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Ovipositional Behavior in Predator and Prey Blowflies

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In this study we analyzed the ovipositional behavior of C. albiceps, C. megacephala *and* L. eximia *in response to previous presence of larvae of different species, both predator and prey. The preference for substrates that previously had had no larvae was predominant for all species. However, the experiments showed that* C. megacephala *and* L. eximia *avoid laying eggs principally in patches with previous presence of* C. albiceps *larvae. The implications of these results for the necrophagous Diptera community dynamics are discussed.*

KEY WORDS: oviposition; population dynamics; blowflies.

INTRODUCTION

Blowflies are carrion breeders and lay eggs usually in batches of 100–300, frequently among eggs of several different species (Smith, 1986). The distribution of immature individuals in discrete breeding sites occurs with the random dispersal of adult females (Blackith and Blackith, 1990) and might influence the level of competition for food and space among the former, with consequences for the viability of resultant adults (De Jong, 1979, 1982) and with a marked effect upon population dynamics, since insect density may differ between patches (Ives and May, 1985; Turchin, 1998).

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Chrysomya (Calliphoridae) is a genus of blowflies that includes about thirty abundant and economically important species (Dear, 1985), with distribution restricted to the Old World and Australasia before 1975 (Guimarães *et al.*, 1978; Baumgartner and Greenberg, 1984; Dear, 1985). *Chrysomya megacephala, C. putoria, C. albiceps* and *C. rufifacies* are the most well studied species on account of their introduction to the Americas thirty years ago, in addition to their rapid dispersal and colonization process (Guimarães *et al.*, 1978, 1979; Baumgartner and Greenberg, 1984; Greenberg, 1988). The introduction of these species has influenced the Brazilian necrophagous Diptera fauna, as shown by the displacement of *Cochliomyia macellaria* (Guimarães *et al.*, 1978, 1979; Prado and Guimarães, 1982).

Interspecific interactions have been studied in blowflies, with results showing strong influences of those introduced on native species with respect to competition for food (Wells and Greenberg, 1992a,b,c; Reis *et al.*, 1999). Larval predation in experimental blowfly populations has also been investigated by Faria *et al.* (1999), Andrade *et al.* (2002) and Reigada and Godoy (2005). They observed that *C. albiceps* third instar larvae attacked *C. macellaria, C. putoria* and *C. megacephala* third instar larvae, indicating the negative impact of the predator species on the survival of the prey species.

Although the studies focused on interspecific interactions have clarified several important points related to larval behavior, the ovipositional behavior of blowflies has received little attention, principally in the context of interspecific interactions. Choice of ovipositional patches and dispersion of eggs by adult insects can vary among host species or substrate type, among individuals within a host population, or among individuals of a particular host population (Dukas *et al.*, 2001; Holland *et al.*, 2004). Oviposition is a very important biological process for flies, because it determines the potential population size for successive generations (Ullyett, 1950; Smith, 1986).

Especially in taxonomic groups in which the predator-prey relationship is predominant, the choice among ovipositional patches can influence the population positively or negatively in terms of dynamics and persistence (Waage and Greathead, 1986). Generalist predators frequently have complex behavioral mechanisms involving the search for, and the choice and consumption of prey, habits which may influence ovipositional behavior (Hagen, 1987; Scott and Barlow, 1990; Hagen *et al.*, 1999).

Despite intensive research focusing on ovipositional behavior in predator species (Albuquerque *et al.*, 1997; Bargen *et al.*, 1998; Hagen *et al.*, 1999; Sadeghi and Gilbert, 2000), few studies have evaluated the consequences of patch preference on predators that consume different prey species and on the population dynamics of prey (Petersen and Hunter, 2002).

Preference for ovipositional patches occurs generally in response to several factors such as suitability of food for offspring, decrease of prey-predator encounters, minimization of risks between natural enemies or prevention of high densities in ephemeral substrates that can be insufficient to support high population sizes (Atkinson and Shorrocks, 1981; Petersen and Hunter, 2002).

