Study of the combined radial post-feeding dispersion of the blowflies *Chrysomya megacephala* (Fabricius) and *C. albicep*s (Wiedemann) (Diptera, Calliphoridae)

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ABSTRACT. Study of the combined radial post-feeding dispersion of the blowflies *Chrysomya megacephala* (Fabricius) and *C. albicep*s (Wiedemann) (Diptera, Calliphoridae). Blowflies use discrete and ephemeral substrates to feed their larvae. After they run out of food, the larvae begin to disperse in order to find adequate places for pupation or additional food sources, a process named post-feeding larval dispersion. Some important aspects of this process were studied in a circular arena allowing the combined radial post-feeding dispersion from the center of the arena of *C. albiceps* and *C. megacephala* larvae. To determine the location of each pupa, the arena was divided in 72 identical sections starting from the center. The distance from the center, the depth and weight of each pupa were evaluated. Statistical tests were done to verify the relation between weight, depth and distance for pupation. From the total an average of 976 larvae released (488 for each species) were collected considering both experiments 456 *C. megacephala* pupae and 488 of *C. albiceps*. This demonstrates that *C. albiceps* probably preyed on 32 *C. megacephala* larvae during post-feeding dispersion. The study of this dispersion process can be used to estimate the postmortem interval (PMI) of human cadavers in legal medicine.

KEYWORDS. Calliphoridae; *C. albiceps*; *C. megacephala*; dispersion; forensic entomology.

RESUMO. Estudo da dispersão radial combinada de *Chrysomya megacephala* (Fabricius) e *C. albicep*s (Wiedemann) (Diptera, Calliphoridae). As moscas- varejeiras utilizam-se de substratos discretos e efêmeros para alimentar suas larvas. Após deixarem o substrato alimentar, as larvas começam a dispersar em busca de locais adequados para pupação e fontes adicionais de alimento, um processo denominado dispersão larval pós-alimentar. Alguns aspectos importantes desse processo foram estudados em uma arena permitindo a dispersão radial combinada de larvas de *C. megacephala* e *C. albiceps*. Para determinar a localização de cada pupa, a arena foi dividida em 72 setores iguais começando do centro. A distância a partir do centro, a profundidade e o peso de cada pupa foram determinados. Testes estatísticos foram feitos para verificar a relação entre peso, profundidade e distância para pupação. De um total em média de 976 larvas soltas (488 de cada espécie) foram coletadas considerando ambos os experimentos 456 larvas de *C. megacephala* e 488 larvas de *C. albiceps*. Isso demonstrou que as larvas de *C. albiceps* provavelmente predaram 32 larvas de *C. megacephala*. O estudo desse processo de dispersão pode auxiliar na estimativa do intervalo pós- morte (IPM) em estudos de medicina legal.

PALAVRAS-CHAVE. Calliphoridae; *C. albiceps*; *C. megacephala*; dispersão; entomologia forense.

Flies of the genus *Chrysomya* have great medico-sanitary importance as they carry enteropathogenics such as viruses, bacteria and helmints (Furlanetto *et al*. 1984; Lima & Luz 1991) and they may cause myiases to animals and men (Zumpt 1965; Guimarães *et al*. 1983). They are also of fundamental importance in forensic entomology studies, as they can be indicators of the decomposition time of human cadavers (Greenberg 1991; Von Zuben *et al*. 1996).

Chrysomya flies have drawn attention for being an exotic species and for their impact on the native community of necrophagous dipterans (Wells & Greenberg 1992). The impact caused by the introduction of exotic species is interesting both to ecologists and evolutionists who study the process of these invasions, which include competition, predation and dispersion as well as stability and extinction of local populations (Hengeveld 1989). The understanding of the phenomena involved in this invasion process depends on the study of certain population parameters and the space-time environmental structure in which these phenomena occur (Wiens 1976; Hengeveld 1989). Besides these, there are other phenomena of small spatial scale like such as the dispersion of immature stages of the invading organisms. In this context and in the specific case of the necrophagous flies, the post-feeding larval dispersion in search of a pupation site may be mentioned.

