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Behavioural plasticity in relation to egg and time limitation: the case of two fly species in the genus *Anastrepha* (Diptera: Tephritidae)

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Reproductive opportunities in insects that deposit their eggs in discrete resource patches are frequently limited because the availability of oviposition substrates is often spatially and temporally restricted. Such environmental variability leads individuals to confront time- or egg-limitation constraints. Additionally, species with different oviposition strategies (i.e. single egg layers vs clutch layers) commonly deal with different structural and ecological characteristics of larval host plants. To test the hypothesis that oviposition strategies such as laying eggs singly or in batches (clutches) are related to these constraints (i.e. egg vs time limitation), we compared the lifetime oviposition patterns of two closely related sympatric species of *Anastrepha* (Diptera: Tephritidae) with different oviposition strategies. We exposed five cohorts of *A. obliqua* and *A. ludens* females, over the course of their adult lifetimes, to three conditions of "habitat quality" (measured as host density per cage): unpredictable habitat quality (host density varied randomly from day to day between 1, 5, 15, 30 and 60 hosts/cage), low habitat quality (fixed density of one host/cage) and high habitat quality (fixed density of 60 hosts/cage).
Responses to host density conditions were strikingly different in the two species. (1) Frequency of host visits and oviposition events increased in *A. obliqua* but not in *A. ludens* when host densities increased. (2) *Anastrepha ludens* females accepted low quality hosts (i.e. fruits on which eggs had already been laid and were therefore partially covered with host marking pheromone) significantly more often than *A. obliqua* females did. (3) Females of *A. obliqua* adjusted their oviposition activity to variations in host density, whereas *A. ludens* females exhibited a constant oviposition pattern (i.e. did not respond to variations in host density). Based on the above, it is likely that in *A. obliqua* oviposition is governed by egg-limitation and in *A. ludens* by time-limitation constraints. We discuss the relationship between the oviposition strategies of each fly species and the fruiting phenology and density of their native host plants. We also address the possible influence of oogenesis modality and parasitism by braconid wasps in shaping oviposition behaviour in these insects.

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Many insects deposit their eggs in discrete patches of food on which their larvae develop. However, since the availability of oviposition resources is often spatially and temporally restricted, such environmental variability can lead individuals to confront time- or egg-limitation constraints. Time limitation refers to the situation in which a female dies or otherwise looses reproductive ability before it has deposited its entire egg complement (Sevenster et al. 1998). Egg limitation occurs when a female runs out of eggs before all oviposition opportu-

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nities have been exhausted (Rosenheim 1996). Host distribution in time and in space is a major source of variability influencing reproductive opportunities. Species that experience situations of low host density (i.e. low habitat quality) will maximise progeny size per unit time (i.e. the cost of finding a host is high relative to the cost of producing an egg). As a result, they behave as time limited. Egg-limited behaviour is found in systems in which host availability is high (i.e. high habitat quality) (i.e. the cost of finding a host is low compared to the cost of producing an egg).

Synovigenic species, (i.e. those that produce mature eggs throughout their lifetime) can suffer, on several occasions during their lifetimes, from egg- or time-limitation restrictions (Driessen and Hemerik 1992). However, since these species are able to replenish their egg supply throughout life, the incidence of egg limitation is lower than time limitation (Ellers et al. 2000). Time limitation may induce females to adopt strategies that increase host encounter rates, even if such strategies result in the exploitation of low-quality oviposition substrates (Stephens and Krebs 1986). In contrast, egg limitation encourages females to become more selective with respect to host quality, even if such selectivity reduces overall oviposition rates (Mangel 1987).

Species with different oviposition strategies (i.e. single egg layers vs clutch layers) also commonly deal with different structural and ecological characteristics of larval host plants. For example, studies with two butterfly species that exploit the same host plants (*Pieris rapae* L. a single egg layer, and *P. brassicae* L. a clutch laying species), suggest that, in these types of insects, egg clustering is an adaptation to deal with spatially clumped hosts, while laying a single egg per oviposition bout is probably more suited for exploiting isolated plants (Davies and Gilbert 1985). It is also known that clutch-laying species exhibit high-realised fecundities as a result of decreased host search time (Courtney 1984).