In Calliphoridae, studies focusing on ovipositional behavior have not been frequent. The principal studies performed until now focused on patch dynamics and distribution of Diptera in different food substrates (Hanski, 1987; D'Almeida and Almeida, 1998). We believe that the blowfly ovipositional behavior occurs in a random manner. However, there has been no study evaluating the influence of the previous presence of different species, principally in case of larval competitor or predator species. The principal reason to investigate this point is because ovipositional behavior may indirectly affect individual fitness, population dynamics, and community structure (Blaustein, 1999).

In the present study we analyzed the ovipositional behavior of *C. albiceps*, *C. megacephala* and *L. eximia* in response to previous presence of different species in the larval stage in both predator and prey. With this experimental design we intend to show how the previous presence of predator and prey larvae can influence or not the ovipositional behavior in blowflies.

METHODS

Specimens of *C. albiceps, C. megacephala* and *L. eximia* were collected in the vicinity of the Campus of Universidade Estadual Paulista, Botucatu, São Paulo, Brazil. Adults were maintained in the laboratory, in cages (30 × 30 × 30 cm) covered with nylon at 25 ± 1°C and were fed water and sugar *ad libitum*. Adult females were fed fresh beef liver to permit the complete development of the gonotrophic cycle (Linhares, 1988). Newly hatched larvae of *C. albiceps, C. megacephala* and *L. eximia* were obtained from eggs of adult flies kept at constant temperature (25°C) and 70% relative humidity, and raised in vials containing ground beef in excess.

Experimental Setting for Ovipositional Patch Choice Behavior

Cylindrical vials (15 × 13 cm) received three *C. albiceps* females with developed gonotrophic cycle. Three vials (4 × 4 cm) were introduced into the larger cylindrical vials to permit oviposition by females of *C. albiceps* (Fig. 1). Each small vial had 20 g of ground beef with two of them also receiving blowfly larvae. One hundred hatched larvae of *L. eximia* were

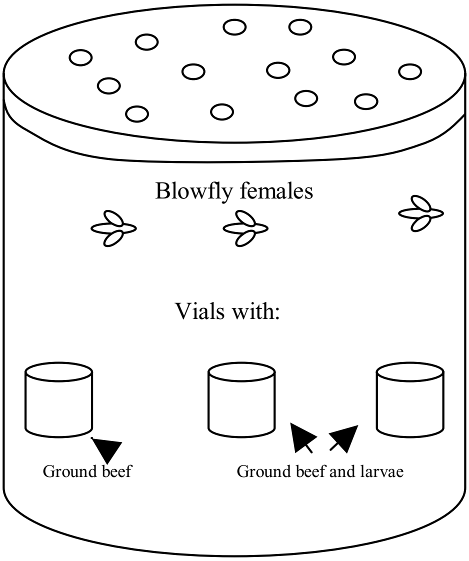

Fig. 1. Experimental design showing ovipositional patch choice experiment.

introduced into the vial and one hundred larvae of *C. megacephala* into the other (Fig. 1). This procedure was adopted to permit different options for oviposition by *C. albiceps*. Thus, *C. albiceps* females could choose among three treatments: ground beef only, ground beef plus *L. eximia* larvae and ground beef plus *C. megacephala* larvae. The number of eggs found in each vial was recorded after 24, 48 and 72 h. Twenty replicates were performed for each treatment. The same experimental protocol was employed to investigate the ovipositional patch choice behavior by *C. megacephala*, with previous presence of *C. albiceps* and *L. eximia* larvae, and to evaluate the patch choice behavior by *L. eximia*, with previous presence of *C. albiceps* and *C. megacephala*.