The substrates in which blowflies develop are called discrete and ephemeral because they are units separated in space and last a short period of time due to the rapid and successive changes they undergo (Atkinson & Shorrocks 1981). Normally these substrates are saturated with insects of one or more species (Beaver 1977), involving an intense competition for resources (Hanski 1987).

The larval stage is the main period when blowflies face limits on food resources. The competition for these resources is generally of the exploitative type (Levot *et al*. 1979; Goodbrod & Goff 1990; Reis *et al*. 1994), where each larva attempts to

Table I. Depth, distance and weight (average and standard deviation) of *Chrysomya megacephala* and *Chrysomya albiceps* pupae in four quadrants of the arena 2 m diameter. The first quadrant corresponds to sectors from 1 to 90°, the second quadrant from 91 to 180°, the third from 181 to 270°, and the forth from 271 to 360°.

Quadrant	1	2	3	4
Average depth ±± SD (cm)	4.13 ±± 1.08	4.46 ±± 2.01	4.69 ±± 1.34	4.12 ±± 2.09
Average distance ±± SD (cm)	31.12 ±± 2.16	24.25 ±± 1.78	29.99 ±± 2.56	34.25 ±± 1.73
Average weight ±± SD (mg)	39.16 ±± 4.66	38.90 ±± 5.96	43.14 ±± 5.12	37.32 ±± 6.98

feed as much as possible before the complete exhaustion of resources (Ullyett 1950; Backer 1961; 1969; De Jong 1976; Levot *et al*. 1979; Lominicki 1988).

Following this competition, the larvae begin to search for a pupation site in the habitat or for another source of food if they do not have enough weight for pupation. This process is called post-feeding larval dispersion (Greenberg 1990).

Some studies on caliphorid larval dispersion have already been done as is the case of Greenberg (1990), Kocarek (2001) and others involving mathematical models as the ones on post-feeding larval dispersion restricted to one direction regarding diffusion equations (Bassanezi *et al*. 1997), on statistical analyses of spatial distribution (Godoy *et al*. 1995; 1996; Von Zuben *et al*. 1996; Gomes *et al.* 2002; Gomes & Von Zuben 2003), and on non-local interactions (Boldrini *et al*. 1997). All of these are a basis for future experimental studies simulating the natural environment, as proposed in this study.

The objective of this study is to investigate the interspecific radial post-feeding larval dispersion considering *C. megacephala* and *C. albiceps*, because this dispersion reflects more accurately the larval dispersion process that occurs in their natural environment compared to former studies which considered only one species at a time.

MATERIAL AND METHODS

C. megacephala and *C. albiceps* specimens were collected around the Biosciences Institute of Unesp in Rio Claro, São Paulo, Brazil. Decaying organic matter was used as bait and the specimens collected were maintained in screen cages in a controlled temperature room at 25 ± 1°C, 60% relative humidity and 12-hour photoperiod.

Larval densities were formed with *C. megacephala* and *C. albiceps* individuals in macerated bovine meat. After the larvae developed, the meat was placed in the center of a circular arena (illuminated, to avoid tendencies) for them to move out of it. Arenas with 2 m in diameter, covered with 5 cm of wood shavings were used. An average of 976 larvae were used in two trials: a test (968 larvae, 484 from each species) and a replicate (984 larvae, 492 from each species).

After the larvae pupated, they were located and removed from the wood shavings. The depth of the pupation site and its distance from the center of the arena were measured with rulers and measuring tapes. The counting was done from the periphery to the center and the arena was divided in 72 sectors of 5 degrees each and four quadrants.

At the same time that pupae were collected, each pupa was weighed on an Ohaus analytical scale before the adults emerged and after individualized in plastic flasks. Pupal weight was measured in milligrams, with a precision of 0.01 mg. After they were weighted, each larva was returned to its individual flask for identification of species and sex of the adults after their emergence. The depth the larvae buried themselves was measured in centimeters. Burial depth was measured as a discrete variable, that is, it is represented by whole numbers from 0 to 5.

