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Competitive Interaction Between Larvae of *Lucilia sericata* (Meigen) and *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae)

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Abstract: Rearing of *L. sericata* and *C. albiceps* in pure cultures of a variety of densities, at four constant temperature regimes, demonstrated an inverse relationship between egg density and the total development ($F_{2,6} = 264.35$ and $F_{2,6} = 71.87$ For *L. sericata* and *C. albiceps*, respectively $p<0.05$), survivorship ($F_{2,9} = 68.41$; $p< 0.001$ for *L. sericata* and $F_{2,9} = 12.35$; $p< 0.05$ for *C. albiceps*) and adult size (For *L. sericata*: males $F_{2,9} = 58.94$ and females $F_{2,9} = 140.09$. For *C. albiceps*: males $F_{2,9} = 43.62$ and females $F_{2,9} = 167.99$. In all cases $p<0.001$) of both species. Addition of *C. albiceps* reduced the development time and survivorship of *L. sericata* at a variety of densities and proportions at 17 and 23°C. While at 29 and 35°C, a complete elimination of *L. sericata* was recorded. Neither egg density nor temperature has a significant effect on the sex ratio of the resulting adults. It seems that the interaction between these species is a highly asymmetric case of competition.

Key words: *Chrysomya albiceps*, *Lucilia sericata*, competition, larvae, culture substrate

INTRODUCTION

Competition in nature is difficult to detect and defining of competition is not straightforward (Paul, 1993). The natural history of carrion flies is thought to include intense competition for larval food (Suenaga, 1959a, b; Beaver, 1973, 1977; Cornaby, 1974; Baxter and Morrison, 1983; So and Dugeon, 1990; Wells and Greenberg, 1992a, b). Almost every aspect of their breeding biology suggests strong selection for rapid location and consumption of this patchy and empheral resource (Beaver, 1984; Hanski, 1987).

Intra- and inter-specific larval competition for food result in larval mortality, reduction in size and weight of individual larvae and pupae and undersized adults with less fecundity and short life (Ullyett, 1950; Putman, 1977; Williams and Richardson, 1983; Shahein, 1986; Goodbrod and Goff, 1990; Omar, 1992; Reis *et al*., 1994; Von Zuben, *et al*., 2001).

The degree to which blowflies species suffer loss of population from the effects of intra and interspecific competition on a carcass is determined by their inherent growth characteristics and by the degree to which they are adapted to withstand the adverse conditions engendered by overcrowding of the larval populations on the available food supply (Ullyett, 1950).

Intra- and inter-specific competition in two species of calliphorids; the common green bottle blow fly *Lucilia sericata* and the African hairy maggot blow fly *Chrysomya albiceps* can be easily cultured and studied in detail under laboratory conditions.

The blow fly *L. sericata* is a communicative eusynathrope, which is widespread throughout the major zoogeographical regions, but is not yet cosmopolitan (Greenberg and Povolny, 1971; Smith, 1986; Spradbery, 1991). It is a Holarctic species distributed over the warmer regions of the temperate zone (Hall and Wall, 1995) and now the dominant species in urban and suburban districts of Australia and Africa (Zumpt, 1965; Wall *et al*., 1992). *L. sericata* is a facultative ectoparasite, which acts as the primary agent of sheep myiasis in Britain and parts of continental Europe (Smith, 1931; Davies, 1934; MacLeod, 1943; Wall *et al*., 1992; Hall and Wall, 1995; Smith and Wall, 1997a), in South Africa (Hepburn, 1943) and Australia (Norris, 1959).

Chrysomya albiceps is a hemisynathropic species, which prefers high temperatures and humidity (Greenberg and Povolny, 1971). This tropical and subtropical species is very common and abundant in Africa, southern Europe, tropical and subtropical Arabia, India and recently central and South America (Zumpt, 1965; Guimarães *et al*., 1978, 1979; Mariluis, 1980, 1981, 1983; Leite *et al*., 1983; Baumgartner and Greenberg, 1984; Baumagartner, 1988; Spradbery, 1991; Hall and Smith, 1993; Grassberger *et al*., 2003).

