

ECOLOGY, BEHAVIOR AND BIONOMICS

The Dynamics of Intraguild Predation in *Chrysomya albiceps* Wied. (Diptera: Calliphoridae): Interactions between Instars and Species under Different Abundances of Food

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A Dinâmica de Predação Intraguilda em *Chrysomya albiceps* Wied. (Diptera: Calliphoridae): Interações entre Instares e Espécies sob Diferentes Abundâncias de Alimento

RESUMO - O padrão de interação larval em moscas-varejeiras na presença de *Chrysomya albiceps* Wied. e *C. rufifacies* Maquart pode ser alterado em função do comportamento predatório das duas espécies, mudando a estratégia de competição do tipo explorativa para competição por interferência. A predação facultativa é um comportamento freqüente em *C. albiceps* e *C. rufifacies* durante o estágio larval. Neste estudo, investigamos a dinâmica de predação intraguilda por *C. albiceps* sobre outras espécies de moscas, em experimentos delineados para analisar a sobrevivência interespecífica e intraespecífica em *C. albiceps*, *C. megacephala* Fabricius e *C. macellaria* Fabricius. O delineamento experimental do estudo permitiu avaliar de que modo fatores como, espécies, densidade e abundância de alimento, influenciaram a sobrevivência das espécies em culturas puras e mistas. Quando *C. albiceps* foi confinada com *C. megacephala* ou *C. macellaria*, somente adultos de *C. albiceps* sobreviveram em diferentes densidades e abundância de alimento. Além disso, a sobrevivência de *C. albiceps* foi superior em culturas mistas se comparada aos experimentos com culturas puras. As implicações desses resultados para a dinâmica de *C. albiceps* foram discutidas.

PALAVRAS-CHAVE: Comportamento larval, mosca-varejeira, competição

ABSTRACT - The pattern of larval interaction in blowflies confined with *Chrysomya albiceps* Wied. and *C. rufifacies* Maquart can be changed in response to the predatory behaviour of the two species to a contest-type process instead of the scramble competition that usually occurs in blowflies. Facultative predation is a frequent behaviour in *C. albiceps* and *C. rufifacies* that occurs as an alternative food source during the larval stage. In this study, we investigated the dynamics of intraguild predation by *C. albiceps* on other fly species in order to analyse interspecific and intraspecific survival in *C. albiceps*, *C. megacephala* and *C. macellaria* Fabricius. The experimental design of the study allowed us to evaluate how factors such as species, density and abundance of food influenced the survival of the calliphorid species. When *C. albiceps* was confined with *C. megacephala* or *C. macellaria*, only adults of *C. albiceps* survived at different larval densities and abundance of food. In addition, the survival of *C. albiceps* was higher in two-species experiments when compared to single species experiments. The implications of these results for the dynamics of *C. albiceps* were discussed.

KEY WORDS: Larval behavior, blowfly, competition

Nearly 30 years ago, three species of blowflies from Africa and Asia, *Chrysomya albiceps* Wiedemann, *C. megacephala* Fabricius and *C. putoria* Wiedemann, became established in the Americas (Guimarães *et al.* 1978). This invasion led to a sudden decline in the numbers of ecologically similar native American species, such as *Cochliomyia macellaria* Fabricius and *Lucilia eximia* Wiedemann (Prado & Guimarães 1982).

C. albiceps, one of the invading species, is a carcass feeder frequently involved in secondary myiasis in sheep (Zumpt 1965).

Blowfly species frequently show different competitive abilities which, when associated with other types of behaviour, such as predation or cannibalism, interfere with coexistence by maintaining different species present in patches in spite

of their population sizes, and by excluding one of them (Goodbrod & Goff 1990, Ulyett 1950). For *C. albiceps* and *C. ruffifacies* Fabricius, local competition can cause the competitor to become an active predator, and can lead to a contest-type process instead of the scramble competition that usually occurs in blowflies (Ulyett 1950, Nicholson 1954). Facultative predation is a good example of the interaction that occurs as an alternative food source, and the blowflies *C. albiceps* and *C. ruffifacies* shows such behavior during the larval stage (Wells & Greenberg 1992a, b, c).

