

## **Influence of Conspecific Presence, Experience, and Host Quality on Oviposition Behavior and Clutch Size Determination in *Anastrepha ludens* (Diptera: Tephritidae)**

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*Females of some insect species adjust the number of ovipositions and clutch size adaptively depending on conspecific density and probably experience. In a series of three experiments, we examined the effect of the presence of conspecifics, host quality, and oviposition experience on oviposition behavior and clutch size determination by females of the polyphagous fruit fly *Anastrepha ludens* (Diptera: Tephritidae). In the first experiment, we determined that grouped (eight females per cage) *A. ludens* females tended to visit and oviposit in more hosts than did solitary females probably as a result of stimulation by the presence of conspecifics. We also determined that females with previous oviposition experience visited and oviposited in more hosts than inexperienced ones. Importantly, when females were grouped, we observed significantly more landings on unoccupied hosts (i.e., devoid of flies) than on occupied ones (i.e., with at least one fly on it). However, oviposition experience, and not female density, was the most important factor affecting clutch size. Naive females deposited larger egg clutches than experienced ones. In the second experiment, we found that oviposition experience and host quality (i.e., clean fruit or fruit covered with a host marking pheromone [HMP] extract), influenced clutch size and the decision of females to defend or not defend the*

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*host. Clutch size and number of fights were greater on clean than on HMP-marked hosts. In the third experiment, we observed that host quality (i.e., size) played a significant role with regard to the number of female fights, host marking behavior, and clutch size. Specifically, females fought and dragged their aculeus longer on small- and medium-sized hosts than on large ones. But this behavior varied according to whether females were kept alone or grouped. Clutch size was greatest in the largest hosts. Considering all the above, we believe that the observed increase in ovipositional activity by grouped *A. ludens* females can be attributed to competition through mutual interference and not social facilitation as has been reported in other tephritid species.*

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**KEY WORDS:** *Anastrepha ludens*; Tephritidae; oviposition behavior; clutch size; experience; host quality; mutual interference.

## INTRODUCTION

Individuals need to accure information about their habitat to make decisions that maximize their fitness. For example, encounters with conspecifics can be used as indicators of the quality and quantity of available resources in a patch (Beuchamp *et al.*, 1997; Giraldeau and Beuchamp, 1999). These encounters can have an inhibitory, a facilitatory, or a neutral effect (Prokopy and Roitberg, 2001). The inhibitory or negative effects of one conspecific upon another are generally associated with competition and resource over-exploitation (Prokopy and Roitberg, 2001). In contrast, through facilitation, a conspecific exercises a positive effect on another one. For example, the presence of one or more conspecifics may stimulate an individual to mate (Reed and Dobson, 1993), synchronize breeding in colonial animals (Emlen and Demong, 1975), or enhance learning about new food items (Forkman, 1991). Such a positive relationship between an individual's fitness and the density of conspecifics has been defined as an Allee effect by Stephens *et al.* (1999). Social facilitation is defined as the behavior exhibited by an individual that is initiated or intensified in the presence of other conspecifics that are performing the same type of behavior (Clayton, 1978) and is a phenomenon observed in animals in which the cost of sharing resource information is less than the cost of searching alone for a resource (Ryer and Olla, 1991, 1992). However, there are situations that can be better interpreted in the context of competition, especially when exhibiting a particular behavior in the presence of conspecifics induces potential negative effects on an individual's fitness.

In insects, both negative (i.e., inhibition) and positive (i.e., facilitation) effects have been documented when individuals are held in groups. For example, it has been observed that females of some species deposit a greater number of eggs when they are in groups than when they are found alone

(Hilker, 1989; Chess *et al.*, 1982; Abernathy *et al.*, 1994). Such an increase in the number of eggs laid has been attributed to social facilitation. Inhibitory effects are reflected in a reduction in search rates and clutch size caused by mutual interference (i.e., any type of interaction between conspecifics that reduces searching efficiency; Visser, 1996; Visser *et al.*, 1999).