In field carrion studies, in Egypt, Tantawi *et al*. (1996) found that *L. sericata* was able to breed successfully in carrion in fall, winter and spring. While in summer, little or no breeding in carrion occurred when the adult population was most abundant. This behavior displayed

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by *L. sericata* was attributed as to avoid intense predation of its larvae by third instars of *C. albiceps* in summer, during which larval development of both species proceeds synchronously. Therefore, it was found necessary to explore this aspect by a series of laboratory experiments.

MATERIALS AND METHODS

Maintenance of laboratory fly colonies: Larvae and adults of the two species were collected from exposed rabbit carcasses at Moharrem Bey District, Alexandria, Egypt. Larvae and adults were identified to species after Tantawi and El-Kady (1997). The flies were held in fly screen cage (50×50×50 cm) at 25±2°C. Adults were supplied with water, granulated sucrose and powdered milk.

Experimental procedures: Gravid females of *L. sericata* or *C. albiceps* were allowed to oviposit on minced meat placed in black 35-mm film cups. This provided a dark and moist environment preferred by female flies for oviposition. Eggs were collected within 30 min of oviposition, so that they would be the same age.

Clumps of eggs were separated by a gentle shaking for 10 min in a tube of 0.1 M NaOH (Sandeman *et al*., 1987). Unseperated eggs, which float unlike the separated eggs and the solution were decanted. The remaining eggs were rinsed twice by filling the tube with distilled water, which then was decanted when the eggs had settled. The eggs were poured with a small amount of water onto a paper towel marked with a grid and counted under a dissecting microscope (Model 41 THRU 48). A piece of towel with the desired number of eggs was then cut out and placed with the eggs down on the meat of the experimental jar. Care was taken that the towel did not dry before the eggs were placed in each experimental jar.

Containers used in these experiments were 1 L jars. Each jar filled, in the following order, with about 5 cm height of moistened sawdust, 140 g of minced meat, the desired combination of calliphorid eggs and dry sawdust to within 2 cm of the top. The mouth of the jar was then covered with a fine mesh cloth, sealed by a rubber band and placed into an incubator at one of the four desired temperature regimes (17, 23, 29 or 35±0.5°C). The quantity of meat used in these experiments was selected according to previous experiments of competition conducted by Ullyett (1950) and Wells and Greenberg (1992a). To estimate hatching success, a number of leftover eggs (at least in hundreds) were kept moist in petri dishes next to the jars. In every case, the hatching success percentage should exceed 90%.

Intra-specific competition (pure cultures): Three treatments of 40, 200 and 1000 eggs of each species were selected. The quantities of food available per larva for these treatments were 3.5, 0.7 and 0.14 g, respectively.

Inter-specific competition (mixed cultures): Nine combinations of 20, 100 or 500 eggs of *L. sericata* or *C. albiceps* were selected and performed in this manner: L20 C20, L20 C100, L20 C500, L100 C20, L100 C100, L100 C 500, L500 C20, L500 C100 and L500 C500.

Development under different temperature regimes: In this study, the minimum duration of total development (from egg to adult eclosion) of each species at each of the four studied temperature regimes in pure and mixed cultures was recorded. As the larvae grew the mean temperature within the center of actively feeding maggots was recorded at regular intervals throughout the entire feeding period by inserting the probe of a calibrated mercury thermometer in the core of the maggot mass. The time range of the adult eclosion was determined from periodical observations at 6 h intervals. This procedure was in triplicates for each egg density at each of the tested temperature regimes.

Survivorship criteria of adults: The effect of larval competitionon the resulting adults was studied as follows: adult flies were killed by refrigerating after 12 h of observing the first fly to eclose, sorted by species and counted. Sexes were determined by examining the flies under a stereomicroscope (Model OLY 31) (Smith, 1986). Samples of adult flies of each sex were randomly collected, dried at 50°C and weighed.

