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Population Dynamics, Life Stage and Ecological Modeling in *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae)

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Abstract

In this study we investigated the population dynamics of *Chrysomya albiceps* (Wiedemann) with laboratory experiments, employing survival analysis and stage structure mathematical models, emphasizing survival among life stages. The study also assessed the theoretical influence of density dependence and cannibalism during immature stages, on the population dynamics of the species. The survival curves were similar, indicating that populations of *C. albiceps* exhibit the same pattern of survival among life stages. A strong nonlinear trend was observed, suggesting density dependence, acting during the first life stages of *C. albiceps*. The time-series simulations produced chaotic oscillations for all life stages, and the cannibalism did not produce qualitative changes in the dynamic behavior. The bifurcation analysis shows that for low values for survival, the population reaches a stable equilibrium, but the cannibalism results in chaotic oscillations practically over all the parametric space. The implications of the patterns of dynamic behavior observed are discussed.

Introduction

One important attribute of insects is the existence of age classes and life stages. Within each age class, the individuals of a species behave differently, and have different types of dependence on the environment and resource needs (Cushing *et al* 2003, Dilão 2006). Several studies have attempted to investigate age-structure problems by examining life tables in which the age of individual insects is determined and used to assess the standing population age structure (Gabre *et al* 2005, Liu *et al* 2008). To describe a population with age classes or life-stages, a discrete formalism can be adopted, where the transition between different age classes or stages is described in a matrix form. One of the advantages of this

type of model is that it can be naturally related to field or laboratory data (Caswell 2001, Dilão 2006).

The Leslie matrix model (Leslie 1945, 1948) has been frequently used to describe the dynamics of age- or stage-structured populations. The Leslie matrix approach leads the modeller to describe the population life history as a sequence of equal-duration age classes, thus effectively precluding the identification of these age classes with functional categories, instars, developmental stages, etc. (Leslie 1945, 1948, Tuljapurkar & Caswell 1997).

Estimates of life-history components, such as the intrinsic rate of increase or mortality rates, are essential for a full understanding of population dynamics in insects (Pitts & Wall 2004). However, quantifying these rates in natural populations is not a trivial task, particularly for

small, short-lived, and highly mobile organisms such as insects (Pitts & Wall 2004). An alternative solution for this problem is to attempt to evaluate life-history parameters in the laboratory or in semi-natural microcosms, where conditions can be controlled and detailed measurements made (Bonsall & Hassell 2005).

Blowflies are characterized by the ability of their larvae to develop in the flesh of vertebrates; some species parasitize invertebrates, while others can complete their larval development in animal detritus (Goodbrod & Goff 1990). However, the overall defining characteristic of blowflies is the requirement for a protein-rich substrate, as provided by animal tissues or by-products, in which the larvae can complete their development (Goodbrod & Goff 1990).

The distribution of immatures in discrete breeding sites occurs through random dispersal of adult females (Blackith & Blackith 1990). This distribution may influence the level of competition for food and space among immatures, with consequences for the viability of the resulting adults (De Jong 1979) and with a marked effect upon the population dynamics, as the density of the animals may differ between patches (De Jong 1979, Ives & May 1985, Turchin 1998). This means of distribution makes the blowfly community a complex system, including many simultaneous processes such as intra- and interspecific competition, besides intraguild predation, cannibalism and parasitism (Rueda & Axtell 1985, Wells & Greenberg 1992a,b,c, Faria *et al* 2004a,b, Rosa *et al* 2006). All of these interactions have a strong impact on the dipteran community, mainly under high larval densities (Goodbrod & Goff 1990, Wells & Greenberg 1992a,c).

High densities may have negative effects on the life history of blowflies (Faria *et al* 1999, 2004a,b, Rosa *et al* 2006). These effects have direct consequences for the development and dynamics of the species (Godoy *et al* 2001, Serra *et al* 2007). A global analysis of population dynamics involving life history parameters is important to evaluate dynamic patterns of temporal oscillation. However, the results produced by this kind of approach do not permit detailed analyses capable of associating the effect produced with the specific life stage in which the event takes place.