Here, we compared the lifetime oviposition patterns of two closely related polyphagous, synovigenic species of *Anastrepha* fruit flies (Diptera: Tephritidae) that belong to the same intrageneric group (the *fraterculus* group which contains the most derived species within *Anastrepha*, Norrbom et al. 2000), and that exhibit similar net fecundity (Liedo et al. 1992), but possess contrasting oviposition strategies. *Anastrepha ludens* (Loew) females can lay single eggs or clutches of up to 40 eggs depending on host size and host fruit species (Aluja et al. 2000), whereas *A. obliqua* (Macquart) females invariably lay one egg per oviposition bout (Aluja 1994). Apparently, the strategy of depositing eggs in clutches is ancestral in this group of insects (F. Díaz-Fleischer, F. Ornelas and M. Aluja, unpubl.). The larvae of both species develop in the pulp of several host plant species although, in the case of *A. ludens*, seed feeding has also been reported (Aluja et al. 2000). Native host plants of *A. obliqua* (e.g. *Spondias mombin* L.) produce between 2500 and 20 000 fruits per tree which mature simultaneously over a two to four week period (Miranda 1952, Aluja and Birke 1993). Fruits weigh between 3.5 and 8.0 g and *A. obliqua* females deposit preferentially one or two eggs per fruit (Sivinski et al. 1997). Conversely, native host fruits of *A. ludens* are more variable in time and space (i.e. they are not as numerous and their fruiting phenology tends to be much less synchronised). For example, *Sargentia gregii* S. Coult, and *Casimiroa edulis* Llave & Lex (both Rutaceae) have fruiting seasons that last between four to five months (Miranda 1952, González-Hernández and Tejada 1979, Aluja et al. 1998, F. Díaz-Fleischer pers. obs.). Fruits of *S. gregii* measure 1.3 to 2 cm diameter and harbour 2 larvae (Plummer et al. 1941, Leyva et al. 1991). Fruits of *C. edulis* weigh on average 150.1 ± 10.5 (SE) g and harbour between 2 and 60 larvae per fruit (López et al. 1999).

Our goal in this study was to test the hypothesis that oviposition strategies in insects (i.e. laying one vs. a clutch of eggs/host) are related to time- or egg-limitation constraints. Based on the high habitat quality encountered by *A. obliqua* adults in nature (described above), we predicted that they would confront egg-limitation constraints. In the case of *A. ludens*, based on the low habitat quality encountered by adults in nature (described above), we predicted that time-limitation constraints would modulate the oviposition behaviour of this species.

Methods

Study site

This study was undertaken at the laboratories of the Programas MoscaMed/MoscaFrut, Subdirección de Desarrollo de Métodos (DGSV-SAGARPA), in Metapa de Domínguez, Chiapas, México. Insects were maintained at a temperature and relative humidity of 25 ± 1°C and 60 ± 10%, respectively and exposed to a 12:12 hr light:darkness cycle (7 a.m. to 7 p.m.).

Biological material

All insects utilised stemmed from field-infested fruit collected in the vicinity of Tapachula, Chiapas, México. Hog plum (*S. mombin*) and grapefruit (*Citrus paradisi* McFadden) were used as sources for *A. obliqua* and *A. ludens*, respectively. Three hundred pupae of each fly species were allowed to emerge in Plexiglas cages ($30 \times 30 \times 40$ cm). Once flies reached 10 days of age (before they started laying eggs), individuals with no visible damage to wings and legs were selected and transferred to observation cages. Three females and one male were placed in each observation cage. Prior to being released

in the cage, females were marked on the thorax with a small spot of vinyl paint to distinguish individuals during the bioassay. Previous observations had indicated that this marking procedure had no discernible effect on female behaviour.

Experimental arena

Observations were carried out using glass cages ($30 \times 30 \times 30$ cm). On one side of each cage, a fine cloth screen was fastened with masking tape to facilitate daily manipulations inside the cage. Cages were placed on shelves at a height of 1.20 m, enabling a seated observer to observe adult flies. A 75 Watt fluorescent tube lamp located 30 cm above the cages served as a light source. Agar spheres (Bacteriological Agar, Sigma Chemical Co., U.S.A.) measuring 2.5 cm in diameter and coloured with green food dye (McCormick-Herdez, México) were used as oviposition substrates (Boller 1968). Spheres were wrapped in Parafilm (American National Can Tm Neenah, U.S.A.) and placed inside the observation arena previous to the initiation of each trial. The observation arena consisted of a Styrofoam platform ($26 \times 26 \times 1.5$ cm) containing 0.5 cm diameter holes, used to support agar spheres, that were distributed in a symmetrical, hexagonal pattern as described by Boller and Aluja (1992). The arrangement of this pattern was invariant among all treatments with more than one host. All artificial hosts were changed on a daily basis to minimise the effect of host-marking pheromone left from previous ovipositions. Artificial host size was chosen based on the native host sizes of both species (Plummer et al. 1941, Sivinski et al. 1997).

Host densities

We evaluated three treatments (i.e. levels of "habitat quality"): (1), a variable host density of 1, 5, 15, 30 or 60 hosts/cage (average $\pm$ SE of 22.3 ± 1.6) (unpredictable habitat quality), (2), a fixed density of one host/cage (low habitat quality), and (3), a fixed density of 60 hosts/cage (high habitat quality). In the case of treatment 1 (i.e. variable host density), host number was selected randomly every day (with the aid of a random numbers table). The aim of this treatment was to ascertain if females of both species would adjust their oviposition activity according to host availability. In the case of treatments 2 and 3 (fixed density of one and 60 hosts/cage, respectively), our aim was to study the oviposition behaviour of *A. ludens* and *A. obliqua* under extreme habitat quality conditions. Specifically, we wanted to determine if females of both species would resort to superparasitism (common in time-limited species) when confronted with an extremely low number of hosts (common scenario very early, or at the end in the fruiting season) or if they would face egg-limitation constraints when confronted with an extremely large number of hosts. Fly cohorts (three females and one male) were assigned to a single treatment that did not change during the lifetime of the individuals under observation. Each treatment was replicated five times.