In the case of fruit flies (Diptera: Tephritidae), it has been reported that females of the tropical, polyphagous species *Bactrocera tryoni* (Froggart) and *Ceratitis capitata* (Wiedemann) and of the temperate species *Rhagoletis pomonella* Walsh tend to visit and oviposit hosts with greater frequency in the presence of ovipositing conspecifics than when alone (Prokopy and Bush, 1973; Prokopy and Duan, 1998; Prokopy and Reynolds, 1998; Prokopy *et al.*, 1999; Rull *et al.*, 2003). *Ceratitis capitata* females also appear to prefer to land on hosts occupied by conspecifics compared with unoccupied fruits (Prokopy *et al.*, 2000; but see Dukas *et al.*, 2001ab). All the above, has been attributed to social facilitation (Prokopy and Duan, 1998; Prokopy and Reynolds, 1998; Prokopy *et al.*, 1999). Such an interpretation appears reasonable if one considers the fact that *C. capitata*, *B. tryoni*, *B. dorsalis* (Hendel), *Rhagoletis boycei* Cresson, and *R. juglandis* Cresson females tend to reuse the punctures left in the epicarp of particularly hard fruit by other conspecifics, to save time and aculeus (ovipositor) wear (Papaj *et al.*, 1992; Papaj and Alonso-Pimentel, 1997; Drew and Romig, 2000; Prokopy and Papaj, 2000). However, Dukas *et al.* (2001ab), working with *C. capitata*, questioned the existence of social facilitation because under more natural conditions, females did not increase their rate of oviposition when in the presence of conspecifics and there was no positive fitness consequence of laying eggs in an already occupied host. Additionally, females of *B. tryoni* and *C. capitata* generally engage in fights when they coincide on the same fruit and these interactions end with the ejection of one of the individuals (generally the newcomer female) from the host (Pritchard, 1969; Papaj and Messing, 1998; Shelly, 1999).

Oviposition experience and host quality can also influence patch time allocation, host selection, and clutch size decisions in fruit flies and some parasitoids (Rosenheim and Rosen, 1991; Visser, 1996; Visser *et al.*, 1992). For example, a *Leptopilina heterotoma* (Thompson) (Hymenoptera: Figitidae) female with previous experience with a low-quality patch or with high interspecific competition will tend to superparasitize even when alone (Visser *et al.*, 1992). In *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae), females with previous oviposition experience deposit smaller clutches than females without experience (Rosenheim and Rosen, 1991). In fruit flies, experienced females localize hosts and discriminate parasitized ones with greater efficiency (Papaj *et al.*, 1989; Roitberg and Prokopy, 1981). In the apple maggot fly (*R. pomonella*), experience is also needed to recognize

the host marking pheromone that is deposited after an oviposition bout (Roitberg and Prokopy, 1981; Papaj *et al.*, 1990).

In the case of our study object, the polyphagous Mexican fruit fly, *A. ludens* (Loew), populations in nature sometimes reach such high numbers that the simultaneous presence of two or more females on a single fruit is not an uncommon phenomenon. When such is the case, two individuals will likely encounter each other given the small size of their purported ancestral hosts. For example, the yellow chapote (*Sargentia greggii* S. Wats) (Rutaceae) has a diameter of approximately 2 cm and normally supports a maximum of two larvae per fruit (Baker *et al.*, 1944). Another common native host, the matasano or white zapote (*Casimiroa edulis* Llave & Lex) (Rutaceae) measures approximately 5 cm in diameter and has been shown to support up to 60 larvae per fruit (F. Díaz-Fleischer and J. Arredondo, unpublished data). As observed in *B. tryoni* and *C. capitata*, some encounters result in aggressive contests between females, usually ending with the ejection from the fruit of one individual. *Anastrepha ludens* females do not reuse the holes left by the aculeus of another conspecific but can lay clutches of up to 40 eggs depending on host fruit characteristics such as size and degree of ripeness (Aluja *et al.*, 2000; Díaz-Fleischer and Aluja, 2003a). Females mark fruit with a HMP after an oviposition bout (Aluja *et al.*, 2000) and are able to adjust the number of marks and the time spent marking depending on host size and HMP concentration on the fruit (Papaj and Aluja, 1993).

Here, we were interested in determining how the presence of conspecifics, oviposition experience, and host quality possibly interact to influence the oviposition behavior and clutch size of *A. ludens* females. While previous work on this topic has dealt with the first two factors, host quality and the possibly interacting effects of all three factors represent new elements in the present study. We predicted that experienced and grouped *A. ludens* females would exhibit increased oviposition activity and superparasitize. Our goal was to gather enough evidence to be able to discern if the predicted increase in oviposition activity and superparasitism behavior was caused by competition or by social facilitation as previously reported by Prokopy and collaborators (Prokopy and Duan, 1998; Prokopy and Reynolds, 1998; Prokopy *et al.*, 1999) working with *B. tryoni*, *C. capitata*, and *R. pomonella*.

## MATERIALS AND METHODS

This study was carried out in laboratories belonging to the Subdirección de Desarrollo de Métodos of the MoscaMed/MoscaFrut Programs, located in Metapa de Domínguez, Chiapas, México. Insects were kept under the following environmental conditions: temperature,  $25 \pm 1^\circ\text{C}$ ; and relative

humidity,  $60 \pm 10\%$ . Flies were exposed to a 12:12-h light/dark cycle (0700 to 1900).

