

# Leafminer egg distribution at decreasing leaf availability levels: do females avoid intraspecific competition?

María Lourdes Aparicio, María Silvina Fenoglio & Martín Videla\*

Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and Centro de Investigaciones Entomológicas de Córdoba (CIEC), Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 1611, (X5016GCA), Córdoba, Argentina

Accepted: 24 April 2015

**Key words:** clumped distribution, exploitative competition, insect performance, *Liriomyza commelinae*, oviposition choices, Diptera, Agromyzidae, Commelinaceae

## Abstract

Female oviposition choices are expected to maximize offspring fitness. Leafminers often lay their eggs in an aggregated fashion, leading to exploitative or interference competition among larvae. However, few studies have explored whether egg distribution patterns vary with leaf availability and whether these changes are an attempt to reduce competition effects on offspring fitness. Here, we evaluated the egg distribution patterns of the specialist leafminer *Liriomyza commelinae* Frost (Diptera: Agromyzidae) for decreasing levels of leaf availability of their host plant *Commelina erecta* L. (Comelinaceae). Competition effects on insect performance were evaluated at various leaf larval densities in the laboratory and egg distribution was investigated for a wide range of leaf availability levels, both in the laboratory and in the field. *Liriomyza commelinae* performance indicated that larvae competed for resources (exploitative competition), with a negative impact on survival and adult size at emergence when four or more larvae shared a leaf. The distribution of the immature stages of the leafminer was aggregated in both the laboratory and in the field. As this pattern did not change with leaf availability, increasing levels of larval competition occurred when available leaves were scarce. Moreover, the proportion of total individuals subjected to the strongest competition level (six or more larvae per leaf) increased exponentially at the lower levels of leaf availability. Competition was found to be irrelevant as a selective force in shaping *L. commelinae* oviposition decisions, as egg distribution was aggregated and did not vary with leaf availability, leading to relatively strong levels of competition. The egg distribution patterns observed in *L. commelinae* may have resulted from trade-offs between competition and factors such as enemy-free space and leaf quality.

## Introduction

The survival and fitness of many phytophagous insect offspring strongly depend on decisions taken by females when evaluating oviposition site suitability (Thompson, 1988). These selections are expected to be adaptive and to maximize offspring fitness (Jaenike, 1978), with host plant quality and quantity, predation, parasitism, and intra- and interspecific competition being among the factors that may affect offspring fitness and provide selective pressure on a female's choice (Ishihara & Ohgushi, 2007; Sugiura et al., 2007; Ishino et al., 2011; Videla et al., 2012). Given the number of potential factors affecting offspring fitness, trade-offs in female decisions are expected to occur

(Scheirs et al., 2000; Ishihara & Ohgushi, 2007). Endophagous insects are ideal systems to study the ecology and evolution of oviposition site selection, as in many species immature stages cannot emigrate from the sites chosen by mothers. Hence, decisions of females with sessile offspring would be expected to be more prone to selective pressure than those made by females with mobile progeny.

Intraspecific competition has often been mentioned as a potential driving force of oviposition choices in endophagous insects such as leafminers (Sugiura et al., 2007). However, several studies have shown that leafminer females lay multiple eggs in the same leaf more often than would be expected by chance (Stiling et al., 1984; Bultman & Faeth, 1986; Faeth, 1990; Hespenheide, 1991; Morris et al., 1992; Cornelissen & Stiling, 2008). This clumped pattern of egg distribution is frequently related to within-plant variation in leaf traits such as size, quality,

\*Correspondence: E-mail: mvidela@com.uncor.edu

and age (Tuomi et al., 1981; Kagata & Ohgushi, 2002). Independent from the causes involved in determining this distribution, detrimental effects on larvae occupying the same leaf arising as a consequence of either exploitative (resource depletion) or interference (cannibalism) competition have frequently been reported (Stiling et al., 1984; Bultman & Faeth, 1986; Faeth, 1990; Morris et al., 1992; Cornelissen & Stiling, 2008). However, benefits from aggregation such as reduced parasitism or increased feeding efficiency have also been found (Low, 2008; Low et al., 2009).

It has been suggested that competition may not be reflected in leafminer distribution at tree, shoot, or leaf level, due to it often being weak at natural densities and hence of minimal effect in driving offspring distribution patterns (Tack et al., 2009). In addition, trade-offs between competition and other factors (e.g., leaf quality) could lead to females preferring to bear the cost of competition, rather than not ovipositing on high quality but already occupied leaves (Gripenberg & Roslin, 2005; Gripenberg et al., 2007).