Observation procedure

Observations were begun when females started to lay eggs (i.e. 15 days of age). One person monitored fly oviposition behaviour in five cages every day (one person was randomly assigned to one of the three treatments every morning). Daily observation periods began at 7:30 a.m. and ended at 6:30 p.m. without breaks. However, because each species exhibited distinct and relatively short peaks in daily ovipositional activity (two in the case of *A. obliqua*) (Aluja and Birke 1993, Aluja et al. 2000), the actual time during which fly activity was recorded was limited to these activity peaks. Observers recorded the number of sphere visits/female and the number of ovipositor drags/female (females of both species drag the ovipositor after each successful oviposition bout, Aluja et al. 2000). The number of spheres on which eggs were laid and the number of eggs deposited per sphere were also recorded.

Statistical analysis

Cage was used as the unit for analysis. We used average activity per cage (i.e. values averaged over the three females in each cage) (Crawley 1993). A two-way ANOVA was used to analyse the variable density treatment (i.e. 1, 5, 15, 30 or 60 hosts/cage) in an attempt to determine whether females adjusted their oviposition according to host availability over their entire lifetimes. The proportion of used hosts was analysed in each of the five host densities. To analyse the temporal distribution of visits and oviposition bouts over time in the fixed-host density treatments (1 vs 60 hosts/cage), we ran a two-way repeated-measures ANOVA (Zar 1984). This analysis included only the first 15 days of observations to fulfil the model assumption of a balanced design (repeated measures tests can't handle missing values, von Ende 1993, Dukas et al. 2001). Since females started to lay eggs at age 15 days, this analysis only covered the period of their lives encompassed by ages 15 to 30 days. After this period, 3 females died in one experimental unit (i.e. cage) and we were therefore unable to use subsequent data for this particular analysis. We felt further justified to proceed in such a manner given the fact that the peak in oviposition activity of *A. ludens* and *A. obliqua* falls within this time period (i.e.

ages 15 to 30 days; Celedonio-Hurtado et al. 1988, Liedo et al. 1992). This was also the case for variable host density treatment, to analyse data on number of eggs per female and eggs per host, we employed a two-way ANOVA (species × host density treatment) in each case. In general, data were transformed to ranks (Conover and Iman 1981, Potvin and Roff 1993) and only those on proportion of hosts used in the variable-density treatment were arc sin $\sqrt{x+1}$ transformed (Zar 1984). For post-hoc analyses we used Fisher's Protected Least Significance Difference test. For ease of interpretation, all figures show untransformed data.

Results

Oviposition patterns under variable host density conditions

The variable host density treatment, which pretended to simulate natural variance in availability of ovipositional resources, generated markedly different egg-laying patterns for the two species. To illustrate this, we compared the number of host visits, ovipositions, eggs per female and eggs per host for each host density (i.e. 1, 5, 15, 30 or 60 hosts/cage) and between species (Fig. 1A, B, C, D). With respect to host visits, we found that females of both species responded differently to daily changes in host density ($F_{4,\ 937} = 5.1$; $P < 0.0005$; Fig. 1A). *A. obliqua* females significantly increased the number of host visits when the number of hosts increased, but this was not the case for *A. ludens*.

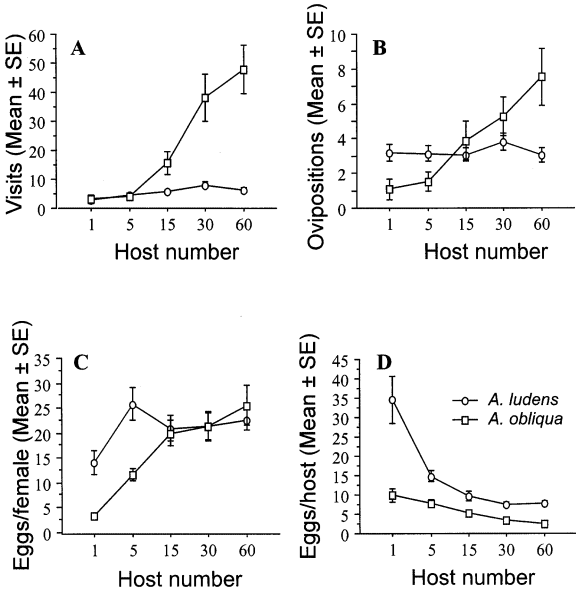

Fig. 1. (A) Lifetime number of host visits, (B) ovipositor drags, (C) eggs oviposited and (D) eggs laid/host by *A. ludens* and *A. obliqua* females exposed to varying host-density levels (host density varied randomly from day to day between 1, 5, 15, 30 and 60 hosts/cage).