Statistical Analysis

Comparison of frequency distribution of eggs among ovipositional patches was performed by using the *G* homogeneity test (Sokal and Rohlf, 1981). The frequency distribution of *C. albiceps, C. megacephala* and *L. eximia* eggs was fitted to the Negative binomial and Poisson distributions in order to determine whether the distribution of eggs was clumped or random. The *k* parameter in the Negative binomial distribution was estimated by the maximum likelihood method (Bliss and Fisher, 1953; Ludwig and

Reynolds, 1988) and the fits of the Negative binomial and Poisson distributions were tested by the Pearson χ^2 statistic (Sokal and Rohlf, 1981). K values close to zero describe the maximum aggregation level. In the Negative binomial distribution the null hypothesis was that the egg distribution of *C. albiceps, C. megacephala* and *L. eximia* exhibits a clumped distribution pattern. In the Poisson distribution the null hypothesis was that the egg distribution follows a random pattern.

RESULTS AND DISCUSSION

Most of the eggs laid by *C. albiceps*, *L. eximia* and *C. megacephala* were found 24 h after the exposure to ovipositional patches. Females of *C. albiceps* produced two egg batches after 24 h, one in the patch which had ground beef plus *C. megacephala* larvae and the other in the patch with only ground beef. Females of *C. megacephala* laid two egg batches in the patch with only ground beef and two in the patch which had ground beef plus *L. eximia* larvae. Females of *L. eximia* produced three egg batches in the patch with only ground beef and one in the patch with ground beef plus *C. albiceps*. The *G* test was employed to analyze the difference among the numbers of eggs found in the three ovipositional patches, through a period of 72 h. The results suggest that the number of eggs laid by the three species differs significantly among the three ovipositional patches (Table I).

Females of *C. albiceps* exhibited preference for the patch in which there were no larvae (Fig. 2). Comparing only the ovipositional patches where there were larvae, the difference between the number of *C. albiceps* eggs laid in each patch was not significant (Table I). With respect to ovipositional habit of *C. albiceps,* our findings indicate a preference for patches containing no larvae, suggesting that *C. albiceps* look for empty patches in which to lay eggs, avoiding the presence of other larvae. This result suggests that the risk of competition for food may be influencing the decision of *C. albiceps*.

Table I. G Test to Analyze the Difference Among Three and Two Ovipositional Patches

	Comparison among three patches			Comparison between two patches		
Parameters	MLB	MAB	LAB	ML	MA	LA
G	79.37	155.25	284.49	22.99	21.88	86.28
df	38	66	82	19	33	41
P	<0.001	<0.001	<0.001	=0.237	=0.930	<0.001

Note. M (ground beef and *C. megacephala* larvae); L (ground beef and *L. eximia* larvae); B (only ground beef); A (ground beef and *C. albiceps* larvae).

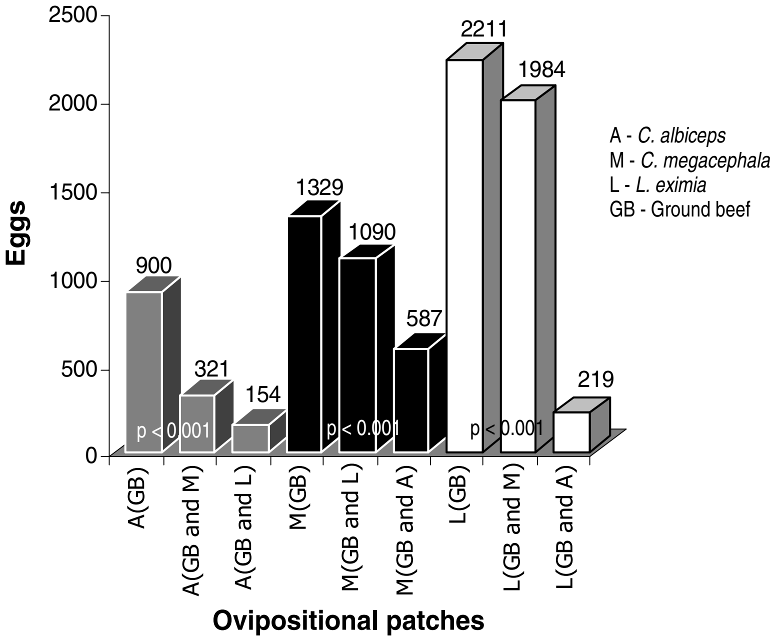

Fig. 2. Number of eggs laid by *C. albiceps* (**A**), *C. megacephala* (**M**) and *L. eximia* (**L**) in three different ovipositional patches.