Although aggregated egg distribution at several spatial scales (plant, branch, and leaf) is common among leafminers, there is some evidence that this pattern changes with insect density. For example, Eber (2004) found that eggs of the holly leafminer *Phytomyza ilicis* Curtis, were randomly distributed within trees when the leafminer density was low, but that this pattern shifted to clumped when the egg density increased toward medium to high levels. Furthermore, aggregation and the incidence of larval competition of *P. ilicis* were dependent on the availability of suitable young leaves for oviposition, indicating that competition was subordinate to leaf quality in driving oviposition choices in the holly leafminer. However, a different outcome would be expected when competition is important in shaping leafminer egg distribution. At increasing population densities, females may lay their eggs uniformly to avoid competition. Moreover, even by ovipositing in an aggregated fashion, females might be able to maintain competition costs for their offspring relatively low by laying eggs at densities below the threshold value beyond which competition impacts on offspring fitness.

Studying egg distribution patterns at decreasing levels of leaf availability provides an opportunity to examine how female egg laying choices are related to the strength of competition their offspring are subjected to. However, most studies have only looked at egg distributions for either low (Bultman & Faeth, 1985; Tack et al., 2009) or relatively high (Stiling et al., 1984; Auerbach & Simberloff, 1989) insect densities, with few investigations having explored this relationship for a wide range of insect densities under natural field conditions. Here, we evaluated the

strength of larval competition and the egg distribution pattern of the specialist leafminer *Liriomyza commelinae* Frost (Diptera: Agromyzidae) in response to decreasing availability of oviposition sites under laboratory and field conditions. Previous studies have reported that *L. commelinae* can display a wide range of egg density levels on its patchily distributed host plant *Commelina erecta* L. (Commelinaceae) under urban conditions (Fenoglio, 2009). Bearing this in mind we specifically asked: (1) What is the threshold value in larval density within a leaf beyond which competition affects offspring fitness? (2) Do egg distribution patterns change with decreasing levels of leaf availability? And if so, (3) are females behaving in a manner that reduces larval competition strength? To answer these questions, we evaluated the competition effects on insect performance at various leaf larval densities for laboratory and egg distribution patterns within a wide range of leaf availability levels in both laboratory and field *C. erecta* plants.

## Materials and methods

### Study system

*Liriomyza commelinae* is a Neotropical oligophagous insect that feeds on plants of the genera *Commelina* and *Tradescantia* (Smith, 1987), with the larvae of this species burrowing into the leaf parenchyma and forming linear and white-colored mines. Its life cycle can be completed in ca. 12 days when the temperature is over 25 °C, and all its immature stages (three larval stages and the pupa) develop inside the leaf (Stegmaier, 1966; Smith, 1987). In our particular study region (Córdoba, Argentina), it appears to be specialized on *C. erecta* (Valladares, 1984). In central Argentina, this leafminer usually first appears in November, reaching peak abundance during February and March (Fenoglio, 2009), with this marked seasonality seeming to coincide with the period of growth of *C. erecta* (Sérsic et al., 2006).

The host plant, *C. erecta*, is a native perennial herbaceous plant extensively distributed in central and northern regions of Argentina. Its leaves are ovate and acute, 3–10 cm wide and 2–3.5 cm long. The species has a patchy distribution, as each plant is capable of producing a variable number of basal tillers. It usually occurs in dry and sandy soils of urban, cultivated and natural environments, with flowering taking place from November to April (Sérsic et al., 2006). Although *C. erecta* can behave as an annual plant in less severe climates, in our study region it disappears after the first winter frosts, before sprouting again from rhizomes by the end of spring (Sérsic et al., 2006).

### Plant and insect rearing

Shoots of *C. erecta* were collected from a single location (Astronomic Observatory of Córdoba) (31°25'S, 64°11'W)

to reduce any possible genetic or developmental variability, and were then transplanted into pots (24 × 18 × 5 cm deep) in the laboratory. Plants, which were easily grown from transplanted tubers, were kept in the laboratory and then used when they had between 80 and 240 leaves.