Statistical analysis: Statistical analysis was performed using the program SAS (Institute Inc (1988), Cary, NC, USA), data were analyzed statistically by using Two-ways analysis of variance (ANOVA) and a *t-test* to detect differences between means (Sokal and Rohlf, 1981).

RESULTS

Development rate: For pure cultures, Table 1 data reveled significant effects ($p<0.05$) of temperature and egg density on the development of both species (For *L. sericata*: $F_{3,6} = 38427.31$ and $F_{2,6} = 264.35$, respectively. For *C. albiceps*: $F_{3,6} = 20736.35$ and $F_{2,6} = 71.87$, respectively).

At all tested temperatures, the maggot mass temperature of each species showed a regular pattern of increase as the number of eggs was increased. In cultures of lower egg densities (40 eggs), the differences between the ambient and maggot mass temperature were slight and showed no detectable pattern. On the other hand, in cultures of higher densities (200 and 1000), strong peaks

in temperature were observed. A maximal temperature of 11°C for *L. sericata* and 13.5°C for *C. albiceps* above ambient was observed in the culture with density of 1000 eggs.

For mixed cultures, the results showed that at higher temperatures (29, 35°C) complete elimination of *L. sericata* was observed from all egg combinations, except at a ratio of 25L: 1C (L500:C20), where *L. sericata* was able to complete development and survive. Analysis of data found a significant decrease in the development time of *L. sericata* with increasing intra- and inter-specific competition in the cultures with 20, 100 and 500 of *C. albiceps* (In all cases $p<0.05$). Concerning the development time of *C. albiceps*, results of ANOVA showed a significant decrease in the development time with increasing only intraspecific competition (In all cases $p<0.05$). On the other hand, when the egg density of *C. albiceps* held constant and that of *L. sericata* increased, insignificant effects of increasing interspecific competition was indicated (In all cases $p>0.05$).

Analysis of the data also revealed that at lower temperatures (17, 23°C) the total development time of *L. sericata* in pure cultures was slower than in mixed cultures of corresponding total egg densities, in all cases $p<0.05$. On the other hand, at 17 and 23°C, the total development time of *C. albiceps* was lengthened significantly ($p<0.05$) in mixed cultures (L100C100, L500C500) than in pure cultures of egg densities (200, 1000). Also at both 29 and 35°C, a significant increase in the development of *C. albiceps* was observed in pure cultures of egg density (1000) than in mixed cultures of egg combinations (L500C500), in all cases $p<0.05$ (Table 1).

Survivorship: The proportion surviving was arcsine transformed and subjected to ANOVA. For pure cultures, the results revealed that adult survivorship of both species declined significantly as the initial egg number was increased ($F_{2,9} = 68.41$; $p<0.001$ for *L. sericata* and $F_{2,9} = 12.35$; $p<0.05$ for *C. albiceps*). It is clear that there was a consistent pattern of higher survivorship at 29°C for both species (Table 2).

For mixed cultures, no statistically true effect of intra- and inter-specific competition on the survivorship of *L. sericata* at cultures of 20 and 100 (In all cases $p>0.05$) but significantly decreased in culture with 500 eggs ($p<0.05$). On the other hand, there was a significant decrease in the survivorship of *C. albiceps* with increasing only the intraspecific competition (In all cases $p<0.05$) (Table 2).

Table 1: Minimal total development times (in hours) of *Lucilia sericata* and *Chrysomya albiceps* raised in pure and mixed cultures of a variety of densities and proportions at different temperature regimes