Distance of burial was measured as a discrete variable, that is, it is represented by whole numbers from 1 to 5, where 1 includes the interval from 0 to 20 cm, 2 includes the interval from 21cm to 40 cm, 3 includes the interval from 41 cm to 60 cm, 4 includes the interval from 61 cm to 80 cm and finally 5 includes the interval from 81 cm to 100 cm from the center of arena. The distance from the center of the circumference to the burial site was also measured in centimeters.

A correlation test were performed to analyze the correlation

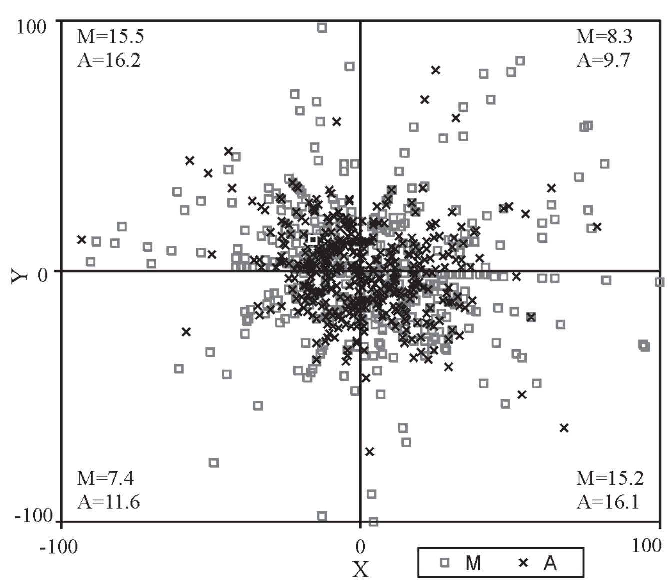

Fig. 1. Species distribution in the dispersion arena (species M = *C. megacephala* and A = *C. albiceps*).

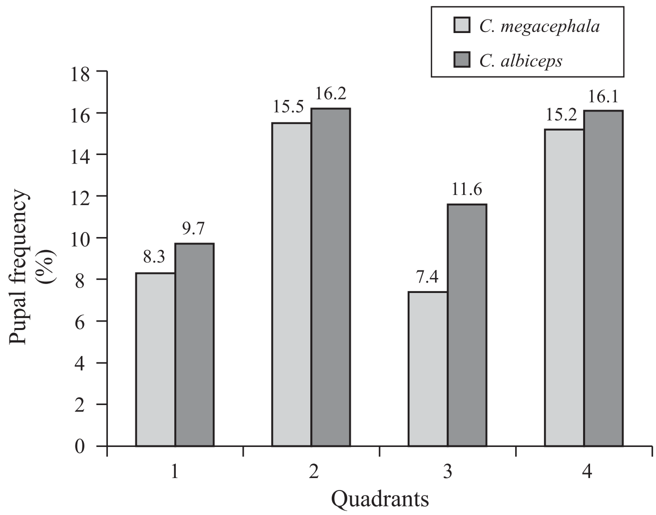

Fig. 2. Pupal frequency (%) per quadrant *C. albiceps* and *C. megacephala*.

among variables and Anova test to check the difference among 2 experiments (Zar, 1999).

RESULTS

Combined radial post-feeding larval dispersion in *Chrysomya megacephala* and *Chrysomya albiceps* (considering both species jointly). Considering both experiments, from the total number of larvae released, 976 were collected on average: 456 *C. megacephala* pupae and 488 *C. albiceps*. This demonstrates that *C. albiceps* probably preyed on 32 *C. megacephala* larvae during the process of post-feeding dispersion because there was no blowfly flying in the room after the end of collecting the pupae.

Average and standard deviation for burial depth, distance from the arena center and weight of the larvae in all four quadrants of the arena are represented on Table I. The first quadrant corresponds to sectors from 1 to 90°, the second quadrant from 91 to 180°, the third from 181 to 270°, and the forth from 271 to 360°.

Considering the distribution of both species jointly in the arena (Fig. 1), 31.7% of the total preferred the quadrant 2 while only 18% went to quadrant 1.