The adults of *L. commelinae* used in the laboratory experiments were obtained from a colony initiated with 50 individuals collected on naturally mined plants growing in various parts of Córdoba city (31°20'S, 64°10'W), and were maintained under controlled conditions on *C. erecta* plants during three generations starting with 50 individuals each. Mined leaves were collected, placed in plastic bags, and checked daily until the emergence of adults, which were then transferred to insect cages (30 × 30 × 30 cm) containing *C. erecta* plants to allow mating and oviposition. All plants were kept in a parasitoid-free environment, at 23 ± 3 °C and L12:D12 photoperiod.

#### Competition effects on insect performance

The effect of competition on *L. commelinae* offspring was evaluated with 1–6 or more larvae per leaf. A minimum of 20 leaves (replicates) per density level was obtained by placing plants of *C. erecta* in insect cages containing different numbers of adult flies.

After being exposed to leafminers, plants were checked daily for the initiation of the mines. Leaves with larvae were then marked using a paper label gently tied to the petiole and examined daily to assess the development time and survival of the various life cycle stages. As each larva excavates a single mine, we took the number of mines to be equivalent to the number of larvae. Mined leaves were kept on the plant until all individuals pupated. Then, leaves with pupae were individually placed in plastic bags and the emerged adults were stored in glass vials plugged with cotton wool (Fenoglio et al., 2010). The experiment lasted ca. 25 days.

Leafminer offspring performance was evaluated through total development time, total survival rate, and adult wing length (discriminated by sex), the latter being used as an estimator of potential fecundity (Honěk, 1993). From these data, we were able to establish the threshold value in larval density beyond which offspring fitness was affected by competition.

#### Egg distribution and leaf availability

Egg distribution was evaluated in the laboratory by offering two pots containing 4–6 tillers each, which represented a *C. erecta* plant, to leafminers in an insect cage for 48 h. By varying the number of leafminer females (3–17) and leaves (81–248), a wide range of leaves available per female—and hence egg density levels (0.6–8.2)—was obtained,

which closely reflected those observed in the field environment. The total numbers of leaves, mined leaves, and mines per leaf were recorded for each of the 10 replicates (cages).

The width and length of each mined leaf were also measured to calculate leaf area following Sugiura et al. (2007), as leafminers often prefer larger leaves to lay their eggs in (Tuomi et al., 1981; Kagata & Ohgushi, 2002). The leaf area of a random sample of 57 leaves was obtained from scanned leaf tracings. Then, a Spearman correlation between the calculated area (width\*length) and the area obtained from the scanned leaf tracings was made, yielding the following equation:

$$Y = 0.62X_1X_2 + 136.36 (r^2 = 0.92, P < 0.0001),$$

where Y, X<sub>1</sub>, and X<sub>2</sub> correspond to the leaf area (mm<sup>2</sup>), leaf length (mm), and leaf width (mm), respectively. This equation was used to estimate the leaf area of the remaining leaves.

Field surveys were also carried out to evaluate the egg distribution patterns of *L. commelinae*. The leafminer was sampled at 16 sites located in various neighborhoods of the city (S31°20', W64°10', elevation 440 m) during its peak abundance. The pavements of each site were checked to search for *C. erecta* plant patches. For each patch (n = 214), the total number of leaves was registered and all mined leaves were collected. In the laboratory, the mines per leaf were counted and leaves were individually placed in plastic bags until the flies emerged. More details of the survey can be found in Fenoglio et al. (2010, 2013).

Leaf availability for each cage (laboratory) and patch (field) was calculated by dividing the total number of leaves by the total number of larvae (leaves per egg). After determining the threshold value of larval density beyond which competition affects offspring fitness, we calculated the proportion of larvae (mines) within a cage (laboratory) or patch (field) subjected to competition. Also, we separately calculated the proportion of larvae competing at each density level.

#### Data analysis

To analyze the effect of larval density treatment on *L. commelinae* performance, Generalized Linear Mixed Models (GLMMs) were used. 'Leaf nested within pot' was included as a random effect in the models, given that leaves coming from the same pot have a greater chance of showing correlated responses (Bolker et al., 2009). We used a Poisson error distribution and a log link function for development time (counting of days). A binomial error distribution with logit as a link function was used for survival, whereas wing length data were analyzed assuming a

normal distribution. The significance of the estimated parameters for the fixed effect was evaluated using likelihood ratio tests (Bolker et al., 2009), with a posteriori Tukey's tests being performed to determine differences between treatments. The mixed models were built using the lme4 (Bates & Maechler, 2009) package in R 2.9.2 (R Development Core Team, 2010).