All *A. ludens* specimens utilized in the experiments stemmed from field-infested grapefruit (*Citrus paradisi* Macfadyn). Pupae were allowed to emerge in Plexiglas cages ( $30 \times 30 \times 40$  cm each). Once all flies had emerged, 30 pairs with no visible wing and leg damage were selected and transferred to  $30 \times 30 \times 30$ -cm Plexiglas cages. Females were marked on the thorax with a small spot of vinyl paint (Vinic, Vinci de México, S.A. de C.V.) to distinguish individuals during the bioassay. Cages were placed on shelves at a height of 1.20 m, enabling a seated person to observe adult flies. A 75-W fluorescent lamp located 30 cm above the cages served as a light source. Agar spheres (Bacteriological Agar, Sigma Chemical Co., St. Louis, MO), colored with green food dye (McCormick-Herdez, México) and wrapped in Parafilm (American National Can Tm, Neenah, WI) (Boller, 1968), were used as artificial hosts. Three sizes (diameter) of artificial hosts were used: 1, 2.5, and 3.5 cm. We note that by using artificial hosts we removed any influence of host odor on female behavior. Because we were interested in determining the effect that conspecifics have on female oviposition behavior, we felt that using odorless oviposition substrates was the most appropriate procedure. Additionally, artificial agar hosts have been proven highly effective when studying clutch size decisions in *A. ludens* (Berrigan *et al.*, 1988, Díaz-Fleischer and Aluja, 2003a).

### **Experiment 1. Effect of Presence of Conspecifics and Oviposition Experience on Host Selection and Oviposition Behavior**

Our objective in this experiment was to determine if the presence of conspecifics and previous oviposition experience would facilitate host selection and oviposition behavior in *A. ludens* females. We predicted that females would choose hosts already occupied by a conspecific and would increase oviposition activity when grouped with other females. We also predicted that experienced females would exhibit increased rates of oviposition activity compared to naive ones. Twenty-day-old individually marked *A. ludens* females, with and without oviposition experience, were used in this experiment. To obtain flies with and without ovipositional experience, only half of the emerged individuals were offered artificial hosts the day prior to testing. One host per female was offered during 10 h to reduce the possibility of habituation to HMP (Roitberg and Prokopy, 1987). To guarantee that the females to be used in the experiment had actually oviposited and were thus experienced, we made sure that the hosts they had been exposed to had eggs inside them. Two female densities were tested: one and eight females per

cage (single and grouped female treatments respectively). To be able to observe an equal number of females per treatment, we simultaneously followed fly activity in nine cages (one cage with eight females and eight cages with one female per cage). Each observation period lasted 1 h and was replicated 21 times, using on each occasion (i.e., replica) a new cohort of flies. Three 2.5-cm-diameter agar spheres were hung from the roof of each cage and distributed 15 cm apart in a triangular pattern. To avoid host position effects, cages were rotated every 20 min, such that each sphere occupied each one of the three possible positions for equal periods of time. The following variables were measured: number of host visits, number of oviposition attempts, and number of successful ovipositions (i.e., after effectively laying eggs, a female drags the aculeus [ovipositor] tip, depositing a HMP). In the case of cages with grouped females, we also recorded visits and clutch size in hosts occupied and unoccupied by conspecifics and the number of fights between females on the same host. A fight consisted of head butting and pushing as well as wing waving displays (Aluja *et al.*, 2000). Data were analyzed as proportions of total number of events registered per female using a two-way MANOVA (experience  $\times$  fly density) and a one-way ANOVA to compare the number of visits to hosts that were either free or already occupied by another fly. For post hoc analyses we used a Bonferroni–Dunn test. When data did not follow the assumptions of a normal distribution, homocedasticity, and independence, we used rank transformations (Conover and Iman, 1981; Potvin and Roff, 1993). To determine the effect of experience in the number of fights among females, we performed a Mann–Whitney test (Zar, 1984).

### **Experiment 2. Effect of Oviposition Experience and Host Quality on Oviposition Behavior and Clutch Size**

Our objective in this experiment was to study the effect of host quality (i.e., clean or fruit covered with a host marking pheromone extract) on the oviposition behavior of grouped *A. ludens* females with and without oviposition experience. We predicted that only females with previous oviposition experience would be influenced by host quality. To test this hypothesis, we performed the following experiment in which only grouped females were used. Fly age and experience conditions as well as the number of hosts per cage and their spatial arrangement were identical to those in Experiment 1. Two types of agar spheres were utilized: (1) treated with HMP (i.e., a methanol extract of *A. ludens* feces at a concentration of 10 mg feces/ml of methanol; ca. 8–10 dragging equivalents [M. Aluja and F. Díaz-Fleischer, unpublished data]) and (2) unmarked (“clean”) spheres. Each of these two treatments

was replicated five times. The following information was recorded: number of host visits, number of oviposition attempts, number of ovipositions, visits to artificial host spheres occupied by a conspecific, visits to hosts unoccupied by a conspecific, clutch size, and number of fights between females that occupied the same host at the same time. Data were analyzed on a per female basis by means of a two-way MANOVA. For post hoc analyses we used the Bonferroni–Dunn test (Zar, 1984).