	Mean minimal development time (±SE)			
Egg density	17°C	23°C	29°C	35°C
Pure cultures				
40	860.21±0.68	331.36±0.29	283.52±0.15	242.17±0.31
	756.05±0.47	382.06±0.14	290.22±0.07	209.36±0.28
200	855.39±0.61	329.25±0.92	278.40±0.37	237.29±0.21
	750.17±0.49	378.33±0.12	286.26±0.09	208.35±0.48
1000	818.49±0.34	294.15±0.87	243.25±0.48	210.06±0.55
	727.54±0.72	356.14±0.12	272.57±0.09	190.49±0.30
Mixed cultures				
L20C20	854.53±0.64	327.36±0.35	—	—
	756.38±0.24	379.03±0.81	292.05±0.89	209.54±0.94
L20C100	851.31±0.92	325.06±0.97	—	—
	755.58±0.44	379.59±0.53	288.56±0.71	209.59±0.45
L20C500	840.11±0.22	321.14±0.12	—	—
	739.52±0.36	362.11±0.57	278.06±0.97	200.11±0.34
L100C20	856.13±0.66	328.33±0.86	—	—
	758.18±0.59	383.39±0.81	291.53±0.23	211.17±0.30
L100C100	847.27±0.32	319.06±0.61	—	—
	757.37±0.58	380.22±0.46	287.51±0.53	210.25±0.54
L100C500	841.18±0.75	309.14±0.42	—	—
	740.00±0.78	362.52±0.89	278.56±0.47	200.53±0.34
L500C20	840.23±0.52	314.51±0.40	262.33±0.13	228.34±0.22
	757.10±0.51	383.55±0.35	291.36±0.79	212.50±0.17
L500C100	838.06±0.92	310.31±0.42	—	—
	759.08±0.52	382.17±0.46	289.54±0.45	210.51±0.60
L500C500	814.53±0.32	296.33±0.89	—	—
	734.20±0.55	364.24±0.28	277.53±0.72	202.28±0.28

Upper figures for *Lucilia sericata*, Lower figures for *Chrysomya albiceps*. Data obtained from 3 replicate rearings

Table 2: Percentage of adult survivorship of *Lucilia sericata* and *Chrysomya albiceps* raised in pure and mixed cultures of a variety of densities and proportions at different temperature regimes

	Mean percentage of adult survivorship (± SE)			
Egg density	17°C	23°C	29°C	35°C
Pure cultures				
40	65.00±0.84	79.17±0.31	83.33±0.42	80.83±0.33
	57.50±0.21	79.00±0.45	81.67±0.31	80.83±0.64
200	55.33±0.60	60.33±0.73	63.83±1.08	61.83±0.60
	42.67±0.36	68.67±0.88	73.33±0.38	71.33±0.25
1000	32.03±0.76	33.23±0.68	35.03±0.24	34.30±0.31
	30.63±0.30	34.53±0.37	40.23±0.26	36.30±0.59
Mixed cultures				
L20C20	56.67±1.77	74.67±0.58	—	—
	55.00±0.56	73.33±1.64	91.67±0.89	80.00±1.23
L20C100	58.33±1.28	51.67±0.89	—	—
	41.33±1.74	69.00±1.00	80.00±1.14	57.67±1.24
L20C500	41.67±1.56	38.33±1.77	—	—
	32.13±1.06	41.40±0.79	70.73±1.11	38.07±1.54
L100C20	35.33±1.11	71.00±1.34	—	—
	51.67±0.55	78.67±1.33	86.67±0.89	71.67±1.77
L100C100	42.67±1.01	61.00±2.00	—	—
	57.67±1.37	77.67±1.51	77.33±1.02	77.67±1.16
L100C500	36.00±1.69	32.33±2.52	—	—
	33.93±1.31	40.93±1.53	64.07±0.91	53.07±2.32
L500C20	34.60±2.13	36.61±1.54	34.40±1.88	15.73±1.78
	53.33±1.53	78.33±1.55	90.00±1.72	70.00±1.00
L500C100	30.13±1.91	31.87±1.13	—	—
	53.00±1.86	72.00±2.77	82.67±2.52	67.00±2.12
L500C500	16.47±1.10	21.93±2.32	—	—
	40.00±1.48	44.53±1.12	59.13±2.01	39.80±2.82

Upper figures for *Lucilia sericata*, Lower figures for *Chrysomya albiceps*, Data obtained from 3 replicate rearings