Facultative predation by *Chrysomya* species was classified as intraguild predation (IGP) by Polis et al. (1989), who suggested that IGP can lead to faster growth and earlier metamorphosis in these organisms. Intraguild predation is usually categorized as a combination of competition and predation that involves the killing and eating of species that use similar, often limiting, resources and are thus potential competitors (Polis et al. 1989). Such predation can be distinguished from traditional concepts of competition by the immediate energetic gains for the predator, and differs from classic predation because the act reduces potential exploitative competition (Polis et al. 1989).

The specific predatory behaviour of *C. albiceps* has been investigated through choice and no-choice experiments designed to evaluate larval predation rates and prey choice by *C. albiceps* (Faria et al. 1999, Faria & Godoy 2001). *C. albiceps* attacks *C. macellaria* more often than *C. megacephala* and *C. putoria* (Faria et al. 1999). However, in the absence of *C. macellaria*, *C. albiceps* attacks *C. putoria* more often than *C. megacephala* (Faria & Godoy 2001). Attacks occur more often within the carcass, but may also occur outside, during larval dispersal (Andrade et al. 2002, Gomes & Von Zuben 2005). Grassberger et al. (2003) reported that the mortality rate of *Lucilia sericata* Meigen caused by predation from *C. albiceps* ranged from 57.6% to 99%, indicating a high susceptibility of *L. sericata* to attack by *C. albiceps*. This type of interaction may have serious implications for the faunal structure of necrophagous flies and, consequently, for forensic entomology in which the abundance and coexistence of species are important data (Gomes & Von Zuben 2005), since carcasses can be almost monopolised by a single predator fly species such as *C. albiceps* (Grassberger et al. 2003).

The negative influence of *C. albiceps* on the abundance of other blowfly species has also been intensely studied, and the results of these investigations clearly suggest that this behaviour can be an important factor in the displacement of native species in the New World (Wells & Greenberg 1992 a,b,c; Faria et al. 1999). However, biological invasions and the colonization of new areas must be evaluated not only by abundance, but also by factors such as patch habitat availability and interspecific interactions (Wells & Greenberg 1992a,b,c; Tilman & Kareiva 1997).

Despite these studies, it is not yet clear how intraguild predation occurs in situations that involve different amounts of food and densities. Important aspects that need to be considered when assessing interaction dynamics and carrying capacity include the influence of larval densities and the amount of food on predator and prey interactions, as

well as the factors that determine a switching of behaviour from competitor to predator. In this study, we investigated the dynamics of intraguild predation by *C. albiceps* larvae on themselves and on the larvae of *C. megacephala* and *C. macellaria* in experiments designed to analyse double and single species survival. The effects of interactions among instars and of food abundance on blowfly survival were also estimated in order to understand what governs the intraguild predation by *C. albiceps* in a context of carrying capacity.

Material and Methods

Laboratory populations. Laboratory populations of *C. albiceps*, *C. macellaria* and *C. megacephala* were established from specimens collected on the campus of the Universidade Estadual Paulista, Botucatu, São Paulo, Brazil. Adult flies were maintained at $25 \pm 1^\circ\text{C}$ in cages (30 cm x 30 cm x 30 cm) covered with nylon and were fed water and sugar *ad libitum*. Adult females were fed fresh beef liver to allow the complete development of the gonotrophic cycle. Hatched larvae of *C. albiceps* were reared on an excess of ground beef until the 3rd instar when they were removed and placed in empty vials (10 cm height x 7 cm wide). These larvae were considered to be predators, since 3rd instar is the life stage at which predation rates have been considered the highest (Wells & Greenberg 1992a, Faria et al. 1999).