### **Experiment 3. Effect of Social Context and Host Size on Oviposition Behavior and Clutch Size**

Our objective was to determine the effect of social context (i.e., absence or presence of conspecifics) on the oviposition behavior of *A. ludens* females exposed to varying host sizes. We used host size as a measure of quality, since it is an indicator to the female of the amount of food available for larvae. Artificial hosts 1, 2.5, and 3.5 cm in diameter were employed in each replica. We predicted that the presence of conspecifics would alter oviposition behavior and clutch size independently of host size and ran the following experiment to test this hypothesis. Individually marked females without oviposition experience were used. The oviposition behavior of each female was observed under two conditions: with a conspecific female present on the host and in a host devoid of other flies. The order of these conditions was alternated in each replicate ( $n = 20$ ).

Our protocol consisted in introducing a single host from one of the three size categories (1-, 2.5- and 3.5-cm-diameter agar spheres) into a cage with 10 females. Once one of the females had landed on a host, it, along with the female, was transferred into another cage to observe its oviposition behavior in the absence of conspecifics. For the treatment corresponding to the previous occurrence of a conspecific female on the host, we proceeded as follows. Once a female landed on an agar sphere, we transferred the sphere with the female to an empty cage. There, the female was left alone for about 5 min, and once it started to exhibit oviposition behavior (i.e., aculeus insertion into sphere) we introduced a second sphere into the cage with 10 females and waited for another female to land on it. Once this second female initiated aculeus insertion motions, it was gently lifted with the help of a mango leaf and transferred to the cage containing the sphere already occupied by the first female. Even though we acknowledge that transferring the second female from one host to another meant that both females were not treated in exactly the same way, this procedure allowed us to guarantee that both test individuals exhibited the same oviposition drive (a critical factor to test our hypothesis). Once on the test host, we observed the behavior of both

females, considering the first female as the “resident” and the second female as the “intruder.” The following data were recorded: number of oviposition attempts, duration of the oviposition bout, number of ovipositor drags, time spent dragging the ovipositor, number of fights between females, duration of fights, and clutch size. We also investigated the effect of host residence status (resident vs. intruder) on clutch size and compared individual female oviposition behavior when the first clutch was laid in the absence of a conspecific and the second in the presence of a conspecific, or vice versa. Data were analyzed by means of a two-way MANOVA (host size  $\times$  social context at moment of oviposition) or a one-way ANOVA (number of fights). For multiple comparisons we used a Bonferroni–Dunn test. Effect of oviposition experience and resident status on outcome of contests was analyzed using a binomial test.

## RESULTS

Grouped (eight individuals per cage) *A. ludens* females tended to visit and oviposit in more hosts than did solitary females probably as a result of stimulation by the presence of conspecifics. Furthermore, females with previous oviposition experience visited and oviposited in more hosts than inexperienced ones. Importantly, when females were grouped, we observed significantly more landings on unoccupied hosts (i.e., devoid of flies) than on occupied ones (i.e., with at least one fly on it). However, oviposition experience, and not female density, was the most important factor affecting clutch size. Naïve females deposited larger egg clutches than experienced ones. Oviposition experience and host quality (i.e., clean fruit or fruit covered with a HMP extract) influenced clutch size and the decision of females to defend or not defend the host. Clutch size and number of fights were greater on clean than on HMP-marked fruits. Finally, we found that host quality (i.e., fruit size) played a significant role with regard to the number of female fights, host marking behavior and clutch size. Specifically, females fought and dragged their aculeus longer on small and medium sized hosts than on large ones. But this behavior varied according to whether females were kept alone or grouped. Clutch size was greatest in the largest hosts.

### **Experiment 1. Effect of Presence of Conspecifics and Oviposition Experience on Host Selection and Oviposition Behavior**

The MANOVA indicated that the relationship among the response variables was mainly influenced by female experience (Wilkinson  $\lambda$ ,  $F_{3,78} = 3.0$ ,  $P = 0.03$ ). However, no significant difference was detected when comparing