Table 3: Percentage of female adults of *Lucilia sericata* and *Chrysomya albiceps* raised in pure and mixed cultures of a variety of densities and proportions at different temperature regimes

	Mean percentage of female adults (±SE)			
Egg density	17°C	23°C	29°C	35°C
Pure cultures				
40	48.54±0.32	68.37±0.94	54.10±0.27	49.40±0.22
	57.31±0.69	66.35±0.22	64.86±0.26	46.03±0.17
200	40.71±0.51	37.23±0.33	51.46±0.42	45.04±0.53
	48.28±0.44	67.93±1.08	48.68±0.46	47.32±1.09
1000	65.66±0.46	39.21±0.51	58.31±0.68	62.14±0.76
	50.93±0.31	52.41±0.40	50.73±0.78	48.49±0.71
Mixed cultures				
L20C20	49.45±1.49	50.58±1.58	—	—
	46.01±2.40	55.44±2.87	67.35±1.89	48.94±1.16
L20C100	52.79±1.26	42.12±0.81	—	—
	42.48±1.27	48.09±0.44	52.97±1.76	48.02±1.52
L20C500	55.56±1.90	53.33±0.64	—	—
	51.14±1.31	45.68±0.92	56.67±0.87	41.55±0.79
L100C20	49.52±1.84	41.61±0.23	—	—
	56.59±2.20	41.03±0.90	67.10±0.78	53.16±0.61
L100C100	58.11±1.35	43.59±0.98	—	—
	53.56±1.95	44.12±1.23	51.99±1.54	49.93±1.35
L100C500	43.28±1.23	39.97±0.52	—	—
	47.07±1.40	44.37±0.45	53.14±0.94	42.09±1.62
L500C20	52.19±1.18	44.92±1.62	64.69±1.42	54.87±0.66
	50.35±1.53	48.69±1.09	47.27±0.89	57.64±0.87
L500C100	62.63±0.76	48.28±0.51	—	—
	45.73±0.57	36.45±1.05	44.30±0.78	53.73±0.74
L500C500	55.37±1.10	42.59±1.54	—	—
	57.69±1.03	47.37±1.00	48.13±0.50	45.99±0.43

Upper figures for *Lucilia sericata*, Lower figures for *Chrysomya albiceps*, Data obtained from 3 replicate

Analysis of the data revealed a significant increase in mortality of *L. sericata*, at 17 and 23°C, in the mixed cultures than in pure cultures of identical total egg densities, in all cases $p<0.05$. On the other hand, at higher

Table 4: Adult size (dry weight in mg) of *Lucilia sericata* and *Chrysomya albiceps* raised in pure and mixed cultures of a variety of densities and proportions at different temperature regimes