The distribution of *L. commelinae* within plants was examined by comparing the observed frequency of leaves with no mines and those with 1–6 or more larvae in each of the 10 cages with the expected frequency assuming random (Poisson) and clumped (negative binomial) distributions using a  $\chi^2$  analysis (Southwood & Henderson, 2000). The same analyses were performed for 10 randomly selected field patches considering a gradient of leaf availability. Also, a regression analysis was performed to evaluate whether aggregation, in terms of the negative binomial aggregation parameter ( $k$ ), was inversely related to leaf availability. In addition, to evaluate whether leaf area had an influence on the number of eggs females laid in laboratory experiments, a GLMM was performed where 'leaf nested within pot' was the random factor and the response variable was modeled using a Poisson distribution and log link function.

The proportion of larvae competing (total and separated by the number of larvae per leaf) was analyzed in relation to leaf availability for both laboratory and field data using Generalized Linear Models (GLMs). As the data were overdispersed, a quasibinomial error distribution and logit as a link function were used (Crawley, 2007).

## Results

### Insect performance

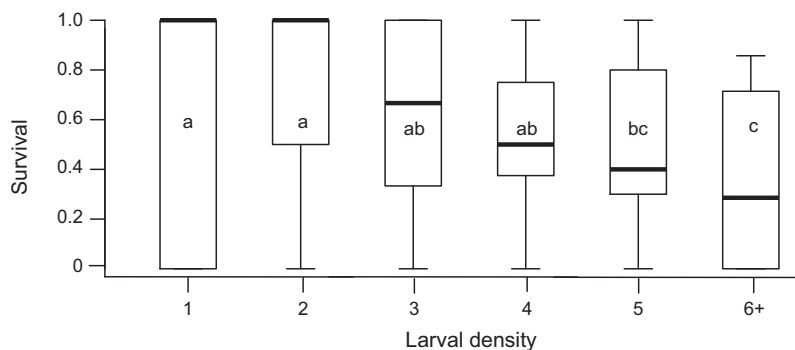
Increases of larval density significantly diminished the total (larvae-adult) survival rates of *L. commelinae* ( $\chi^2 = 43.71$ , d.f. = 5,375,  $P < 0.0001$ ). Almost all individuals developing alone or in pairs reached the adult stage, whereas nearly 40% of larvae in leaves with five or six (or

more) individuals survived, with intermediate survival values being registered in leaves with three or four larvae (Figure 1). The number of larvae per leaf was also associated with a reduction in wing length of females ( $\chi^2 = 26.96$ , d.f. = 5,375,  $P < 0.0001$ ) as well as males ( $\chi^2 = 16.30$ , d.f. = 5,375,  $P < 0.0001$ ) (Figure 2). Females that emerged from leaves with four and six or more larvae were nearly 8% smaller than those from leaves with one or two individuals, whereas males emerging from leaves with six or more larvae were 5% smaller than those from leaves with 1–3 larvae. Larval density had no effect on total development time of *L. commelinae* ( $\chi^2 = 1.11$ , d.f. = 5,375,  $P = 0.95$ ), which was about 20 days for all treatments.

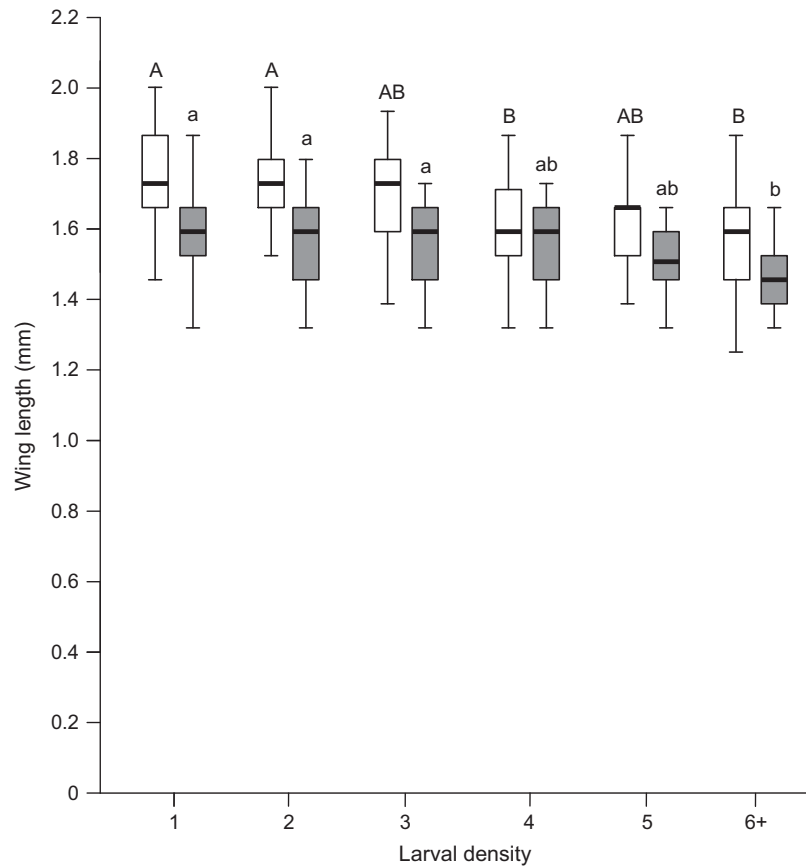
### Egg distribution and leaf availability