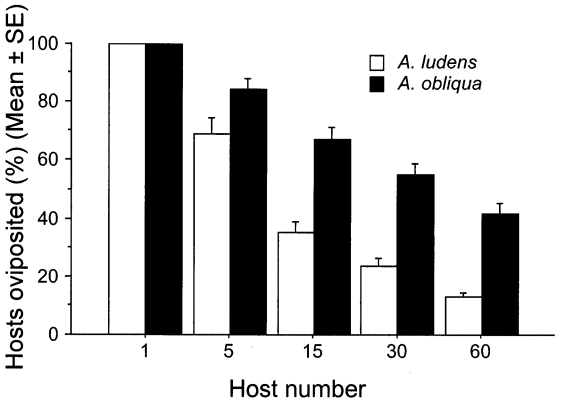

Fig. 2. Number of hosts used for oviposition by *A. ludens* and *A. obliqua* females as influenced by host density (expressed as percent of total used based on total available).

With regards to ovipositional bouts (as evidenced by ovipositional drags), the significance of the interaction between species and host density ($F_{4,\ 937} = 4.3$; $P < 0.005$; Fig. 1B) implies that the latter factor influenced the response of females of the two species in different ways. In the case of *A. ludens* the number of ovipositions among treatments was almost constant. In sharp contrast, *A. obliqua* females significantly increased their number of ovipositions as host number increased.

When looking at the number of eggs laid per female, the interaction between species and host density was also significant ($F_{4,\ 338} = 3.5$; $P < 0.005$; Fig. 1C). Host density affected females of each species in different ways. *A. ludens* clearly laid a similar number of eggs per female across all host densities. In sharp contrast, females of *A. obliqua* deposited very few eggs at low host densities, and many more eggs when more hosts were available.

With respect to the number of eggs per host, females of *A. ludens* deposited more eggs per host than did *A. obliqua* ($F_{1,\ 338} = 153.9$; $P < 0.0001$; Fig. 1D). Females of the two species laid more eggs per host when exposed to 1 and 5 hosts ($F_{4,\ 338} = 20.5$; $P < 0.0001$ Fig. 1D). In this case, the interaction between species and host density was not significant ($F_{4,\ 338} = 1.8$; $P = 0.13$; Fig. 1D).

Finally, with respect to the proportion of hosts used, we found a significant interaction between species and host density ($F_{4,\ 338} = 7.8$; $P < 0.0001$; Fig. 2). The two species tended to use a lower proportion of hosts when more were available, however, *A. obliqua* females used a significantly higher proportion of hosts than *A. ludens* females.

Oviposition patterns under constant host density conditions

We found significant differences in the number of visits and ovipositions between *A. obliqua* and *A. ludens* over