the effect of fly density on oviposition behavior (Wilkinson's  $\lambda$ ,  $F_{3,78} = 0.2$ ,  $P = 0.92$ ). The interaction between experience and fly density was also not significant (Wilkinson's  $\lambda$ ,  $F_{3,78} = 0.3$ ,  $P = 0.87$ ). Female density had a significant effect on at least two of the parameters examined. Grouped females tended to visit more hosts per female ( $F_{1,80} = 4.2$ ,  $P = 0.04$ ) and attempted to oviposit more often (measured on a per female basis) than solitary females ( $F_{1,80} = 5.1$ ,  $P = 0.03$ ). However, we found no significant differences when comparing the number of ovipositions per fly when females were kept alone or in groups ( $F_{1,80} = 4.4$ ,  $P = 0.06$ ) (Table I). Further, females with oviposition experience tended to visit more hosts ( $F_{1,80} = 4.1$ ,  $P < 0.008$ ) and attempted to bore with a higher frequency than naive ones ( $F_{1,80} = 7.4$ ,  $P = 0.05$ ) (Table I). No significant differences were found for the number of effective ovipositions (i.e., aculeus insertion followed by dragging behavior) between experienced and naive flies ( $F_{1,80} = 0.6$ ,  $P = 0.4$ ) (Table I). With respect to clutch size, females without oviposition experience deposited significantly more eggs per clutch than females with experience ( $F_{1,80} = 9.7$ ,  $P = 0.002$ ) (Table I). However, we did not find significant interactions between fly density and fly experience for visits ( $F_{1,80} = 0.2$ ,  $P = 0.64$ ), oviposition attempts ( $F_{1,80} = 0.003$ ,  $P = 0.95$ ), ovipositions ( $F_{1,80} = 0.1$ ,  $P = 0.75$ ), and clutch size ( $F_{1,80} = 0.01$ ,  $P = 0.91$ ). Oviposition experience also played an important role in terms of the number of aggressive interactions between females that occupied the same host simultaneously. Experienced females tended to engage in a greater number of fights than inexperienced females ( $U = 69$ ,  $P < 0.05$ ) (Table I). Importantly, when females were grouped (eight females per cage) we observed more landings on unoccupied hosts than on occupied ones ( $F_{1,43} = 14.5$ ,  $P < 0.05$ ).

**Table I.** Effect of Social Context and Oviposition Experience on Individual Female Oviposition Activity in *A. ludens* (Mean  $\pm$  SE)<sup>a</sup>

	Fly density			
	1 female		8 females	
	Experienced	Naive	Experienced	Naive
Visits	6.5 ( $\pm 1.3$ ) a	3.7 ( $\pm 0.7$ ) b	9.6 ( $\pm 1.5$ ) a	5.7 ( $\pm 1.1$ ) a
Oviposition attempts	16.7 ( $\pm 4.1$ ) a	8.8 ( $\pm 2.6$ ) b	23.7 ( $\pm 4.8$ ) a	16.2 ( $\pm 3.2$ ) a
Ovipositions	2.7 ( $\pm 0.7$ ) a	2.2 ( $\pm 0.6$ ) a	4.7 ( $\pm 0.9$ ) a	3.3 ( $\pm 0.7$ ) a
Number of fights			14.4 ( $\pm 2.0$ ) b	7.9 ( $\pm 2.4$ ) a
Clutch size	5.5 ( $\pm 0.3$ ) b	7.6 ( $\pm 0.9$ ) a	5.5 ( $\pm 0.3$ ) b	7.1 ( $\pm 0.7$ ) a

<sup>a</sup>Means within a row followed by the same letter are not different at a 0.05 level of significance (Bonferroni–Dunn test).

### Experiment 2. Effect of Oviposition Experience and Host Quality on Oviposition Behavior and Clutch Size

As was the case in Experiment 1, the MANOVA indicated that the relationship among the response variables was mainly influenced by female experience (Wilkinson  $\lambda$ ,  $F_{5,12} = 24.9$ ,  $P = 0.0001$ ). No statistically significant effect of host quality (presence or absence of HMP on fruit) was detected on fly oviposition behavior (Wilkinson  $\lambda$ ,  $F_{5,12} = 2.2$ ,  $P = 0.12$ ). However, in this experiment, the interaction of experience and host quality was significant (Wilkinson  $\lambda$ ,  $F_{5,12} = 6.8$ ,  $P = 0.0031$ ). As in the previous experiment, the number of host visits was significantly greater in females with oviposition experience than in those without it ( $F_{1,16} = 16.7$ ,  $P = 0.0008$ ) (Table II). Experienced females attempted to bore with greater frequency than naive flies regardless of host quality ( $F_{1,16} = 6.0$ ,  $P = 0.02$ ) (Table II). However, the number of successful ovipositions (i.e. boring followed by aculeus dragging behavior) was not significantly different between naive and experienced flies ( $F_{1,16} = 0.4$ ,  $P = 0.5$ ) (Table II). As was the case in the previous experiment, naive females deposited larger clutches than experienced ones ( $F_{1,16} = 8.8$ ,  $P = 0.009$ ) (Table II). Experienced flies fought more often than inexperienced ones ( $F_{1,16} = 4.9$ ,  $P = 0.04$ ). There were no significant differences in number of host visits ( $F_{1,16} = 0.2$ ,  $P = 0.6$ ) and in number of oviposition attempts ( $F_{1,16} = 0.2$ ,  $P = 0.6$ ) between marked and unmarked hosts (Table II). More fights were observed on clean than on HMP marked hosts ( $F_{1,16} = 10.7$ ,  $P = 0.005$ ). As was the case before, we did not detect any significant interaction for visits ( $F_{1,16} = 0.6$ ,  $P = 0.4$ ), oviposition attempts ( $F_{1,16} = 2.2$ ,  $P = 0.1$ ), and ovipositions ( $F_{1,16} = 0.8$ ,  $P = 0.1$ ). However, a significant interaction was observed when clean and HMP marked hosts were offered. Experienced flies significantly reduced

