Larval Dispersal and Predation in Experimental Populations of *Chrysomya albiceps* and *Cochliomyia macellaria* (Diptera: Calliphoridae)

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In this study we investigated the larval dispersal associated with larval predation in experimental populations of Chrysomya albiceps *and* Cochliomyia macellaria. *Frequency distribution of sampling units (G test) in the substrate was used to evaluate variation in larval dispersal. An experimental acrylic channel (1 x 0.1 x 0.2 m) covered with wood shavings was used to observe larval dispersal prior to pupation. The acrylic channel was graduated at 0.05 m intervals, each representing a sampling unit; hence, 20 sampling units were set up. A Petri dish containing third instar larvae of single and double species was deposited at one edge of the acrylic channel allowing larvae to disperse. The number of buried pupae (0, 1, 2, ...n) present in each sampling unit was recorded. For double species, the number of recovered larvae of* C. albiceps *was similar to the number initially released on the dish Petri. On the other hand, the number of recovered larvae of* C. macellaria *was significantly smaller than the initially released number. The results show that* C. albiceps *attacks* C. macellaria *larvae during the larval dispersal process. The larval distribution of* C. albiceps *did not differ significantly from* C. macellaria *in double species, but it differed significantly in single species. The larval aggregation level of* C. macellaria *decreased when* C. albiceps *was present and the larval aggregation level of* C. albiceps *increased when* C. macellaria *was present. The implications of such findings for the population dynamics of these species are discussed.*

Key words: larval dispersal - predation - frequency distribution - blowflies

Larval dispersal is an important process in the life cycle of blowflies since during this period larvae leave their food substrate looking for a suitable place to bury and pupate (Levot et al. 1979). During this phase, the blowfly larvae may be at risk of predation, parasitation and desiccation (Legner 1977, Peschke et al. 1987). In two previous studies, Godoy et al. (1995, 1996) investigated the dispersal of post-feeding larvae of *Chrysomya megacephala* (Fabricius), *C. putoria* (Wiedemann) and *Cochliomyia macellaria* (Fabricius). They found that most larvae of *C. megacephala, C. putoria* and *C. macellaria* pupated close to the food source, although the maximum distance traveled by the larvae differed among the three species, with *C. megacephala* and *C. putoria* larvae reaching a greater maximum dispersal distance than *C. macellaria*.

Statistical analysis of the frequency distribution of dispersing blowfly larvae revealed that aggregated patterns of distribution emerge as a consequence of dispersal,

and *C. macellaria* has higher aggregation levels than *C. megacephala* and *C. putoria* (Godoy et al. 1996). Thus, aggregated patterns of distribution during the larval dispersal process may have important implications for the ecology of these species. Predation of post-feeding larvae by Coleoptera and attack by parasitoids occur primarily in the neighborhood of the food source (Peschke et al. 1987) and can also contribute in reducing fitness. It has been estimated that predation and parasitation during pre-adult stages, mainly pre-pupae and pupae, can raise mortality rates up to 60% in some blowfly species (Putman 1977).

Chrysomya albiceps (Wiedemann) is a facultative predator of other dipteran larvae (Fuller 1934, Coe 1978, Gagné 1981, Erzinçlioglu & Whitcombe 1983) and this habit probably has important effects on such prey species, particularly in communities where reduction in population size of native species is evident (Hanski 1977, Goodbrod & Goff 1990, Wells & Greenberg 1992a,b,c). Recently, Faria et al. (1999) and Faria and Godoy (2001) investigated facultative predation rates on third instar larvae of *C. macellaria, C. putoria* and *C. megacephala* by third instar larvae of *C. albiceps* in no-choice, two-choice and three-choice situations. The highest predation rate occurred for *C. macellaria* larvae, suggesting that *C. albiceps* has a higher predation impact on *C. macellaria* than the other prey species.

Although several studies regarding population interactions between the introduced species *C. albiceps, C.*

rufifacies (Macquart), *C. putoria* and *C. megacephala,* and the native species *C. macellaria* have been carried out (Wells & Greenberg 1992a,b,c, Faria et al. 1999, Reis et al. 1999, Faria & Godoy 2001), no systematic study associating blowfly larval predation and dispersal is available in the literature. Here, we investigated the larval aggregation patterns of *C. albiceps* and *C. macellaria* in single and double species experiments in order to evaluate the possible associations between predation and dispersal.

