T3 there were no infested fruit, 37.3% of fruits fell either by abortion or by unknown causes. In T1, insect attack was 4.57 times more likely than for the control (value obtained from the exponential of the coefficient for the treatment effects, i.e., $\exp(152) = 4.57$, Table 1; for more details on this approach see Hosmer and Lemeshow (2000)). Similarly, the probability of a fruit being attacked in T2 was 7.3 times greater than the control. For T4, where fruits were exposed to attacks by all insects insects and other uncontrolled factors, the probability of attack was 74.44 times greater than the control. The percentage of fruits infested by different species varied distinctly per treatment; in T1 7.2 and 4.2% of fruits were infested by the tortricid sp. number 1 and by the gelechiid *Coleotechnites* sp., respectively. For T2 44.3% of fruits were infested by *A. spatulata*. The effect of competition among these species was seen in T4, in which 1.6, 1, and 5.1% of fruits were infested by the tortricid sp. number 1, by the gelechiid moth *Coleotechnites* and by *A. spatulata*, respectively.

In T3 62.7% of fruits yielded seed. In contrast, in T1 only 28.9% of fruits produced seeds and in T2 it decreased to 20.6%. In T4 only 2.6% of fruits produced seed, a level similar to the field survey (Study # 1).
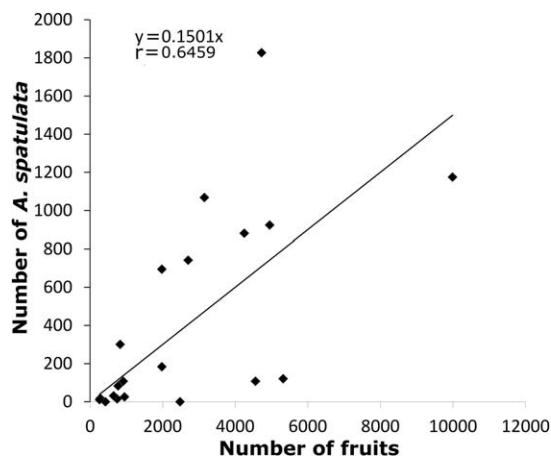

Fig. 3. Relationship between the number of fruits collected per unit area and the number of fruit flies (*A. spatulata*) emerging from them ($P = 0.0020$, y = number of *A. spatulata* and x = number of fruits).
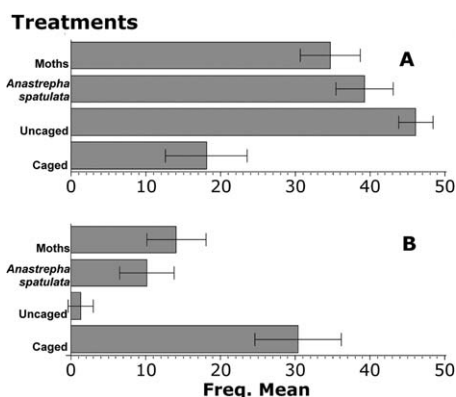
Fig. 4. Comparison among treatments of study number 2 (exclusion of selected herbivores) in terms of (A) average percentage of fruits attacked in each treatment and (B) percentage of fruits with viable seeds at the end of experiment, were 1 = moths present (two species), 2 = *A. spatulata* introduced into closed sleeve cages, 3 = Control (no access for any insects), and 4 = uncaged control (access for all insects).

Study Number 3. The model (2) indicates that fruit length does not affect fruit selection, so a reduced model that includes only fruit weight and width was refitted. These results indicate that fruit selection for oviposition was significantly affected by fruit weight ($T = 2.97$, df = 794, $P \leq 0.003$) and width ($T = 5.00$, df = 794, $P \leq 0.0001$) (Table 2). Flies preferred narrower and heavier fruit (Fig. 5), and for each millimeter of width increase, the probability of oviposition was ca. reduced by half ($\exp[1 \times -0.7930 = 0.4524]$), whereas other variables remained constant. For fruit weight the model indicated that for each 0.023-mg increase in weight, the probability of oviposition doubled ($\exp[0.023 \times 31.0245] = 2.04$). Eight hundred fruits measured and width varied between 2.610 and 5.840 mm, and weight between 0.0150 and 0.0900 mg. Finally, females of *A. spatulata* preferred to oviposit on fruit with an average weight of 0.0618 ± 0.0005 mg, and width of 4.1261 ± 0.0272 mm (mean $\pm$ SE) ($n = 160$).