Of a total of 2 131 leaves offered to *L. commelinae*, 382 were mined in laboratory tests. Larval distribution among leaves significantly differed from a random pattern (Poisson), and adjusted in most of the cases (different cages) to a negative binomial distribution (Table 1). This indicates that the distribution of the immature stages of *L. commelinae* was aggregated, as more leaves were without mines, fewer leaves had just one larva, and more leaves had multiple larvae than expected by chance. The same clumped distribution was observed for field patches (Table 1). Aggregation level was not related to leaf availability in field ( $F_{1,6} = 2.26$ ,  $P = 0.18$ ) or laboratory ( $F_{1,6} = 3.38$ ,  $P = 0.11$ ) conditions. Oviposition was biased toward larger leaves in laboratory tests as indicated by the positive relationship ( $\chi^2 = 19.18$ , d.f. = 1,379,  $P < 0.0001$ ) between leaf area and the number of larvae per leaf.

Our results on *L. commelinae* performance indicated that competition affected at least one offspring fitness parameter when four or more larvae shared a leaf. Taking this value as a threshold, we found that 49.4% (with a total deviance change of 63.27 out of 128.03) of the variation in the proportion of total larvae that were in competition was explained by leaf availability ( $P = 0.004$ ) in the laboratory



**Figure 1** Total survival (from larva to adult) rates of *Liriomyza commelinae* in leaves of *Commelina erecta* with different numbers of conspecifics (larval density). Different letters in the boxes indicate significant differences among treatments (Tukey's tests:  $P < 0.05$ ). Bold line: median; box: lower and upper quartiles; whiskers: smallest and largest non-outlier observations.



**Figure 2** Wing length (mm) of *Liriomyza commelinae* females (white) and males (gray) emerged from leaves of *Commelina erecta* with different numbers of conspecifics (larval density). Different letters (within sex) capping the boxes indicate significant differences among treatments (Tukey's tests:  $P < 0.05$ ). Bold line: median; box: lower and upper quartiles; whiskers: smallest and largest non-outlier observations.

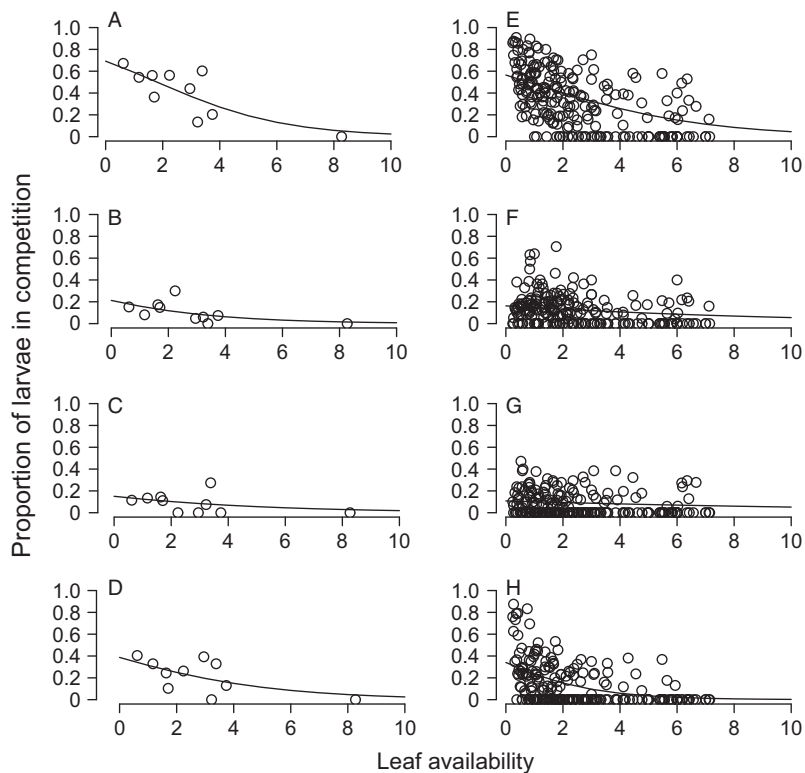
**Table 1** *Liriomyza commelinae* egg distribution among leaves of *Commelina erecta* plants in laboratory (unit: cage) and field conditions (unit: patch) tested against a random (Poisson) and clumped (negative binomial) distribution