MATERIALS AND METHODS

Laboratory studies - Newly hatched larvae of *C. albiceps* and *C. macellaria* were obtained from adult flies kept at constant temperature (25ºC) and 80% relative humidity, and raised in vials containing 50 g of ground beef. An experimental acrylic channel (1 m long, 10 cm high, and 20 cm wide) covered with wood shavings was used to observe larval dispersal prior to pupation. The acrylic channel was graduated at 0.05 m intervals, each representing a sampling unit; hence, 20 sampling units were set up. A Petri dish containing third instar larvae of single and double species was deposited at one edge of the acrylic channel allowing larvae to disperse. The number of found pupae (0, 1, 2, …n) present in each sampling unit was recorded and plotted against its relative distance from the initial releasing point to assess the larval distribution pattern of each species. Two replicates per species were run, with 120 and 60 larvae in each replicate for single *C. albiceps* (120) and *C. macellaria* (120) and double *C. albiceps* (60) and *C. macellaria* (60) species, respectively.

Statistical analysis - Differences in larval dispersal patterns of postfeeding larvae between single and double blowfly species were evaluated by the *G* test (Sokal & Rohlf 1981). The frequency distribution of *C. albiceps* and *C. macellaria* pupae was fitted to the negative binomial distribution in order to determine whether larval dispersal was aggregated. The *k* parameter in the negative binomial distribution was estimated by the maximum likelihood method (Bliss & Fisher 1953, Ludwig & Reynolds 1988) and the fit of the negative binomial distribution was tested by the Pearson χ^2 statistic (Sokal & Rohlf 1981).

RESULTS AND DISCUSSION

C. albiceps larvae attacked *C. macellaria* larvae during their dispersal process. This result is interesting because no systematic study focusing on the description of larval predation outside the food substrate is available. The impact on *C. macellaria* was demonstrated by larval recovery. For double species we observed that the mean predation rate by *C. albiceps* on *C. macellaria* was 74%, suggesting that larval predation also occurs after the postfeeding period and particularly during larval migration. It is the first time that this kind of behavior is experimentally shown. This result is also relevant because *Chrysomya* species are implicated in a recent biological invasion process. Four *Chrysomya* species were introduced to the Americas about 25 years ago and probably displaced the native species *C. macellaria* (Guimarães et al. 1978, 1979). We strongly believe that the predatory habit of *C. albiceps* had an important impact on the survival rates of *C. macellaria*.

Most of *C. albiceps* and *C. macellaria* larvae were found near the point of larval release (Figs 1-3). For blowfly dispersal experiments, Greenberg (1990) and Godoy et al. (1995) observed similar results. The distribution of larvae differed significantly between species when *C. albiceps* and *C. macellaria* were released as single species ($G_H = 105.92$, first replicate; $G_H = 91.57$, second replicate; df = 19, P < 0.05) (Figs 2, 3). Godoy et al. (1995) and Boldrini et al. (1997) also observed a variation in the dispersal patterns among the blowfly species *C. megacephala, C. putoria* and *C. macellaria.* They found at least two different distribution patterns in the species studied. The first pattern was defined as a damping oscillation, with bimodal distribution in *C. megacephala* and *C. putoria* (Godoy et al. 1995, Boldrini et al. 1997), and the second showed no oscillation and could be defined as a regular diffusion process (Boldrini et al. 1997). In our experiments we found no clear oscillation for *C. albiceps* and *C. macellaria* and we believe that the oscillation patterns found by Godoy et al. (1995) and Boldrini et al. (1997) do not occur for these species.
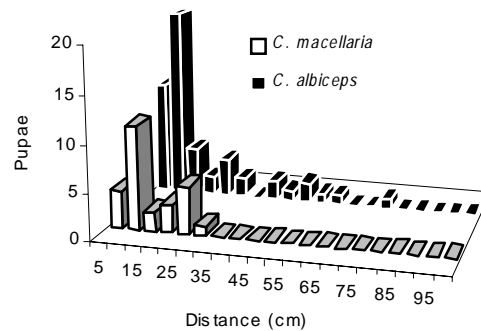