**Table II.** Effect of Host Quality and Oviposition Experience on Individual Female Oviposition Behavior in *A. ludens* (Mean  $\pm$  SE)<sup>a</sup>

	Clean host		HMP marked host	
	Experienced	Naive	Experienced	Naive
Visits	4.4 ( $\pm 0.8$ ) a	2.2 ( $\pm 0.7$ ) b	5.2 ( $\pm 0.4$ ) a	2.0 ( $\pm 0.6$ ) b
Oviposition attempts	18.4 ( $\pm 5.5$ ) a	6.0 ( $\pm 2.6$ ) b	15.2 ( $\pm 3.3$ ) a	12.2 ( $\pm 3.0$ ) b
Ovipositions	8.8 ( $\pm 1.6$ ) a	5.8 ( $\pm 2.3$ ) a	5.4 ( $\pm 2.1$ ) a	5.0 ( $\pm 1.5$ ) a
Number of fights	9.8 ( $\pm 0.3$ ) a	2.4 ( $\pm 0.9$ ) b	1.0 ( $\pm 0.5$ ) b	2.4 ( $\pm 1.7$ ) b
Clutch size	7.3 ( $\pm 0.9$ ) a	8.6 ( $\pm 1.5$ ) a	4.6 ( $\pm 0.6$ ) b	8.8 ( $\pm 1.1$ ) a

<sup>a</sup> Means within a row followed by the same letter are not different at a 0.05 level of significance (Bonferroni–Dunn test).

the number of eggs per clutch ( $F_{1,16} = 9.6$ ,  $P = 0.007$ ) (Table II). Finally, we detected a significant interaction when looking at the number of fights between females that simultaneously occupied the same host ( $F_{1,16} = 10.7$ ,  $P = 0.005$ ). While experienced females fought more often on clean hosts than on marked hosts, naive ones fought equally on both types of hosts (Table II).

### Experiment 3. Effect of Presence of Conspecifics and Host Size on Oviposition Behavior and Clutch Size

The MANOVA indicated that the relationship among the response variables was mainly influenced by the effect of host size (Wilkinson  $\lambda$ ,  $F_{4,226} = 8.4$ ,  $P = 0.0001$ ). No statistical effect was observed for fly density (pair or alone) on fly oviposition behavior (Wilkinson  $\lambda$ ,  $F_{4,226} = 0.97$ ,  $P = 0.42$ ). Furthermore, the interaction between host size and fly density was also not significant (Wilkinson  $\lambda$ ,  $F_{4,226} = 0.7$ ,  $P = 0.65$ ). We found that the number of oviposition attempts were not significantly different when comparing female behavior on hosts of varying diameters (1, 2.5, and 3.5 cm) ( $F_{2,230} = 1.6$ ,  $P = 0.19$ ) or in the presence or absence of conspecifics ( $F_{1,230} = 1.4$ ,  $P = 0.23$ ) (Table III). Similarly, no differences in oviposition time (i.e., from insertion to withdrawal of aculeus) were detected between hosts of different sizes ( $F_{2,230} = 2.0$ ,  $P = 0.14$ ) and when conspecifics were present or absent ( $F_{1,230} = 0.2$ ,  $P = 0.67$ ) (Table III). Interestingly, flies dragged their aculeus over significantly shorter periods of time on larger hosts when alone (i.e., in the absence of a conspecific) than when grouped ( $F_{2,230} = 4.3$ ,  $P = 0.01$ ) (Table III). Clutch size was affected only by host size, larger clutches being found on larger hosts ( $F_{2,224} = 24.7$ ,  $P < 0.001$ ) (Table III). We did not find significant interactions between host size and fly condition for oviposition attempts ( $F_{2,230} = 1.11$ ,  $P = 0.33$ ), oviposition time ( $F_{2,230} = 0.12$ ,  $P = 0.88$ ), dragging time ( $F_{2,230} = 0.29$ ,  $P = 0.75$ ), and clutch size ( $F_{2,224} = 0.31$ ,  $P = 0.73$ ). Furthermore, the number of fights were not significantly different among the three host sizes ( $F_{2,115} = 1.2$ ,  $P = 0.29$ ). However, flies fought significantly longer on small- and medium-sized hosts than on large ones ( $F_{2,115} = 3.8$ ,  $P = 0.02$ ). Resident status played an important role in determining the outcome of fights. Resident females were able to expel the intruder more often than were intruder females able to expel resident ones (Table IV). Also, resident females that oviposited first when alone (gaining experience) and then oviposited in the presence of a conspecific, were more successful in defending a host than those females whose first oviposition experience took place in the presence of a conspecific (Table IV).