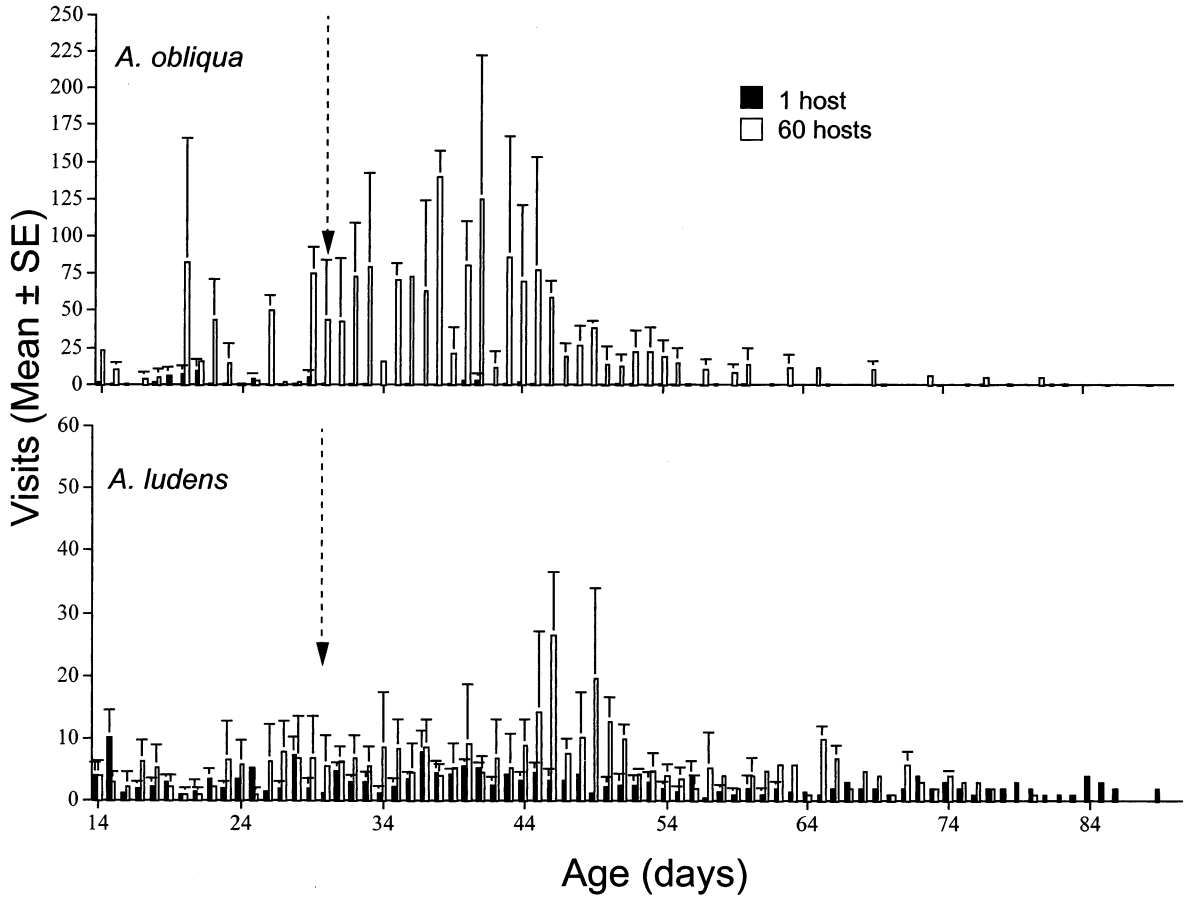

Fig. 3. Number of host visits per day by *A. ludens* and *A. obliqua* females exposed to two contrasting fixed host densities during the peak oviposition period in their lifetime. Arrow indicates cut-off point after which data were not included in repeated measures ANOVA to fulfil model assumption of a balanced design (details in text). Different scale used in case of *A. ludens* for ease of interpretation (activity in this species was significantly lower than in *A. obliqua*).

We found significant differences in the number of visits and ovipositions between *A. obliqua* and *A. ludens* over the 15-day period we used for analysing this pattern ($F_{1,\ 224} = 9.7$; $P < 0.005$, $F_{1,\ 224} = 4.5$; $P < 0.05$; Figs. 3 and 4, respectively). Hosts in the fixed 60 host/cage treatment received more visits and ovipositions than in the fixed 1 host/cage treatment ($F_{1,\ 224} = 10.7$; $P < 0.005$, $F_{1,\ 224} = 9.6$; $P < 0.01$, respectively). The interaction between species and host density was significant, indicating that the females of each species responded in different ways to host density ($F_{1,\ 224} = 9.5$; $P < 0.05$, $F_{1,\ 224} = 9.2$; $P < 0.05$, visits and ovipositions, respectively) (Table 1). Host visits and ovipositions varied significantly among days ($F_{14,\ 224} = 2.5$; $P < 0.05$, $F_{1,\ 224} = 1.8$; $P < 0.05$, visits and ovipositions, respectively). *A. obliqua* females visited more hosts and oviposited more than *A. ludens* females in the high-density treatment. The interaction between the time (i.e. days) and treatments (i.e. 1 vs 60 hosts/cage) was significant for host visits but not for ovipositions ($F_{14,\ 224} = 2.3$; $P < 0.05$, $F_{14,\ 224} = 1.5$; $P = 0.11$, visits and ovipositions, respectively) (Table 1). The interaction between species and time (i.e. days) for the response variables host visits and ovipositions was significant ($F_{14,\ 224} = 2.6$; $P < 0.005$, $F_{14,\ 224} = 2.3$; $P < 0.05$, visits and ovipositions, respectively) (Table 1). Finally, the three-level interaction between time (i.e. days), host density and species was significant when comparing the number of host visits and ovipositions ($F_{14,\ 224} = 2.3$; $P < 0.05$, $F_{14,\ 224} = 1.8$; $P < 0.05$, respectively) (Table 1). When 60 hosts were available, we observed that on any given day, *A. obliqua* females visited and oviposited in a larger number of hosts than *A. ludens* females did. Importantly, the number of host visits and ovipositions by *A. obliqua* varied from day to day during the 15-day period we considered for this analysis. In contrast, *A. ludens* females exhibited a remarkably constant pattern of host visits and ovipositions in both treatments (1 vs 60 hosts/cage).