	Mean dry weight (±SE)							
	17°C		23°C		29°C		35°C	
Egg density	♂	♀	♂	♀	♂	♀	♂	♀
Pure cultures								
40	6.18±0.27	7.58±0.13	6.48±0.09	7.76 ± 0.20	7.10±0.08	8.22±0.09	7.12±0.29	8.26±0.10
	6.36±0.32	7.82±0.39	7.52±0.09	8.02 ± 0.05	7.60±0.50	8.62±0.24	7.92±0.08	8.64±0.10
200	5.64±0.11	7.04±0.13	5.92±0.13	7.12 ± 0.09	6.16±0.03	7.28±0.26	6.30±0.09	7.34±0.13
	5.78±0.19	7.18±0.37	5.94±0.06	7.18 ± 0.05	6.20±0.08	7.32±0.27	6.38±0.08	7.50±0.09
1000	2.58±0.13	3.92±0.15	2.62±0.17	3.08 ± 0.05	3.30±0.13	4.20±0.24	3.98±0.17	4.18±0.09
	2.96±0.11	4.30±0.23	3.60±0.11	4.26 ± 0.09	4.12±0.13	4.74±0.13	4.34±0.09	4.76±0.17
Mixed cultures								
L20C20	5.50±0.24	7.06±0.05	6.20±0.27	7.68±0.37	—	—	—	—
	6.58±0.16	7.18±0.23	7.74±0.27	8.22±0.19	7.84±0.05	8.46±0.09	7.70±0.27	8.26±0.77
L20C100	5.36±0.34	6.72±0.23	6.18±0.29	7.72±0.46	—	—	—	—
	6.64±0.30	7.00±0.12	7.16±0.39	8.08±0.45	7.30±0.12	8.22±0.25	7.16±0.21	8.00±0.41
L20C500	5.28±0.47	6.56±0.33	6.48±0.29	7.66±0.27	—	—	—	—
	4.90±0.29	5.74±0.15	5.54±0.34	5.96±0.42	5.62±0.26	6.10±0.57	5.96±0.54	6.26±0.42
L100C20	5.88±0.29	7.06±0.15	6.10±0.20	6.86±0.44	—	—	—	—
	6.68±0.15	7.34±0.27	7.82±0.19	8.28±0.19	7.87±0.42	8.20±0.25	7.76±0.33	8.22±0.36
L100C100	5.46±0.49	6.84±0.40	5.96±0.30	7.64±0.26	—	—	—	—
	6.82±0.18	7.00±0.20	7.74±0.29	8.34±0.23	7.36±0.52	8.14±0.20	7.36±0.34	8.16±0.52
L100C500	5.60±0.38	6.98±0.29	6.00±0.20	6.78±0.35	—	—	—	—
	5.14±0.22	5.92±0.22	5.64±0.36	6.16±0.31	5.80±0.07	6.24±0.23	6.28±0.59	6.70±0.85
L500C20	5.02±0.24	5.82±0.28	5.00±0.46	6.00±0.49	5.08±0.54	5.52±0.49	5.66±0.27	5.84±0.26
	6.84±0.15	7.66±0.26	7.94±0.27	8.34±0.26	7.36±0.20	8.24±0.21	7.84±0.51	8.40±0.17
L500C100	4.88±0.23	5.74±0.26	4.94±0.21	6.02±0.51	—	—	—	—
	6.88±0.26	7.36±0.15	7.42±0.41	8.66±0.51	7.48±0.30	8.30±0.29	7.54±0.26	8.08±0.25
L500C500	4.66±0.19	4.74±0.23	4.80±0.22	5.60±0.14	—	—	—	—
	4.98±0.22	6.02±0.24	5.74±0.32	6.16±0.54	5.98±0.22	6.52±0.35	6.28±0.28	7.14±0.25

Upper figures for *Lucilia sericata*, Lower figures for *Chrysomya albiceps*, Data obtained from 3 replicate rearings

temperatures (29, 35°C), the survivorship of *C. albiceps* was significantly greater in the mixed culture than that in the pure cultures, in all cases $p<0.05$ (Table 2).

Sex ratio: For both pure and mixed cultures, it can be noticed that the percentage of surviving females of both species was nearly around the value of 50%. Analysis of data revealed that the percentage of surviving females were insignificantly affected by either egg density or temperature and there were insignificant differences in the percentages females of each species from pure or mixed cultures, in all cases $p>0.05$ (Table 3).

Size: In pure cultures, there was a significant decrease in adult size of both sexes of each species as the initial number of eggs was increased (For *L. sericata*: males $F_{2,9} = 58.94$ and females $F_{2,9} = 140.09$. For *C. albiceps*: males $F_{2,9} = 43.62$ and females $F_{2,9} = 167.99$. In all cases $p<0.001$) (Table 4).

For mixed cultures, the adult size of *L. sericata* significantly decreased with increasing both intra- and inter-specific competition (In all cases $p<0.05$). For *C. albiceps*, the adult size significantly decreased only with increasing intraspecific competition. In contrast, a significant increase in the adult size of *C. albiceps* was recorded with increasing interspecific competition in cultures of 500 eggs (Table 4).