Females of *L. eximia* also showed preference for patches that had no larvae (Fig. 2). However, where there were larvae of *C. albiceps* the number of *L. eximia* eggs was clearly lower than in the other patches (Fig. 2). Compared to the ovipositional patches where there were larvae, the difference between the number of eggs of *L. eximia* also was not significant (Table I). Females of *C. megacephala* exhibited a slight preference for the ovipositional patch that had only ground beef, followed by the patch with ground beef plus *L. eximia* larvae (Fig. 2). There was a significant difference between the two ovipositional patches with larvae (Table I). Egg distribution by *C. albiceps, C. megacephala* and *L. eximia* in the ovipositional patches trended to a clumped pattern ($P < 0.05$), independent of patch content; and the Negative binomial model seemed to provide a good fit for the data exhibiting K values between 0.01 and 0.07.

It is interesting to note that, although all species showed a preference for patches where there was only ground beef, *C. albiceps* appears to have been a species that rejected more substrates in which other species had been present previously. In these cases its ovipositional behavior resulted in no more than 321 eggs, versus a higher number of eggs laid by the other species in patches with previous presence of larvae (Fig. 2). Both *C. megacephala* and *L. eximia* laid significantly fewer eggs where *C. albiceps* larvae were previously present, suggesting an ovipositional inhibition when their females faced *C. albiceps* larvae.

On the other hand, when *C. megacephala* females faced *L. eximia* larvae or *L. eximia* faced *C. megacephala* larvae, the number of eggs laid was not excessively low. It is possible that the ovipositional avoidance occurred in response to the movement of *C. albiceps* larvae, which during the third larval instar move vigorously on the substrate searching for food or prey larvae (Faria *et al.*, 1999; Reigada and Godoy, 2005). Hence, our results suggest that the previous presence of *C. albiceps* larvae can influence the ovipositional behavior of *L. eximia* and *C. megacephala*.

Ovipositional behavior has been studied in Diptera, but the emphasis given to previous presence of predator and prey has not been directed to Calliphoridae species (Solar and Ruiz, 1992; Prokopy and Reynolds, 1998; Dukas *et al.*, 2001; Joachim-Bravo *et al.*, 2001). Although these species belong to other taxonomic groups, the results of these studies suggest that the risk of predation can influence the ovipositional behavior of Diptera females.

Of all Calliphoridae species *C. albiceps* has been the most abundant species in Brazil in recent years (Souza *et al.*, 1997; Carvalho *et al.*, 2001, 2004). We believe that the highly seasonal and spatial abundance of *C. albiceps* in fact is related to its predatory habit since the larval predation is an interaction capable of influencing the necrophagous fauna composition (Faria *et al.*, 1999). Confronting the results recently found in previous investigations performed in Brazil with other countries, it is possible to conclude that *C. albiceps* is a species, which has exhibited a remarkable performance in terms of abundance. In this sense we also suppose that the ovipositional behavior of prey species mentioned herein also contributes to the results recorded in the several studies.

This is the first time that ovipositional behavior in Diptera (Calliphoridae) has been evaluated by taking into account the previous presence of prey and predator. Several studies have focused on prey-predator interaction in Calliphoridae, but all were designed to analyze larval interactions (Faria *et al.*, 1999; Faria *et al.*, 2004a,b; Rosa *et al.*, 2004; Reigada and Godoy, 2005). Larval predation in blowflies frequently results in important consequences for community dynamics of necrophagous Diptera since it may significantly influence the abundance of several species (Faria *et al.*, 1999). In addition, the necrophagous fauna composition appears to exhibit expressive variations with respect to diversity, making the interspecific interaction a very important factor to be considered in forensic entomology

(Grassberger *et al.*, 2003). In this sense, the focus of the present study, evolving adult behavior, makes an important contribution to the database applied to population ecology and forensic science, since the population potential for future generations essentially depends on ovipositional behavior of the flies.

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