**Table III.** Effect of Host Size and the Presence of Conspecifics on Individual Female Oviposition Activity in *A. luteus*

Host size	Alone			With a conspecific		
	Small	Medium	Large	Small	Medium	Large
Oviposition attempts	5.3 ( $\pm 0.8$ ) a	5.0 ( $\pm 1.3$ ) a	5.3 ( $\pm 1.1$ ) a	6.5 ( $\pm 1.4$ ) a	4.4 ( $\pm 0.8$ ) a	6.6 ( $\pm 1.2$ ) a
Time attempting (s)	202.8 ( $\pm 24.7$ ) a	277.5 ( $\pm 55.2$ ) a	325.4 ( $\pm 59.1$ ) a	272.2 ( $\pm 61.4$ ) a	278.1 ( $\pm 57.9$ ) a	355.6 ( $\pm 67.3$ ) a
Time dragging (s)	164.5 ( $\pm 36.7$ ) a	155.3 ( $\pm 27.5$ ) a	89.8 ( $\pm 9.9$ ) b	118.5 ( $\pm 21.5$ ) a	125.1 ( $\pm 18.7$ ) a	148.1 ( $\pm 58.5$ ) a
Number of fights				1.9 ( $\pm 0.3$ ) a	1.7 ( $\pm 0.3$ ) a	1.3 ( $\pm 0.2$ ) a
Time fighting (s)				7.9 ( $\pm 1.4$ ) ab	12.5 ( $\pm 2.2$ ) a	5.9 ( $\pm 1.3$ ) b
Clutch size	6.4 ( $\pm 0.3$ ) a	7.2 ( $\pm 0.5$ ) b	9.4 ( $\pm 0.6$ ) b	6.9 ( $\pm 0.3$ ) a	7.2 ( $\pm 0.3$ ) b	10.4 ( $\pm 0.7$ ) b

<sup>a</sup>Means within a row followed by the same letter are not different at a 0.05 level of significance (Bonferroni–Dunn test).

**Table IV.** Effect of Oviposition Experience and Resident Status on Outcome of Contests in Experimental Manipulations with *A. ludens* Females

Host size	Fly condition	Winner			<i>n</i>	One-tail binomial test
		Resident	Invader	Draw		
Small	Naive	12	8	1	21	0.25
Small	Experienced	16	2	2	20	0.0025
Medium	Naive	14	3	2	19	0.01
Medium	Experienced	18	4	0	22	0.005
Large	Naive	11	6	2	19	0.25
Large	Experienced	15	4	1	20	0.025

## DISCUSSION

We were able to show that conspecific presence, oviposition experience, and host quality influenced the oviposition behavior of *A. ludens* females. As predicted, on a per female basis, grouped females tended to visit hosts and oviposit into them more often than those kept singly. Interestingly, when females were grouped (eight females per cage), we observed more landings per female on unoccupied spheres than on occupied ones. Experienced *A. ludens* females visited hosts and oviposited significantly more often than naive ones, but naive females deposited significantly larger clutches than experienced ones. Experienced flies also better assessed host quality and engaged in fights more often on clean and smaller hosts than on larger ones or those marked with a HMP methanolic extract. Further, flies with previous oviposition experience fought longer and defended their hosts more successfully than naive ones. As was reported before (Papaj and Messing, 1998), resident status conferred a competitive advantage to females while defending an oviposition resource. Unexpectedly, we did not find any significant interaction among the factors evaluated in relation to clutch size. For example, we expected a significant interaction between experience and presence of HMP. The latter because in other fruit fly species (e.g., *R. pomonella* and *C. capitata*), females need experience to recognize HMP and reduce clutch size when ovipositing in hosts marked with this infochemical (Roitberg and Prokopy, 1981; Papaj *et al.*, 1989; Papaj and Messing, 1996).