Hatched larvae of *C. macellaria* and *C. megacephala* were reared as described for *C. albiceps*, but were only allowed to reach the 2nd instar since they were considered prey. Strong predator-prey interactions classically imply differences in size, with predators generally being larger than prey (Faria et al. 1999, Faria & Godoy 2001). The larval instars were determined using accepted morphological characters to identify the various developmental stages (Prins 1982). One and two-species interaction experiments were set up, with 50% of larvae for each instar, i.e. 50% being 3rd instar (predators) and 50% being 2nd instar (prey).

The experiments were also conducted with larval densities of 200 and 1000 at the 1:1 proportion of predators (3rd-instar larva of *C. albiceps*) and prey (2nd-instar larva). For two-species experiments, the following treatments were performed: 100 3rd-instar larvae of *C. albiceps* with 100 2nd-instar larvae of *C. megacephala*, 100 3rd-instar larvae of *C. albiceps* with 100 2nd-instar larvae of *C. macellaria*, 500 3rd-instar larvae of *C. albiceps* with 500 2nd-instar larvae of *C. megacephala*, and 500 3rd-instar larvae of *C. albiceps* with 500 2nd-instar larvae of *C. macellaria*. Each larval density was studied under three levels of food abundance, namely, no food (1), moderate food abundance (2) and high food abundance (3), which corresponded to 0, 25 and 50 g of ground beef, respectively. The survival was estimated for each larval density and treatment by recording the number of adults obtained in the experiments. Three replicates (Grassberger et al. 2003) were used for the density of 200 and five for the density of 1000 based on a previous work (Reis et al. 1999).

Statistical analysis. The results were expressed as the

mean \pm S. D. Statistical comparisons were performed by using a three-way ANOVA with food abundance, species and densities as the factors. The Tukey test was used for multiple comparisons. The analyses were done using the SAS software (SAS Institute 1989). Values of $P < 0.05$ indicated significance (Table 1).

Results and Discussion

When *C. albiceps* was confined with *C. megacephala* or with *C. macellaria*, the only survivors at the two densities and three treatments were adults of *C. albiceps* (Figs. 1 and 2). Since two-species experiments of *C. albiceps* completely eliminated *C. megacephala* and *C. macellaria* individuals, no statistical comparisons were done between one and two-species experiments. *C. albiceps* had a higher survival in double compared to single species cultures at a density of 200 for the three treatments (Fig. 3). At a density of 1000, only one case of double culture (*C. albiceps* \times *C. megacephala*, treatment 2) had a lower survival than the single culture for *C. albiceps* (Fig. 3). The survival for *C. albiceps* at a density of 1000 was higher when this species was confined with *C. megacephala* in treatment 1, and with *C. macellaria* in treatments 2 and 3 (Fig. 3).

The sources of variation, degrees freedom, F - values and P -values are shown in Table 1. The difference among the survival percentages was significant for all sources of variation shown in Table 1, except for the factor species, when separately analysed. The survival percentages did not differ significantly among single species when analysed without consider the factors abundance and availability of food, which are narrowly associated with the environmental carrying capacity. Both density and different levels of

Table 1. Statistics for the three way ANOVA and Tukey test for multiple comparisons.

Source of variation	DF	F	P-value
Treatment	2	80.22	0.000
Species	2	0.52	0.596
Density	1	27.68	0.000
Treatment x species	4	4.23	0.004
Treatment x density	2	23.49	0.000
Species x density	2	5.24	0.008
Treatment x species x density	4	6.42	0.003

abundance, expressed in this study as treatments, influenced significantly the survival percentages (Table 1). This kind of influence has been also observed in experiments focused on intraspecific larval competition, where survival rates among blowfly species were very similar, leading to identical results in terms of dynamic behaviour, investigated by mathematical models of population growth (Godoy *et al.* 1993, Von Zuben *et al.* 1993).