DISCUSSION

Development rate: Due to the rapid deterioration of the carrion habitat, the relative success of larvae will depend on how quickly they attain the minimum weight for viable pupation (Ullyett, 1950; Levot *et al*., 1979). For both species, the development time decreased with increasing the number of eggs was increased. Reduction of the development time as the initial number of eggs was increased has been observed in other dipterans (Ullyett, 1950; Baxter *et al*., 1973; Baxter and Morrison, 1983; Hutton and Wasti, 1980; So and Dudgeon, 1989a, b and 1990; Goodbrod and Goff, 1990; Ribeiro *et al*., 1993; Saunders and Bee, 1995).

It has been shown in the study by Baxter and Morrison (1983) that fly larvae reared in crowded conditions may benefit from the presence of others through elevation of temperature, accumulation of digestive enzymes and physical alterations of the carcasses which will facilitate feeding. The present study reported excess heat in maggot mass of *L. sericata* and *C. albiceps* which peaked at 11.0 and 13.5°C, respectively above the ambient temperature. In the study of flies development on dead bodies, a process of larvae mass self heating was observed owing to metabolic heat release and results in an up to 50% shortening of the

development in a certain period of pre-imago stages, compared to the time on the environmental temperature data (Marchenko, 1973; Zvereva and Marchenko, 1987). Elevation of maggot mass temperature is common in many carrion flies (Marchenko 1985; Lord *et al*., 1986; Early and Goff, 1986; Goodbrod and Goff, 1990; Cianci and Sheldon 1990). The present study adds support to the view of Goodbrod and Goff (1990) who mentioned that maggot mass could be another factor for consideration when estimating postmortem intervals (PMI), based on maggot development.

The current results of mixed cultures indicate that, at a variety of densities and proportions at temperatures 29 and 35°C, *L. sericata* was completely eliminated. This result is in accordance to Hutton and Wasti (1980) and Furman *et al*. (1959). This elimination could be explained in view of Tantawi *et al*. (1996) that *L. sericata* breed successfully in carrion in fall, winter and spring. However, in summer, no breeding in carrion occurred when the adult population of *L. sericata* was most abundant. This behaviour of *L. sericata* avoided intense predation of its larvae by third instar of *C. albiceps*, in summer, during which larval development of both species proceeds synchronously. Larval predation by *C. albiceps* has been reported, in laboratory experiments, by several authors (Coe, 1978; Gagné, 1981; Erzinçlioglu and Whitcombe, 1983; Faria and Godoy, 2001).

It also found that the development of *C. albiceps* was not significantly influenced in cultures where *C. albiceps* density was held constant and that of *L. sericata* increased. This result contradicts that obtained by Wells and Greenberg (1992a) who recorded a prolongation in the development of *C. rufifacies* with increasing interspecific density of *C. macellaria*. Comparison between pure and mixed cultures indicates that, at all the density level tested, the development of *L. sericata* was shortened significantly in mixed than in pure cultures, the reverse was true for *C. albiceps*, at higher egg density. We believe that prolongation of *C. albiceps* development in mixed cultures may be attributed to the ability of *C. albiceps*, under food scarceness, to change its behaviour attacking *L. sericata* larvae. Thus the feeding larvae of *C. albiceps* spent much longer time during the feeding process. This result is in agreement with Wells and Greenberg (1992a) and *Aguiar-Coelho* and Milward-de-Azevedo (1998).

Survivorship: Presented data of single-species cultures indicated that survivorship at each tested temperature decreased as a function of increasing egg densities in both species. This result in accordance with (Ullyett, 1950; Miller, 1964; Klomp, 1964; Wasti *et al*., 1975and b; Moon, 1980; Shahein, 1986; So and Dudgeon, 1989a; Ribeiro, 1990; Goodbrod and Goff, 1990; Godoy *et al*., 1993; Von Zuben *et al*., 1993; Smith and Wall, 1997b; Aguiar-Coelho and Milward-de-Azevedo, 1998; Silva *et al*., 2003). In contrast, Wells and Greenberg (1992a) reported insignificant effect of density on survival of *C. macellaria* and *C. rufifacies* in pure culture experiments. Explanations for decreasing survival at higher egg densities have been forward by De Jong, (1976); Baxter and Morrison (1983); Hanski (1987); Lominicki (1988); Godoy *et al*. (1993) and Reis *et al*. (1994, 1996 and 1999). These authors have emphasized the importance of increasing levels of exploitative competition for limited resources among larvae.