The Fig. 2 shows the presence of pupae (976) of each species in each quadrant. The presence of *C. albiceps* is greater in all quadrants, which may indicate that *C. albiceps* larvae preyed on *C. megacephala* larvae. Considering the presence of pupae on different depths, both species preferred to pupate deeper (Fig. 3).

The distribution and frequency of pupae in relation to their distance from the arena's center were also analyzed. Distances between 0 and 20 cm correspond to the first interval, the second interval from 21 to 40 cm, up to the fifth level, which corresponds to an interval from 81 to 100 cm of distance. Most pupae were concentrated in levels 1 and 2 (Fig. 4).

The larval weight distribution is shown in Fig. 5.

Average pupation weight was 39.2 mg and most larvae (700 approximately) weighed between 37 and 43 mg. Table II reinforces both previous graphs regarding sex distribution, because it demonstrates how each blowfly species was located according to gender. From 488 *C. albiceps* larvae, 265 females were located at an average distance of 23.44 cm whereas 223 males reached 20.44 cm in average. From 456 *C. megacephala* larvae, 224 females were located at an average distance of 31.93 cm whereas 232 males reached 31.83 cm on average. Regarding burial depth, *C. albiceps* males buried deeper than females, reaching an average depth of 4.02 cm, while *C. megacephala* females buried deeper than males (4.20 cm). Despite these differences, *C. megacephala* larvae presented greater average results for all variables, particularly distance, which was 31.88 cm for *C. megacephala* and 22.02 cm for *C. albiceps*. *C. albiceps* larvae preyed on 32 *C. megacephala* larvae considering both experiments. There was no significant difference between the two experiments (Stat t = 1.2).

Statistical analysis of data considering both species together. To check if there is a correlation between the variables analyzed, a correlation test was applied along with the t Student statistical test with 1% and 5% significance. The Variance test was also used to check the variance equality of the variables weight, depth and distance between the species. Considering an interval from –1.6 to 1.6 for the Stat t test (standardized t Student test), there is equality for the variables.

Thus, considering both species together, the correlation between distance and depth is -0.38, which indicates a significant correlation due to sample size (976). When the t Student test was applied, a value of –8.59 was obtained with 1% as well as 5%, which means that the more distant from the center of the arena the larvae were, the less deep they buried.

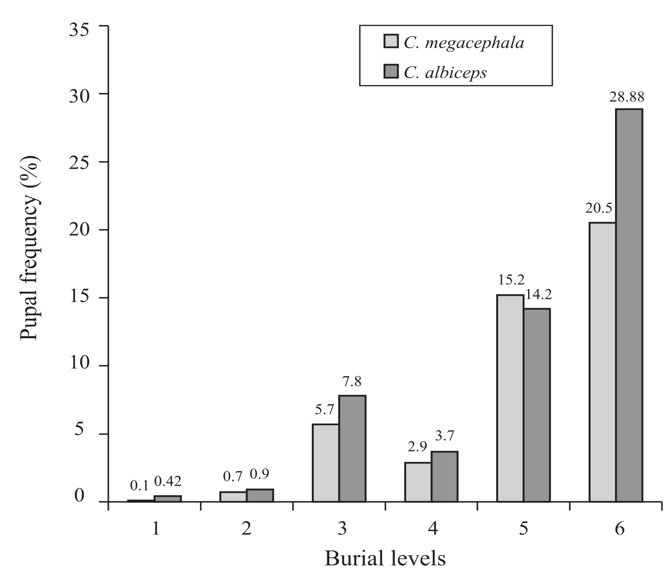

Fig. 3. Pupal frequency (n = 976) of *C. albiceps* and *C. megacephala* at different burial levels.