The dynamic behaviour in insects can be understood as the temporal trajectory pattern exhibited by the population, expressed frequently by different types of oscillations, which are strongly influenced by demographic parameters, such as survival and fecundity (Prout & McChesney 1985, Godoy *et al.* 2001). Density-dependent mechanisms generally are associated to variation of demographic values, and consequently of dynamic behaviour in blowflies (Godoy *et al.* 1996). In our study, both the three way ANOVA and the Tukey test for multiple comparisons showed that

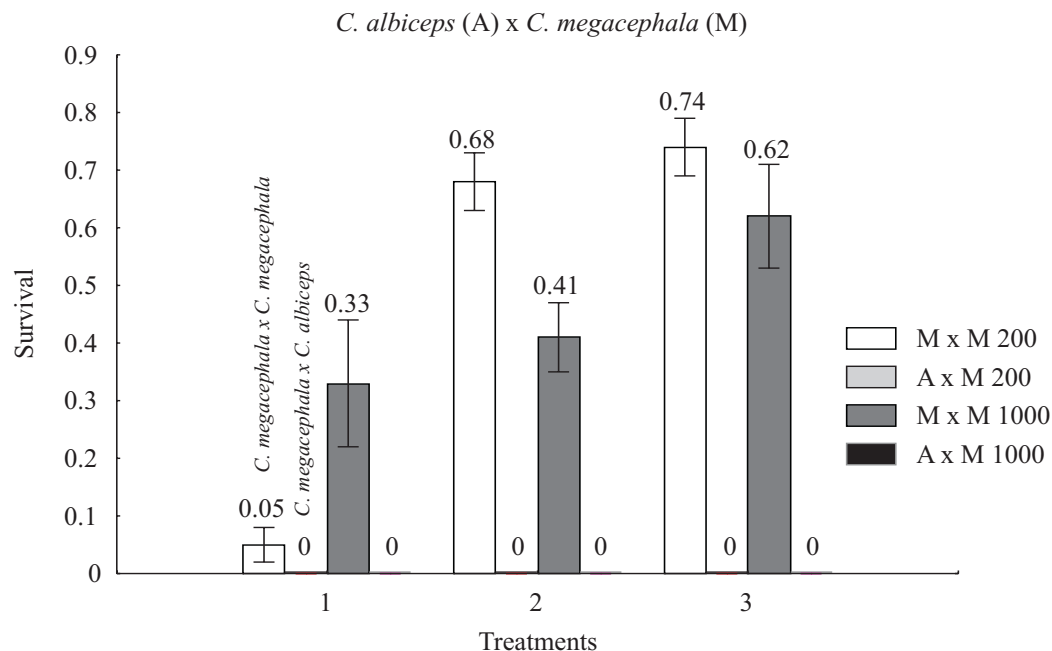


Fig. 1. Survival percentage for different treatments (g of food), and different larval densities of *C. megacephala*. Treatment 1, no meat; treatment 2, 25 g of meat; treatment 3, 50 g of meat.