It is not unusual for grouped females to be more active than solitary ones since encounters with conspecifics might serve as indicators of high resource quality and quantity in a patch (Beuchamp *et al.*, 1997; Giraldeau and Beuchamp, 1999). Encountering high densities of conspecifics might also serve as a signal of a greater risk of resource competition to a foraging individual. For example, superparasitism and patch time allocation increases

when several conspecific female parasitoids are exploring the same patch at the same time (Visser *et al.*, 1990; van Alphen and Visser, 1990) or when a foraging individual encounters a conspecific prior to patch exploration (Visser *et al.*, 1990; Hoffmeister *et al.*, 2000). However, differing from Prokopy *et al.* (2000) and Rull *et al.* (2003) who worked with *C. capitata*, we found that grouped *A. ludens* females visited significantly more empty than already occupied hosts (i.e., those already occupied by one or more conspecifics). Assuming that the existence of social facilitation is real (see Dukas *et al.* [2001b] for details), this difference might be due to the type of oviposition behavior exhibited by the females of both species. While for a *C. capitata* female landing on a host already occupied by a conspecific could be advantageous because it could be able to locate and use holes previously bored by another female (Papaj *et al.*, 1992, Papaj and Messing, 1996), this benefit does not exist in the case of *A. ludens* (F. Díaz-Fleischer and M. Aluja, unpublished data). For *A. ludens*, when two females encounter each other on a host, one (generally the newcomer) is ejected. Thus, selecting an already occupied fruit may represent a double cost for *A. ludens* females: on the one hand, for the parents that have to expend energy fighting for the resource and, on the other hand, for the offspring that will have to compete for food. Choosing an already occupied host could therefore be cost-effective only in the case of extreme resource scarcity (Díaz-Fleischer and Aluja, 2003b) or if the oviposition substrate contains toxic allelochemicals that can be overcome only by large numbers of larvae generating a more “benevolent” microenvironment (Díaz-Fleischer and Aluja, 2003a).

Experienced females visited and attempted to oviposit significantly more often than naive ones. Experienced flies also recognized and rejected HMP-marked hosts while naive flies did not. This is not surprising, since Roitberg and Prokopy (1981) and Papaj *et al.* (1989), working with *R. pomonella* and *C. capitata*, respectively, demonstrated that experienced females not only locate hosts with greater efficiency but also reject previously used ones. In this study, experience also influenced the clutch size of *A. ludens*. However, this result may be attributed to differences in physiological state (i.e., egg load) between experienced and naive individuals. *Anastrepha ludens* is a synovigenic species whose females mature eggs after copulation on a continuous basis and do not reabsorb them if hosts are not available (Aluja *et al.*, 2001a). Based on this, females without oviposition experiences should carry a greater egg load, and as a result, deposit larger clutches when they have the opportunity to do so. In general terms, it is well documented that when faced with host scarcity, insects generally increase clutch size (Pilson and Rausher, 1988; Heard 1998). In addition, and contrary to our prediction, clutch size was not affected by the presence of conspecifics. We had predicted that when faced with competition (i.e.,

presence of conspecifics on a host), *A. ludens* females would lay fewer eggs per clutch. Instead, fruit size was the most important factor regulating clutch size, aculeus dragging, and duration of female fights.

Females fought longer on small- and medium-sized hosts than on large ones, but clutch size was greater in large hosts. Interestingly, when females were alone (i.e., in the absence of conspecifics), they dragged their aculeus longer after an oviposition bout in small hosts (compared to large ones). Conversely, we did not detect significant differences in dragging time on the three different-sized hosts when females oviposited in the presence of conspecifics. These results could be explained by the well-established fact that in frugivorous tephritids, females obtain information on host quality after landing on it (Fletcher and Prokopy, 1991; Díaz-Fleischer *et al.*, 2000). With this information, they may assess time to invest on the host before a contest with a conspecific takes place. For example, host quality, represented in our experiments by the presence or absence of a host marking pheromone extract, was found to influence the behavior of experienced *A. ludens* females but not of naive ones. In fact, the number of fights was significantly greater on clean hosts than on marked ones. In sum, it appears that when the cost of competition to potential progeny is very high (as would be the case in a “defendable” small host), females will fight to drive away other females. On the other hand, when the resource is abundant (e.g., a large host), females will invest less time and energy in fights and more in trying to monopolize the resource by laying a larger clutch.

Based on our results, we conclude that it is difficult to attribute the observed increase in ovipositional activity by grouped *A. ludens* females to a phenomenon such as social facilitation which was purportedly observed (details given by Dukas *et al.*, 2001b) in other tephritid species such as *C. capitata* and *B. tryoni* (Prokopy and Duan, 1998; Prokopy *et al.*, 1999). We rather believe that the observed increase in ovipositional activity by grouped *A. ludens* females, which fought for a resource already occupied by a conspecific, can be attributed to the effect of competition and mutual interference, as observed by Visser *et al.* (1990) in parasitoids. The fact that *A. ludens* females with previous oviposition experience were more influenced than naive individuals by the presence of conspecifics, supports our inference. Previous “knowledge” on, for example, host quality and availability, allowed experienced females, to better assess a situation of competition or host scarcity.

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