With respect to the total number of eggs laid per female there was a significant interaction between host density (1 vs 60 hosts/cage) and fly species ($F_{1,\ 652} =$

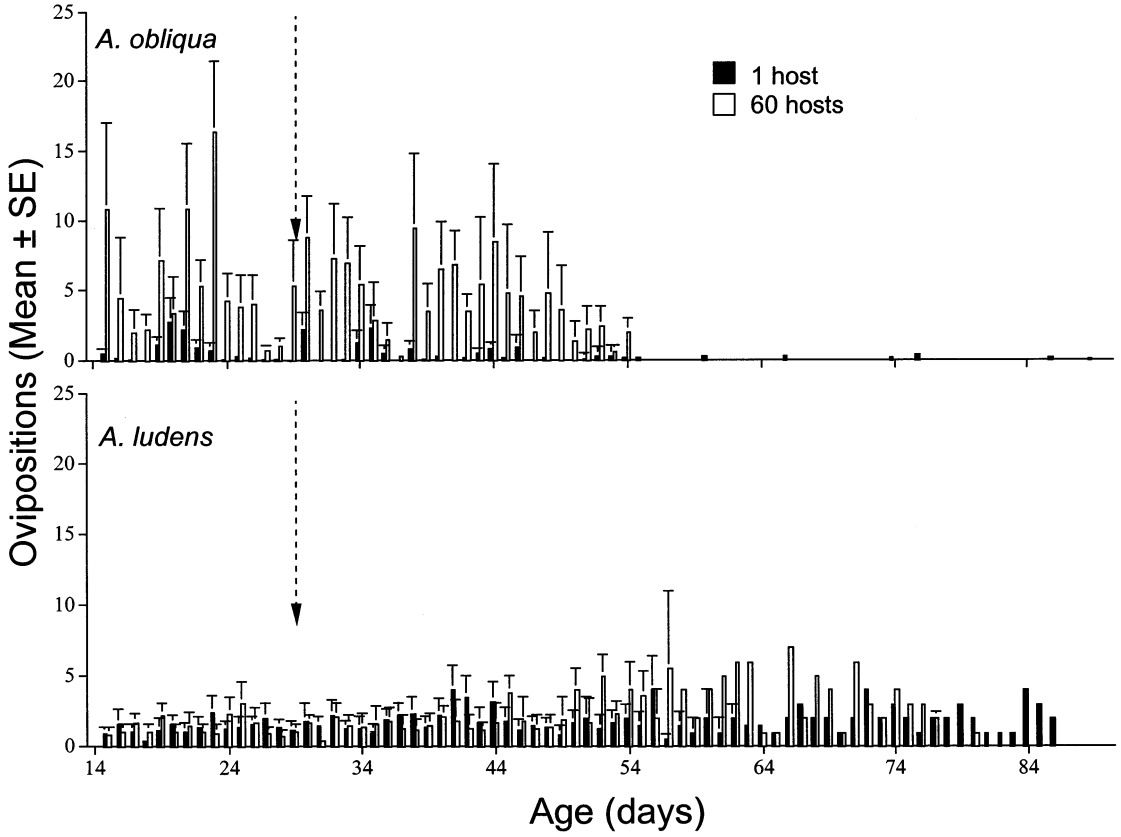

Fig. 4. Number of ovipositions per day by *A. ludens* and *A. obliqua* females exposed to two contrasting fixed host densities during the peak oviposition period in their lifetime. Arrow indicates cut-off point after which data were not included in repeated measures ANOVA to fulfil model assumption of a balanced design.

14.4; $P < 0.0005$; Fig. 5A). *A. obliqua* females oviposited significantly more eggs when exposed to 60 hosts/cage than to 1 host/cage. In contrast, *A. ludens* females laid similar numbers of eggs regardless of host density/cage.

Finally, in the case of the number of eggs per host, the interaction between host density and fly species was also significant ($F_{1, 652} = 12.9$; $P < 0.0005$; Fig. 5B). *A. ludens* females laid significantly more eggs than *A. obliqua* females in the two treatments. Most eggs per host were laid in the one-host, constant density treatment.

Table 1. Results of two-way repeated measures ANOVA comparing the number of host visits and ovipositions under two fixed host density conditions (one or 60 hosts exposed to *A. ludens* and *A. obliqua* females during their lifetime). This analysis included only the first 15 days of observations to fulfil the model assumption of a balanced design (since females started to lay eggs at age 15 days, the analysis covered a period of their lives that encompassed ages 15 to 30 days).

Factor	Visits	Ovipositions
Species	$P < 0.005$	$P < 0.05$
Treatment	$P < 0.005$	$P < 0.01$
Treatment × species	$P < 0.05$	$P < 0.05$
Days	$P < 0.05$	$P < 0.05$
Days × Treatment	$P < 0.05$	NS
Days × Species	$P < 0.005$	$P < 0.05$
Days × Treatment × Species	$P < 0.05$	$P < 0.05$

Discussion

Our data support the notion that species with different oviposition strategies respond differently to varying patterns of resource availability. As predicted, females of the single egg-laying species (*A. obliqua*) seemed to be restricted by egg-limitation constraints. Females of this species visited fewer hosts and reduced the rate of eggs laid per female when exposed to a low host density (1 or 5 hosts/cage). In contrast, and partially fulfilling our prediction, females of the clutch laying *A. ludens*, accepted already used hosts (i.e. low-quality hosts) more often than *A. obliqua* females when exposed to extremely low host densities (i.e. they behaved as if time limited). Nevertheless, when exposed to a large number of hosts, they distributed their eggs among many hosts (i.e. they behaved as if egg limited). Finally, in contrast to *A. obliqua*, *A. ludens* females deposited a uniform rate of eggs/female independent of host density.