Unit	Laboratory			Field		
	Poisson ( $\chi^2$ )	Negative binomial ( $\chi^2$ )	k	Poisson ( $\chi^2$ )	Negative binomial ( $\chi^2$ )	k
1	$10.68 \times 10^{8***}$	13.38 ns	0.11	52.76***	7.67 ns	1.97
2	$98.70 \times 10^3***$	26.5*	–	43.45***	7.87 ns	5.11
3	$22.69 \times 10^3***$	9.24 ns	0.40	7.07 ns	0.37 ns	0.64
4	$68.10 \times 10^6***$	13.08 ns	0.22	12.99**	1.22 ns	0.70
5	315.1***	10.84 ns	0.34	121.7***	2.83 ns	0.30
6	295.1***	9.84 ns	0.11	253.5***	24.86***	–
7	$33.43 \times 10^4***$	19.04*	–	$12.27 \times 10^4***$	7.43 ns	0.14
8	$22.62 \times 10^4***$	12.66 ns	0.18	17.67***	7.62**	–
9	$22.85 \times 10^3***$	5.79 ns	0.36	153.2***	1.79 ns	0.29
10	$18.55 \times 10^3***$	20.31 ns	0.31	$14.94 \times 10^3***$	1.16 ns	0.09

'k' is the estimated parameter of the negative binomial distribution.  
\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ ; ns, not significant.

tests. Values from 0 to 70% of individuals in competition were registered at the lowest and highest levels of leaf availability, respectively (Figure 3A). In addition, a similar trend was found for field data (Figure 3E) although with a

higher variability in the response variable, with 78% (total deviance change was 1 790.90 of 2 291.10) of the variation in the proportion of total larvae that were in competition being explained by leaf availability ( $P < 0.0001$ ). When the



**Figure 3** Relationship between *Commelina erecta* leaf availability (no. leaves per egg) and the proportion of *Liriomyza commelinae* larvae in competition in plants in laboratory (left panels) and field (right panels). (A, E) Overall proportion of larvae in competition (4+ conspecifics) and the fraction of larvae in leaves with (B, F) 4, (C, G) 5, and (D, H) 6+ conspecifics. Dots and lines show observed values and fitted values from generalized linear models with logit link and quasibinomial distribution of error variance.

proportion of larvae in competition was analyzed separately according to the number of competitors, no significant relationships to leaf availability were observed in laboratory trials (Figure 3B–D) for four ( $P = 0.11$ ), five ( $P = 0.38$ ), or six or more larvae per leaf ( $P = 0.09$ ). However, in field patches (Figure 3F–H), the proportions of leaves containing four and six or more larvae were increased at lower levels of leaf availability ( $P = 0.005$  and  $P < 0.0001$ , respectively), although no such relationship was observed when five larvae were in the same leaf ( $P = 0.13$ ).

## Discussion

The distribution of *L. commelinae* eggs among leaves was aggregated under both laboratory and field conditions, as has been reported frequently for other leafminer species (Stiling et al., 1984; Bultman & Faeth, 1986; Faeth, 1990; Morris et al., 1992; Cornelissen & Stiling, 2008). This pattern did not change with leaf availability, leading to increasing levels of larval competition when available leaves were scarce. Moreover, the proportion of total individuals subjected to the strongest competition level (six or more larvae per leaf) increased exponentially at lower levels of leaf availability. These results indicate that *L. commelinae* females did not avoid intraspecific competition when laying their eggs.