Old World flies of the genus *Chrysomya* are important mechanic vectors of pathogenic organisms, causers of myiasis and forensic indicators (Zumpt 1965, Baumgartner & Greenberg 1984, Arnaldos *et al* 2005). They have become widespread and abundant in the Neotropical region, displacing native species (Guimarães *et al* 1978). Of all the exotic species, *Chrysomya albiceps* (Wiedemann) deserves special attention because it is an intraguild predator of other blowfly species and is also cannibalistic during larval stage (Faria *et al* 1999, 2004a,b). Intraguild predation and cannibalism

in blowflies have affected not only the native blowfly fauna in Brazil (Rosa *et al* 2006, Gião & Godoy 2007), but in several areas, *C. albiceps* and a similar species, *Chrysomya rufifacies* (Macquart), have influenced the local fauna (Wells & Greenberg 1992a,b,c, Grassberger *et al* 2003, Shiao & Yeh 2008). Cannibalism has been considered particularly influential on the population dynamics of insects (Costantino *et al* 1995), affecting population stability, and altering competitive interactions by decreasing the number of competitors or increasing the food quality (Dong & Polis 1992).

Several aspects of the biology and ecology of *C. albiceps* have been investigated with respect to population dynamics and interspecific interactions (Faria *et al* 1999, 2004a,b, Serra *et al* 2007). However, no systematic study of the stage structure and distribution of immatures has been performed in blowflies, especially combining laboratory experiments with ecological modelling.

The objective of the present study was to investigate the population dynamics of *C. albiceps*, employing a combination of mathematical models, survival analysis, and laboratory experiments, focusing on survival among life stages and their structure. The study also considered the theoretical influence of density dependence and cannibalism during immature stage on the population dynamics of *C. albiceps*.

Material and Methods

Laboratory populations of *C. albiceps* were founded 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. The experiments were performed using the F2 generation, which is the progeny of one generation that completed its life cycle in laboratory.

Survival was estimated for each life stage, including egg, larva, pupa, and adult. Three larval stages were investigated, which correspond to three instars, L1, L2, and L3. The instars were determined using accepted morphological characters to identify the various developmental stages (Prins 1982). The survival rate was estimated by recording the number of individuals recovered in each life stage.

Ten couples were placed in cylindrical plastic cages (10 cm high x 7 cm wide), and received water, sugar, and fresh beef liver. Subsequently, 12 g of ground beef was offered to females as an ovipositional substrate. The eggs recovered were removed and transferred to Petri dishes provided with filter paper. A 1% sodium hyposulfite solution was added to the mass of eggs to aid in their

separation and recording. The eggs were returned to Petri dishes containing a 0.85% NaCl solution to allow them to hatch. They were maintained at 25 ± 1°C, 70% relative humidity, and 12h photophase.

The number of larvae and pupae recovered in each development stage was recorded. After the adults emerged, males and females were also recorded. Adult females were fed fresh beef liver to permit the complete development of the gonotrophic cycle (Linhares 1988). Fecundity was measured by recording the number of eggs per female, expressed as mean fecundity per five females.

Statistical analysis

A survival analysis was run to compare survival curves from each replicate, using Kaplan-Meier survival curves and a Log-Rank test. The general equation for the Kaplan-Meier survival probability at failure time t(j) can be written as

$$\hat{S}(t_{(j)}) = \hat{S}(t_{(j-1)}) \times \Pr(\hat{T} > t_{(j)} | T > t_{(j-1)})$$

This equation gives the probability of surviving past the previous failure time t(j-1), multiplied by the conditional probability of surviving past time t(j), given survival to at least time t(j). All analyses were performed using SAS for Windows, v. 9.2. A density-dependence test was applied to the data obtained from matrix simulations (see Matrix model section) in order to investigate if the population dynamics of each life stage was density-independent (Roughgarden 1998). To detect this response, a Chi-square test was applied to estimate whether the geometric growth factor (R) in each life stage was dependent on population size (N). Basically, the test consisted of checking whether the low R's matched up with high N's and the high R's with low N's. The mean N and the geometric mean of all the R's for each life stage, over all the data generated by the matrix simulations, were estimated. The results were expressed as a contingency table (Zar 1999). Exponential and linear regressions were also fitted to the survival data, to investigate its negative decrease pattern as a function of the transition among life stages (Sokal & Rohlf 1981).