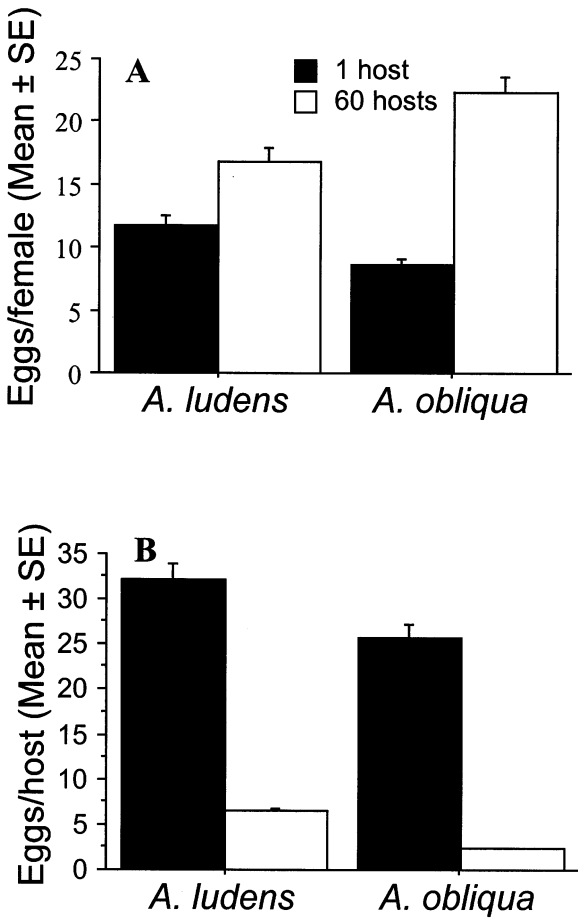

Fig. 5. (A) Mean (± SE) lifetime number of eggs oviposited by *A. ludens* and *A. obliqua* females exposed to two contrasting fixed host densities. Both species deposited more eggs when more hosts were available. (B) Mean (± SE) lifetime number of eggs oviposited per host by *A. ludens* and *A. obliqua* females exposed to two host densities. *A. ludens* deposited more eggs/host than *A. obliqua*.

Based on the above, it appears likely that these two fly species have evolved egg loads and oviposition strategies that allow them to effectively confront varying habitat-quality conditions as is the case with many synovigenic parasitoid species (Ellers et al. 2000). As noted in the introduction, *A. ludens* normally has to cope with a habitat of low quality (i.e. few patchily distributed hosts ripening over long periods of time) and in response, maximises the number of progeny per unit time (i.e. lays clutches; but see below). In contrast, *A. obliqua* deals with habitats of high quality (i.e. many clumped hosts ripening in synchrony) and as a result faces egg-limitation constraints. As mentioned before, in this species adults commonly encounter, at the beginning of the fruiting season, trees with more than 20 000 densely packed fruits that ripen within a relatively short time period (Aluja and Birke 1993, Sivinski et al. 1997). Under these circumstances, the cost of finding a host is likely low compared to the cost of producing an egg. Importantly, under our study conditions, when habitat quality was high (i.e. constant availability of a high number of hosts), both species behaved as if egg limited. That is, *A. obliqua* as well as *A. ludens* appeared to spread their eggs to reduce superparasitism. This observation supports the arguments of Roitberg (1989), Rosenheim (1999), and more recently Casas et al. (2000) against the static view implicit in the time- vs egg-limitation dichotomy usually applied when dealing with synovigenic species (reviewed by Rosenheim 1999). Even though we believe that this dichotomy is conceptually very useful, we need to recognise that there are insect species that exhibit a certain degree of plasticity with respect to oviposition strategies. Plasticity in the case of *A. ludens* is exhibited not only with respect to oviposition strategies over time (as discussed above), but also in the number of eggs oviposited per clutch. As noted in the introduction, females of this species lay between 1 and 40 eggs per clutch, depending on host quality (e.g. size, firmness). Therefore, another dichotomy, in this case commonly applied to tephritid flies, should also be reconsidered. Fruit fly species are often divided into single egg vs clutch layers (Aluja and Norrbom 2000). We would find it more useful to argue in terms of inelastic and plastic strategies. That is, there are species such as *A. obliqua* in which females invariably lay one egg and those like *A. ludens* or *A. serpentina* that can lay one or several eggs per clutch (Aluja et al. 2000).