Both, exploitative and interference competition have been reported for leafminers (Hespenheide, 1991). Resource competition, but not cannibalism, was observed in our laboratory experiments, which caused significant decreases in offspring fitness in terms of survival and body size. In many insect species, reductions in body size have been associated with diminished realized fecundity (Honěk, 1993). In addition, for *Liriomyza trifolii* (Burgess), a closely related species to *L. commelinae* (Parrella, 1983), reductions in feeding capacity and longevity in smaller females have been shown.

It has been proposed that competition may not be reflected in leafminer egg distribution as it is often weak at natural densities, with a consequent low impact on offspring fitness and hence being trivial in shaping female oviposition choices (Tack et al., 2009). However, our results on *L. commelinae* egg distribution do not support this hypothesis—intraspecific competition was found to be common in *C. erecta* urban patches. In fact, in almost half the patches, 40% of larvae occurred at densities at which competition is likely. Moreover, competition caused a significant decrease in offspring fitness, particularly in survival, but also in body size. However, a preliminary study of the *L. commelinae* distribution in patches located within a natural reserve showed that competition was virtually absent. Only 77 mined leaves were collected

from 224 inspected patches, and in just three of these were four or more larvae found in the same leaf (M Videla, unpubl.).

Parasitoids are often regarded as being responsible for maintaining leafminer populations far below levels at which intraspecific competition would occur, and it has been shown that their absence in nature can lead to a regular egg distribution of leafminers (Faeth & Simberloff, 1981; Sugiura et al., 2007). Nevertheless, the occurrence and strength of competition we observed in urban patches could not be attributed to a decrease in top-down control, as parasitism levels on *L. commelinae* in our study region were found to be similar in urban and natural environments (Cagnolo, 2006; Fenoglio et al., 2013; Rossetti et al., 2013). Therefore, bottom-up factors (i.e., leaf quality) probably were responsible for the differences encountered in *L. commelinae* population levels among environments.

Competition may also not be mirrored in leafminer egg distribution if trade-offs exist between competition and other factors (e.g., leaf quality; Tack et al., 2009). For example, females might prefer to bear the cost of competition rather than to renounce ovipositing on already occupied high-quality leaves (Gripenberg & Roslin, 2005; Gripenberg et al., 2007).

Leafminers frequently select larger leaves to lay their eggs, as they are often more suitable for offspring development in terms of nutritional quality than smaller ones (Tumomi et al., 1981; Kagata & Ohgushi, 2002). In our laboratory test, *C. erecta* leaves received more eggs as their size increased, indicating that *L. commelinae* females preferred larger leaves for oviposition. This suggests that the egg distribution patterns we observed may have resulted from a trade-off between competition and leaf quality. However, offspring fitness depends not only on bottom-up factors (leaf quality) but also on top-down ones (third trophic level), so trade-offs between both factors and competition in female oviposition decisions could be expected. Another study performed using the same urban patches found that larval parasitism on *L. commelinae* was inversely density-dependent at leaf scale (MS Fenoglio, unpubl.). Thus, the probability of an individual larva being parasitized decreased as the number of larvae per leaf increased, indicating that the negative impact of competition could (partly) be compensated for by a larger enemy-free space. Trade-offs between enemy impact and competition have also been reported for other leafminer species, although they are less frequent than for leaf quality and competition (Gripenberg & Roslin, 2008; Low 2008).

Summing up, our results indicate that competition was irrelevant as a selective force in shaping *L. commelinae* oviposition decisions, as egg distribution was aggregated and

did not change with leaf availability. Although egg clumping may not have negative consequences for leafminer offspring fitness in natural environments, it caused a significant decrease in survival and size in urban environments. However, whether egg laying decisions by *L. commelinae* maximize offspring fitness remains to be elucidated. Further studies are also necessary to determine whether fitness costs due to competition in larger leaves are lower than those resulting from ovipositing in smaller unoccupied leaves, by considering both leaf quality and enemy impact.

Many phytophagous insects, especially leafminers, distribute their eggs in an aggregated fashion with trade-offs between selective forces possibly implicated in the shaping of this pattern. The study of these forces for varying conditions (such as leaf availability) will help improve our understanding of their relative roles in shaping egg laying decisions.

## Acknowledgements

The authors wish to acknowledge the assistance of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Centro de Investigaciones Entomológicas de Córdoba (CIEC), both of which supported the facilities used in this investigation. Special thanks to Dr. Paul Hobson for reviewing the manuscript.

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