Discussion

The results of this study show that there was a division of resources among the three fruit-attacking

Table 1. Estimated coefficients for the model (1) of attack on fruit for study number 2 (exclusion of selected herbivores), comparing each treatment with the control (T3)

Treatment		Estimate	Standard error	t	P
Intercept		−0.1155	0.1593	−0.73	0.6005
Moth (two species)	1	1.5219	0.1159	13.13	0.0010
A. spatulata	2	1.9999	0.1206	16.58	0.0005
Uncovered	4	4.3149	0.2233	19.32	0.0003
Control	3	0	.	.	.

Attack rates are highest in the uncovered treatment (T4), where fruits are attacked by all species of seed predators.

Table 2. Estimated coefficients for the model for study no. 3 on variables affecting fruit selection (of *S. schreberi*) by *Anastrepha spatulata*

Variable	Estimate	Standard error	t	P
Width	−0.7930	0.1585	−5.00	0.0001
Weight	31.0245	10.4426	2.97	0.0031

insects, which allowed certain level of coexistence among them. Fruit production was greater at OT than at CM, which was reflected in the greater numbers at the more productive site. Differences may have been because of climatic factors (OT exhibits higher temperature and lower precipitation), site vegetation, or both, which has been suggested for other species (Hobbs and Yates 2003, Agren et al. 2008, Günter et al. 2008). Also, the level of fruit availability at the study sites indicates enough available resource for the three insect species. However, their reproductive behavior seems to exert certain limitations for other insect species (Barat et al. 2007, Van Klinken and Flack 2008). We obtained 15 *A. spatulata* individuals per 100 fruits; the rest of the infested fruit were divided between the two moth species, even though there may be additional causes determining the observed pattern of fruit abortion (Stephenson 1981). We did not study the interactions among these species and with others that could have influenced herbivore (e.g., Ohgushi et al. 2007, López and Cervantes 2010, Track et al. 2012), and result in the low number of fruits actually producing viable seed.

Anastrepha spatulata was a superior intrinsic exploiter over the two moth species studied, and therefore the ability of these species to avoid displacement and remain in the system must lie elsewhere (e.g., fecundity or flight capacity). Our results suggest different periods of maximum fruiting between sampling sites (OT, CM), which may differentially affect the insect–host plant synchronicity (Fig. 2a and c). Mem-
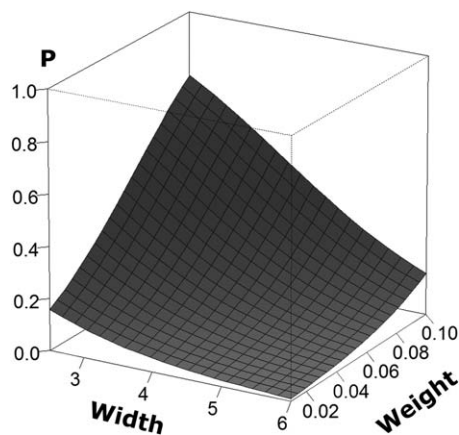

Fig. 5. Probability of attack on fruits of *S. schreberi* by *A. spatulata* in terms of fruit weight and width, modeled as

$$p = \frac{\exp(-0.7930\,Width + 31.0245\,Weight)}{1 + \exp(-0.7930\,Width + 31.0245\,Weight)},$$ with coefficients estimated from the hierarchical binary mode.

bers of the fruit-feeding guild must use their common resource in some distinctive way to coexist. The two moth species, for instance, exhibited different spatio–temporal patterns in resource use (e.g., Vet and Van Alphen 1985, Kaplan and Denno 2007). Also, to reduce interference with *A. spatulata* and *Coleotechnites* sp., the tortricid moth sp. number 1 had its highest incidence on early fruits. Although the moth *Coleotechnites* sp. attacked fruits at the same stage of development as the other moth, we suggest that the moths were able to coexist because of fruit abundance in the period and fruit persistence during the season (Fig. 2b and d).