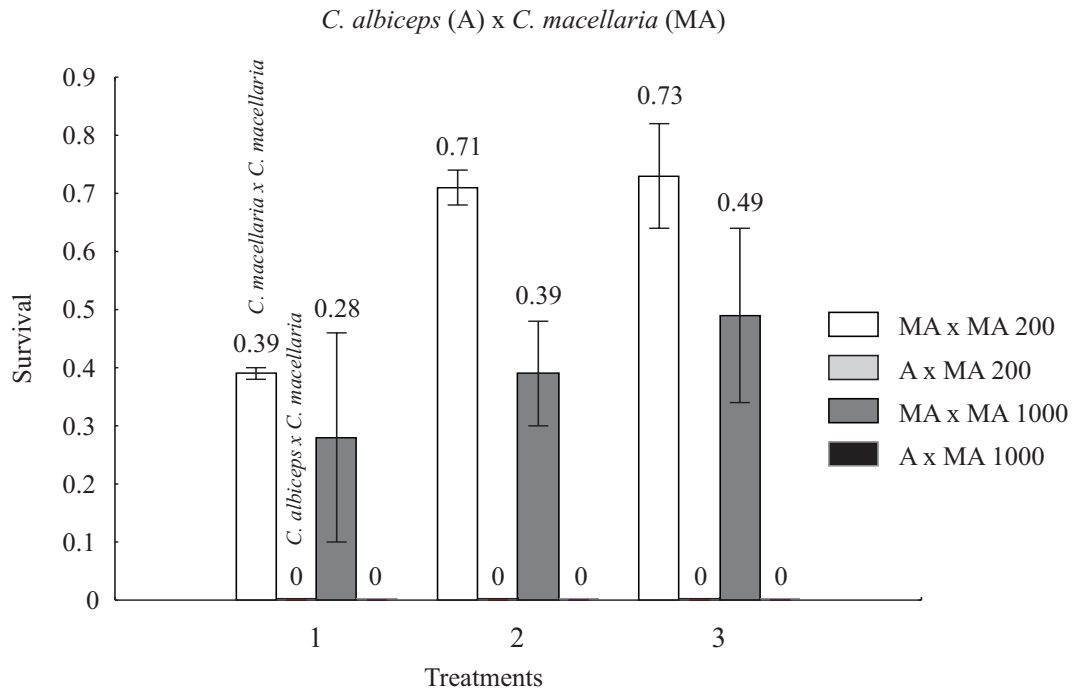


Fig. 2. Survival percentage for different treatments (g of food), and different intra and interspecific densities of *C. macellaria*. Treatment 1, no meat; treatment 2, 25 g of meat; treatment 3, 50 g of meat.