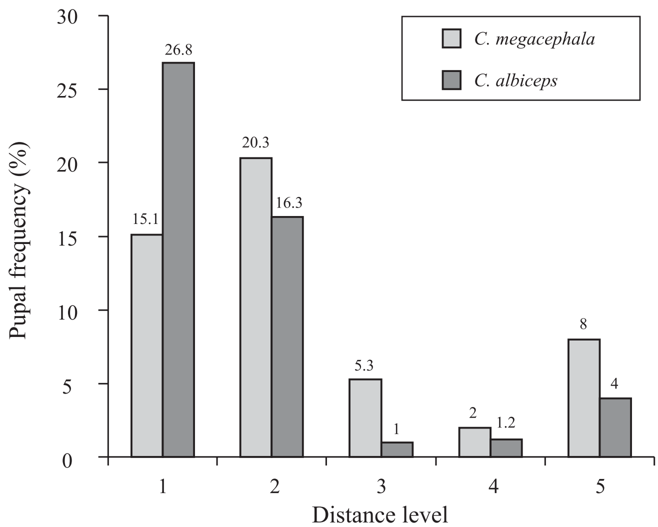

Fig. 4. Pupal frequency (n = 976) of *C. albiceps* and *C. megacephala* per distance level, where 1 includes the interval from 0 to 20 cm, 2 includes the interval from 21cm to 40 cm, 3 includes the interval from 41 cm to 60 cm, 4 includes the interval from 61 cm to 80 cm and finally 5 includes the interval from 81 cm to 100 cm from the center of arena.

Considering depth and weight, a correlation of 0.4 was obtained, demonstrating that there is a strong and significant correlation between these variables. When the t Student test was applied, a value of 5.498 was obtained with 1% and 5%, meaning that the heavier the larvae, the deeper they bury.

Finally, considering the variables of weight and distance, a significant correlation of –0.11 was obtained. The t Student test yielded a value of –13.23 with both 1% and 5% demonstrating that the farther the larvae are from the center, the less they weigh.

Variance test checking the equality of the different variables. Considering the variable distance between both species, a Stat t value of –7.78 was obtained, indicating that the mean distances the two species traveled are not equal.

Regarding depth, *C. albiceps* larvae reached an average of 4.01 cm and *C. megacephala* reached 4.05 cm, which corresponds to a Stat t value of 0.65, showing that the average depth reached by both species was equal.

Finally, considering weight, the mean values obtained were 41.34 mg for *C. albiceps* and 46.57 mg for *C. megacephala*, with a corresponding Stat t value of 1.92 indicating that the weight averages of the two species are not close. This is different from the others works (Gomes & Von Zuben 2003) where mean values of 42.89 mg for *C. albiceps* and 42.41 mg for *C. megacephala* were obtained, with a Stat t value of 1.22 indicating close values in terms of weight.

DISCUSSION

This study demonstrated some general aspects on the dispersion process of larvae in a circular arena and confirmed former results using deeper arenas of smaller diameter. The lightest larvae tend to move longer distances, perhaps searching for new sources of food, and not for a site to pupate (Gomes *et al.* 2002).

The greatest concentration of pupae was found in distances greater than 15 cm (Figure 3) and 26 larvae reached the maximum distance from the center (1 m). Apparently, what limited larval movement the most in this study was burial depth, not distance from the center. The use of an arena with 2 m in diameter and 5 cm of depth allowed the larvae to travel longer distances than other recent studies where the arena had 50 cm in diameter and 20 cm depth (Gomes *et al*. 2003). Larval movement probably took place mainly to find a pupation site, even though the possibility that some pupae were searching for an additional source of food cannot be discarded (Gomes *et al*. 2002).

With regard to the distribution of larvae per quadrant, quadrant 2 was preferred, while in other experiments where only one species was considered, an average of 31.17% preferred quadrant 1 and only 15.25% preferred quadrant 2 (Gomes & Von Zuben 2002; Gomes *et al.* 2003). This might mean that larvae do not have any preference in distributing themselves in the quadrants, to be confirmed in future experiments.

Former studies had considered a trough 3 m long and 30 cm wide for the larval dispersion process. This trough allowed larval movements in only two directions (Godoy *et al*. 1995, 1996; Bassanezi *et al*. 1997). With the use of a circular arena, this study reflects better the conditions of the natural environment the larvae will face when they abandon their feeding substrate in search of a site to pupate (Ullyett 1950). A circular arena allows a radial dispersion from a central feeding substrate unlike the dispersion in only two directions allowed by a trough.