Superparasitism has been proven adaptive under certain circumstances. For example, when there is a shortage of hosts or when several females have depleted a resource-patch simultaneously (van Alphen and Visser 1990). In fruit flies, superparasitism can lead to a serious reduction in fitness because of larval competition (Averill and Prokopy 1987). However, there are some cases when females obtained advantages by superparasitizing. For example, *Rhagoletis pomonella* (Walsh) and *R. completa* (Cresson) females are known to superparasitize hosts when they are unripe and hard (Averill and Prokopy 1989, Lalonde and Mangel 1994). Females obtained fitness advantages by saving time and aculeus wear when ovipositing in this type of fruit (Papaj and Alonso-Pimentel 1997). However, when ripe soft hosts are more abundant, such females distribute their eggs uniformly to reduce larval competition (Averill and Prokopy 1989, Lalonde and Mangel 1994). In the case of *A. ludens* and other clutch laying species such as *Ceratitis capitata* Wiedemann (medfly), superparasitization can, on occasion, have small costs in terms of larval fitness. To illustrate, survival and pupal size in the medfly remained relatively high at densities of up to eight eggs per host fruit (the small-sized kumquat, *Fortunella japonica* Thunb.) (Papaj et al. 1989; but see Dukas et al. 2001). Additionally, pupal size, which was positively correlated with adult lifetime

fecundity, decreased very little even at densities of up to 32 eggs per fruit (Papaj et al. 1989, Dukas et al. 2001). The strategy of depositing egg clutches and adjusting clutch size according to host firmness (a measure of host quality) is adaptive in the sense that it allows larvae to survive in a poor nutritional and possibly toxic micro-environment (F. Díaz-Fleischer and M. Aluja, unpublished data).

In our opinion, the fact that oogenesis in *A. obliqua* and *A. ludens* is governed by different biotic and abiotic factors (Aluja et al. 2001) can partially explain the contrasting oviposition behaviours we observed in this study. In the case of *A. obliqua* the presence of chemical and physical stimulants (i.e. host fruit volatiles and presence of hosts) appears to drive the rate of ovarian maturation, but in *A. ludens*, however, ovarian development is influenced by female age and social context (Aluja et al. 2001). Consistent with this, one would predict that *A. obliqua* females, upon being exposed to a flush of rapidly maturing hosts (with the concomitant massive release of volatiles), would become active foragers and would deposit a large amount of eggs in a short period of time (until the "supply" in the ovaries runs out). In the case of *A. ludens*, rarely exposed to a large, concentrated mass of hosts (and volatiles), a very different phenomenon would be expected. Faced with the constraints imposed by their own type of oogenesis, *A. ludens* females must deal with an egg load that is continually high. The latter, added to the stochastic nature of host availability confronted by this species, leads *A. ludens* females to face repeated time-limitation situations during a lifetime (Minkenberg et al. 1992, Papaj 2000). Under these circumstances, superparasitism becomes a viable oviposition strategy.

Parasitism by braconid wasps could also be a driving force underlying oviposition behaviour (particularly in the case of *A. obliqua*). Parasitism rates are known to be very high in some *A. obliqua* host plants. For example, in *S. mombin*, parasitism varies between 68.3 and 83.8% (López et al. 1999). In sharp contrast to this, in *A. ludens*, parasitism levels only reach 6% in *S. greggii* and are almost non-existent in *C. edulis* (González-Hernández and Tejada 1979, López et al. 1999). Based on this, laying one egg per oviposition bout and reducing the number of eggs per fruit or patch (as *A. obliqua* does), can become an effective risk-spreading strategy that permits females to lower parasitism in their progeny (Stamp 1980, Godfray 1987 and Ayal and Green 1993 for a general discussion of the above).

In conclusion, our results support the postulates of Ellers et al. (2000), who indicated that habitat quality is the most important factor determining if a species will be time or egg limited. When confronted with a high quality habitat (i.e. high host density), *A. ludens* and *A. obliqua* females behaved as if egg limited. However, in low quality habitats (i.e. low host density), the oviposition behaviour of females of these two fly species differed. While *A. ludens* females behaved as if time limited, and maintained a constant rate of oviposition, *A. obliqua* females reduced the rate of oviposition (behaving as if egg limited). As noted by Stamp (1980) and Courtney (1984), oviposition strategies in insects are related to different structural and ecological characteristics of the larval host plants. In the case of *A. obliqua* and *A. ludens*, the fruiting phenologies of native hosts generate different reproductive opportunities. Considering that both species possess a similar net fecundity, but that host availability in nature is different for each fly species, we suggest, on the one hand, that opportunities to reproduce in the case of *A. ludens* females are often time limited due to the low density and extended fruiting periods of their hosts. *A. obliqua* females, on the other hand, oviposit on plants with a much greater number of fruits that become available only during a brief window in time. The response observed in *A. obliqua* probably corresponds to an innate strategy of parasitizing as many host fruits as possible before they become unsuitable for larval development. Consequently, it is more likely that females of this species will confront egg-limitation constraints. We hope that more comparative studies like ours here will help further clarify how host ecology has influenced insect oviposition strategies and their relation with time or egg limitation.

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