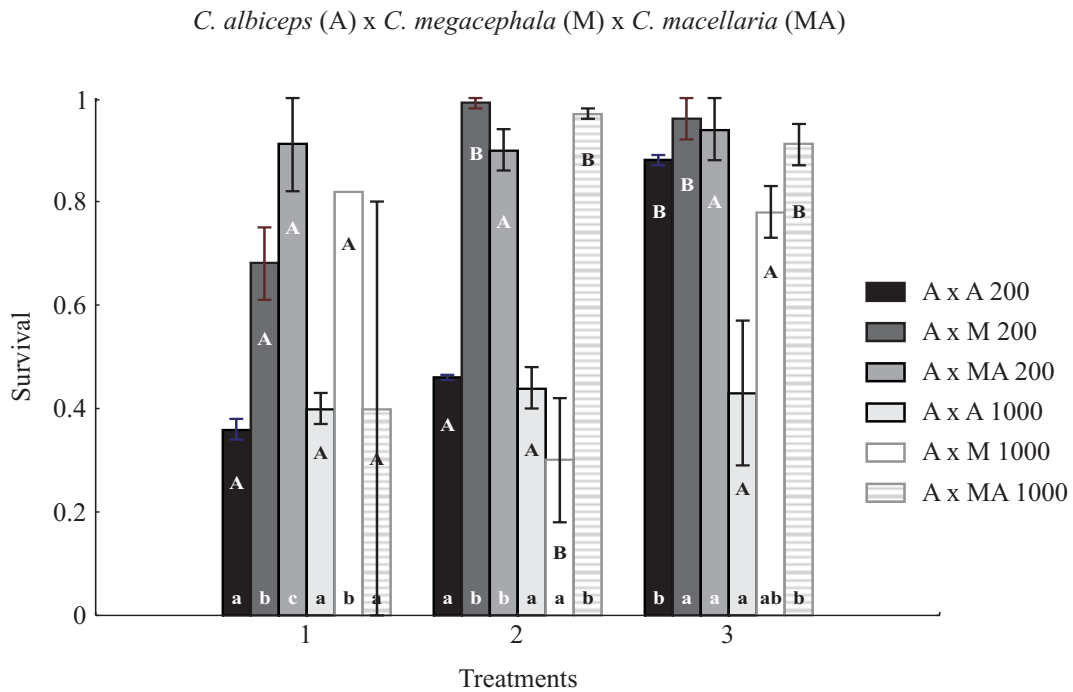


Fig. 3. Survival percentage for different treatments (g of food), species and intra and interspecific densities of *C. albiceps*. Treatment 1, no meat; treatment 2, 25 g of meat; treatment 3, 50 g of meat. Bars with different letters, (capital letters to compare treatments and small letters to compare species) differ significantly ($P < 0.05$, ANOVA and Tukey test).

the influence of the factorial interaction on the survival percentages is significant, indicating that treatment, densities and species are factors capable to change the demographic values in blowflies, with probable consequences for the species population dynamics.

The results suggested that, intraguild predation by *C. albiceps* occurred in the interactions, since no larvae of *C. megacephala* or *C. macellaria* were found after the confinements. Theoretical studies have shown that intraguild predation can affect population dynamics because the intraguild prey have difficulty to survive in food webs where they compete for food and are subjected to predation (Holt & Polis 1997, McCann & Hastings 1997). Based on an isocline analysis of an intraguild predation model, Polis *et al.* (1989) showed that if two species coexist without intraguild predation then adding intraguild predation can lead to exclusion of the intraguild prey from the system. Reis *et al.* (1999) observed that *C. putoria* and *C. macellaria* coexisted where there is no *C. albiceps* larvae. Both intraguild predators and prey can coexist only if the intraguild predators are less inferior than the intraguild prey in exploiting a common resource (Holt & Polis 1997). Moreover, if the intraguild predator is an efficient competitor for shared resources then, even without intraguild predation, the intraguild prey will be eliminated. Holt & Polis (1997) also argued that if intraguild predators follow optimal foraging theory rules, then coexistence might be achieved by dropping the intraguild prey from the predator's diet when food is abundant.

Intraguild predation by *C. albiceps* and *C. rufifacies* has also been observed on other fly species (Ullyett 1950; Wells & Greenberg 1992 a,b,c). In this study, *C. albiceps* showed higher survival in most of the two-species experiments, suggesting that predation offers more advantages to *C. albiceps* than competition for food and cannibalism (Faria *et al.* 1999, 2004). However, interspecific competition might be more advantageous than intraspecific competition, with the preference generally depending on the strength of the interactions between the species (Reis *et al.* 1999).

Intraguild predation provides an alternative resource, when food is scarce, resulting in a decrease of competition for food if one of the competitor species also acts as a predator (Hanski 1981, Polis *et al.* 1989). Many predators are also cannibals, including *C. albiceps* (Faria *et al.* 2004), and the offspring size, growth rate, longevity and reproductive phenology may influence the strength and direction of intraguild predation (Reaka 1987). Intraguild predators can benefit from reduced competition, especially competition for local resources (Mabelis 1984). In some cases, intraguild predation is sufficiently severe to reduce or eliminate the prey population, including insects that feed on carcasses (Polis *et al.* 1989).

At the initial stages of confinement, larvae of both *C. megacephala* and *C. macellaria* avoid interaction with *C. albiceps* larvae by migrating to the vial walls or penetrating the food substrate (Rosa *et al.* 2004). Population theory suggests that a stable coexistence amongst competing species is only possible if the species are sufficiently ecologically distinct, i.e. they must have different roles in order to live in the same community (Zhang & Hanski 1998).

Based on the results of this study, we conclude that the

three factors analysed here (species, amount of food and density) were all important for the interactions amongst blowflies. Competition, predation and cannibalism in experimental and natural populations are interactions that, in association with food abundance, may produce a variety of effects on the natural pattern of interactions in necrophagous dipteran communities, in order to understand what governs the intraguild predation and the population dynamics of these groups.

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