Our results also suggest that the ability of *A. spatulata* to find viable fruits for oviposition was both demonstrated by the highest level of fruit infestation of the three insects considered and by the positive correlation between the number of flies produced and that of available fruits. Interestingly, although 35% of immature fruits aborted naturally (T2), 44.3% of fruits produced flies and 20.6% produced viable seeds, whereas in T3, 62.7% of fruits produced seeds. This similarity when compared with T2 suggests that flies were able to discriminate against 35% of fruits likely to abort naturally. The selection of viable fruits was enhanced under conditions of unlimited resource availability (Fig. 1, fruit differed significantly in weight and size), which further conditioned the flies' preferences. Results of several studies have similar results. For instance, Ostergard et al. (2007) report that *Bruchus atomarius* L. (Coleoptera: Bruchidae) is able to detect fruits likely to abort based on fruit position and phenology. *Anastrepha spatulata* prefers fruits within certain width and weight ranges (Table 2; Fig. 5). Plants may be using defense immunity, recognizing herbivores via mechanical and chemical cues (Erb et al. 2012) and possibly promoting rapid fruit growth, while the insect's strategy is to use the highest quality fruits within a certain size range. Very large fruits may have physiological or phytochemical deficiencies, making them less desirable (Janzen 1975, Juenger et al. 2005). Studies on other species strongly indicate that insects judge the quality of the fruits they attack. For example, Marchand and McNeil (2006) report that females of *Acrobasis vaccinii* (Riley) (Lepidoptera: Pyralidae) prefer to oviposit only on very large fruits, whereas *Curculio elephas* Gyllenhal (Coleoptera: Curculionidae) appears to only attack hosts of high quality, regardless of whether or not the resource is already occupied (Desouhant 1998).

Spatial heterogeneity (i.e., differences between the two study sites) had an effect on insect abundance and dynamics. However, it had no effect on the number of viable seeds produced. Seeds were produced over a long period (February through May; Fig. 2a and c), indicating that the plant has the potential minimize insect attack. Although we did not study the defensive strategy of the plant, the fact that it produces many flower and fruit suggests that pollination may be critical (M.L.-O., unpublished observation). Despres and Cherif (2004) have shown that a greater investment in fruit production can compensate for the effects of seed

predation. Also, Kolb et al. (2007) showed that the magnitude of seed predation and compensatory changes in production levels may vary in both time and space.

There seems to be a close association between insect life histories and plant seed production. Any one insect acting alone would have only a moderate impact on the plant's seed production (Fig. 4b). Takahashi and Huntly (2010) showed that the removal of herbivores increased seed production in *Artemisia tridentata* L. (Asteraceae). The effect of competition among species was recorded in T4, also the treatment with the joint effects of the three seed predators resulted in very restricted seed production (Fig. 4) making it difficult to single the effect of each species. Consequently, we suggest that the abundance and dynamics of the seed predators of *S. schreberi* limit seed production (Fig. 2) and can be an important influence on the growth and dispersion of these populations (e.g., Crawley and Akhteruzzaman 1988, Maron and Crone 2006, Lewis and Gripenberg 2008).

Even though further studies are needed, our results suggest that the timing and abundance of fruits were important factors determining the abundance of the three insects studied. The fact that *A. spatulata* was the most abundant seed predator, suggests that it is better synchronized with its host's fruiting cycle and has a high capacity to find viable fruits, and the rate of attack on fruits by seed feeding insects or a guild of other factors had an important impact on seed formation, which make the reproductive success of *S. schreberi* variable and uncertain.

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