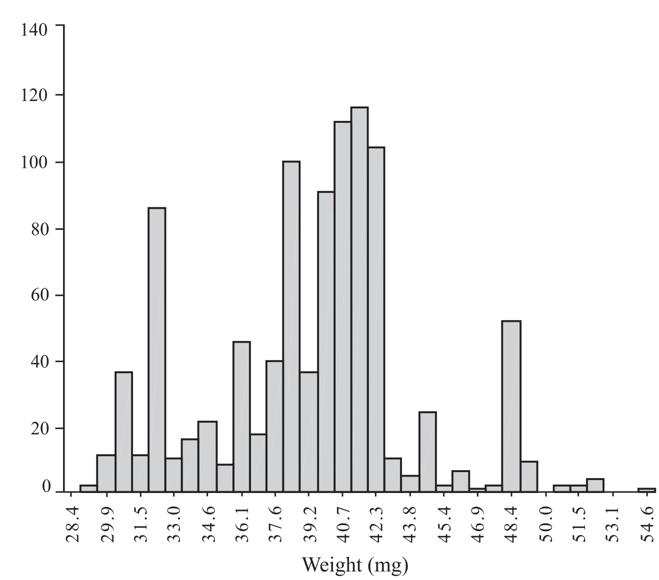

Fig. 5. Number of *C. albiceps* and *C. megacephala* pupae per weight class (Std. Dev = 4.69; Mean 39.2; N= 976).

Table II. Distribution of *C. albiceps* and *C. megacephala* males (M) and females (F) according to each variable tested.

Species		Gender	Number of larvae	Average
C. albiceps	Distance (cm)	F	265	23.44
		M	223	20.34
		Total	488	22.02
	Depth (cm)	F	265	4.00
		M	223	4.02
		Total	488	4.01
	Weight (mg)	F	265	38.97
		M	223	39.02
		Total	488	39.00
C. megacephala	Distance (cm)	F	224	31.93
		M	232	31.83
		Total	456	31.88
	Depth (cm)	F	224	4.20
		M	232	3.90
		Total	456	4.05
	Weight (mg)	F	224	39.57
		M	232	39.55
		Total	456	39.56

Godoy *et al*. (1995, 1996) observed an oscillation in pupal frequency as a function of distance from the feeding substrate for *C. megacephala* (F.) as well as for *C. putoria* (Wied.). According to Boldrini *et al*. (1997), these oscillations would be a consequence of the creation of larval aggregations in certain sites of the pupation substrate. It could be possible that the dispersing larvae can somehow feel the density of other larvae already buried in a certain area of the substrate, and that would cause those larvae to move further in search of more distant pupation sites.

The post-feeding larval dispersion behavior and the consequent pattern of spatial distribution of pupae in pupation sites could have implications on greater or lesser larval susceptibility to predator or parasitoid attacks on natural environment populations (Peschke *et al*. 1987; Legner 1997). *Chrysomya albiceps* larvae prey on *C. megacephala* larvae during larval dispersion and that the latter probably disperse farther and deeper, precisely to escape predation (Goodbrod & Goof 1990; Wells & Greenberg 1992; Hanski 1997; Faria *et al*. 1999, 2001).

Another fact is that the larvae do not distribute themselves uniformly into the arena, which differs from former experiments (Gomes *et al*. 2003). *Chrysomya albiceps* larvae concentrated closer to the center of the arena and did not show, therefore, a uniform distribution (uniformity vector of 0.1, not significant) as in study of Gomes & Von Zuben 2003, while *C. megacephala* larvae present a uniform distribution (uniformity vector of 0.19, significant) (Gomes *et al.* 2003).

It is interesting to note that these dispersion studies could have important implications for medico-criminal investigations as the presence of larvae and pupae in or around human corpses could help estimate the time interval between the person's death and the moment the body was found, called postmortem interval (PMI). This estimation is one of the most important aspects of legal medicine (Smith 1986), because it could be underestimated if the dispersing larvae are not taken into account (Von Zuben *et al*. 1998).

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