In double-species cultures, the high survivorship of *C. albiceps* and the zero survivorship of *L. sericata*, in all egg combinations at both temperatures 29 and 35°C are indicative of the predatory behaviour of *C. albiceps* third instar against *L. sericata* larvae. The greater survival ability of *C. albiceps* larvae was attributed to their greater competitive ability and predatory activity in mixed cultures against larvae from other dipteran (Ullyett, 1950 and Marckenko, 1985). At temperatures 17 and 23°C, for mixed cultures, as the proportion of a species is decreased the influence of intraspecific interaction on survivorship becomes less important and that of interspecific interaction more important. Wells and Greenberg (1992a) found that the interaction between *C. rufifacies* and *C. macellaria* larvae significantly decreased *C. macellaria* survivorship but no effect in the reverse direction. Goodbrod and Goff (1990) and Reis *et al*. (1999) mixed *C. rufifacies* and *C. megacephala*, *C. putoria* and *C. macellaria*, respectively. They found that the interaction increased the survivorship of the former species and decreased that of the latter species.

Sex ratio: In this study, neither egg density nor temperature has a significant effect on the sex ratio of both species raised in pure and mixed cultures. Similar observation was recorded for *C. rufifacies* and *C. macellaria* (Wells and Greenberg, 1992a). It is evident from previous studies, that the density levels did not show any remarkable effect on the sex ratio of various dipteran species; *M. domestica* (Sullivan and Sokal, 1963); *L. sericata* (Klomp, 1964); *D. melanogaster* (Miller, 1964); *M. autumnalis* (Moon, 1980); *C. erythrocephala* (Shahein, 1986). Amano (1989) attributed this due to the density would affect male and female larvae to the same extent as for pupariation. In contrast, in a similar study, Omar (1992) observed that the sex ratio of *C. albiceps* was

significantly affected by egg density since the males number predominates with the appearance of a few females as the larval densities increase.

Size: The present results indicated that adult size of both species reduced in higher densities than in lower densities. Declines in adult size in favour of larval survivorship is common in many Diptera colonizing ephemeral habitats (such as carrion, dung and decaying fruit; Ullyett, 1950; Kitaoka, 1957; Bakker, 1961; Sullivan and Sokal, 1963; Manoukas and Tsiropoulos, 1977; Atkinson, 1979; Butlin and Day, 1984; Sigurjonsdottir, 1984). Explanation for smaller body size, mediated by competition has already been demonstrated by Sullivan and Sokal (1963). So and Dudgeon (1989b) reported that reduced food individual ration to *Boettcherisca formosensis* larvae in crowded cultures produced undersized adults.

Comparison between adult size in pure and mixed cultures shows that, for *L. sericata*, the size of both sexes decreased more rapidly with increasing egg density in the mixed cultures than in the pure cultures. The reverse was true for *C. albiceps*. Hence, in terms of a reduction in adult size, the data suggest that *L. sericata* experienced higher levels of competition in the mixed than in the pure cultures.

It was shown here that *L. sericata* is competitively inferior species, although coexistence between *L. sericata* and *C. albiceps* does occur in nature. Tantawi *et al.* (1996), reported that *L. sericata* was able to breed successfully in carrion in fall, winter and spring, but during summer months, no breeding in carrion occurred. This behaviour of *L. sericata* avoided intense predation by *C. albiceps* third instar. Therefore, extinction of *L. sericata* is unlikely in field due to avoiding breeding in summer during which both species developed synchronously.

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