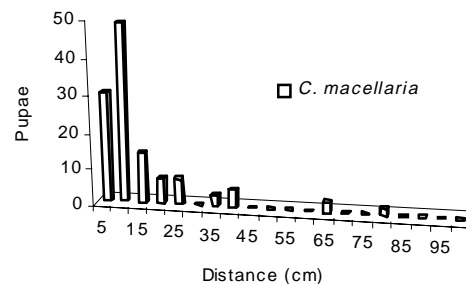Fig. 1: larval dispersal in *Chrysomya albiceps* and *Cochliomyia macellaria.*

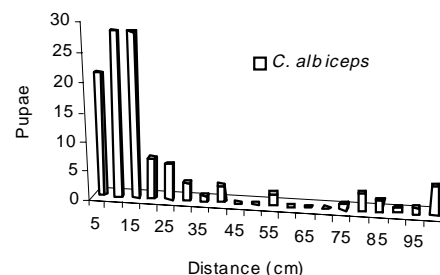Fig. 2: larval dispersal in *Cochliomyia macellaria.*

Fig. 3: larval dispersal in *Chrysomya albiceps.*

TABLE

Statistical analysis of test (first column) and replicate (second column) of the number of pupae in the 20 sampling units for the two blowfly species: *Chrysomya albiceps* and *Cochliomyia macellaria*

Parameters	Double species (rep. 1)		Double species (rep. 2)		Single species (rep. 1)		Single species (rep. 2)	
	C. albiceps	*C. macellaria*	*C. albiceps*	*C. macellaria*	*C. albiceps*	*C. macellaria*	*C. albiceps*	*C. macellaria*
Mean	2.65	1.3	2.6	12.3	5.74	2	3.45	3.45
Variance	24.45	7.48	9.94	79.12	84.65	12.42	24.68	26.05
K	0.49	0.16	1.26	0.83	0.55	0.16	1.73	0.21
χ^2	10.77	13.14	10.03	9.28	14.7	5.29	22.96	14.22
d.f.	13	9	9	14	20	5	10	9

When the two species were released together, no significant difference was found regarding frequency distribution ($G_H = 10.49$, first replicate; $G_H = 11.53$, second replicate, $df = 19$, $P > 0.05$) (Fig. 1). This result suggests some kind of association between the two species. In addition, for double and single experimental settings, both species exhibited an aggregated pattern of distribution since the negative binomial model was fitted to the data (Table). The presence of *C. albiceps* close to *C. macellaria* in order to attack it could explain the similar distribution found. Post-feeding larvae of *C. albiceps* leave the food substrate after consuming the whole food resource. Nevertheless, they may attack *C. macellaria* larvae prior to pupation (Faria et al. 1999).

We used frequency distribution to understand the association between larval predation and aggregation since aggregated distribution has been frequently employed in studies focusing on spatial patterns in the distribution of invertebrates, mainly parasites and insects (Atkinson & Shorrocks 1984, Shorrocks et al. 1984, Kneidel 1985, Ives 1988, Rosewell et al. 1990, Poulin 1993, Sréter et al. 1994, Umoru 1994).

Observing the mean *k* values we noticed that *C. macellaria* exhibited higher aggregation level in single than in double species, whereas *C. albiceps* showed higher aggregation level in double than in single species. These results suggest that *C. macellaria* larvae are more aggregated in the absence of *C. albiceps* and, when attacked by *C. albiceps*, their aggregation level decreases because the larvae try to escape or are killed and ingested by *C. albiceps*. In contrast, *C. albiceps* larvae exhibited a smaller aggregation level in absence of *C. macellaria*, and when searched and caught *C. macellaria* they became more aggregated. This assumption was confirmed by the *G* test which detected no significant difference between predator and prey distribution for double species. We believe that the results reported here may raise relevant questions about larval predation and dispersal of blowflies.

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