Matrix model

We used MATLAB 5.0 (The Mathworks 2004) to define a hundred-generation stage-classified model, where S is the mean constant probability of survival from x to x + 1. Six stages were defined as follows: egg, L1, L2, L3 (larval instars), pupa, and adult, where g_k = stage-specific transition (or 'growth') probabilities and f_k = stage-specific reproduction. Therefore, the population projection matrix takes the form:

$$M = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & f_6 & f_7 & f_8 \\ g_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & g_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & g_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & g_7 & 0 \end{pmatrix}$$

Survival among life stages and fecundity estimated in the laboratory were used as parameter values in the simulations. Fecundity was assumed to be constant.

A deterministic and density-dependent matrix model was employed to project blowfly populations through time (Caswell 2001). Non-linearity was introduced into the matrix model based on the formulations of Ricker (1952) and Prout & McChesney (1985), which employed exponential functions to describe the nonlinear decrease of demographic parameters as a function of immature densities.

Cannibalism between life stages was incorporated into the matrix model by introducing the exponential term based on the LPA model (Costantino et al 1995) into the matrix model. By using an exponential function, the introduced term described the cannibalism by third-instars on second-instars, an intraspecific interaction previously demonstrated for *C. albiceps* in the laboratory (Faria et al 2004b). The estimate of the cannibalism rate (0.13) was obtained from the study by Faria et al (2004b). The matrix model was structured to analyze the population dynamics of *C. albiceps*, considering life stages as follows:

$$M = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & F & F \\ EL1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & L1L2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & L2L3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & L3P & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & SPA & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & SAA & 0 \end{bmatrix}$$

where

F = fecundity

EL1 = S exp (-0.01 n(1)): survival probability from egg to L1 including density dependence

L1L2 = S exp (-0.01 n(1)): survival probability from L1 to L2

L2L3 = S exp (-c): survival probability from L2 to L3 including cannibalism by L3 on L2

L3P = survival probability from L3 to pupa

SPA = survival probability from pupa to adult

SAA = survival probability from adult to adult
 c = cannibalism rate

A sensitivity analysis was applied to investigate the parametrical space of survival and cannibalism. The values used in these simulations were chosen based on the encounter of parametrical regions where the changes of equilibrium takes place. The analysis was conducted by employing the bifurcation theory (May & Oster 1976). The bifurcation theory provides an important analysis by using bifurcation diagrams to show the behaviour of systems in response to changes of parameter values (May & Oster 1976). Usually, different values of demographic parameters may produce different equilibria. In bifurcation diagrams, the horizontal axis gives the parameter value (survival or cannibalism in the current study) and the vertical axis represents the magnitudes of the steady state of the equation. Bifurcations represent new steady states (May & Oster 1976). Two stable branches indicate the existence of a stable period two orbit, four stable branches a period four orbit, and so on.

Results

The experiments designed to estimate the mean survival (between life stages) and fecundity (*F*) of *C. albiceps* resulted in *F* = 281, *EL1* (survival from egg to L1) = 0.88, *L2L3* (from L2 to L3) = 0.86, *L3P* (from L3 to pupa) = 0.81, *PA* (from pupa to adult) = 0.79, and *AA* (young adult to mature adult) = 0.77. The survival curves were similar, and the statistical analysis suggested no significant difference among replicates. The results also indicate that the most important mortality occurred between the egg and the first instar. The exponential function produced a better fit ($r^2 = 0.84$, $P < 0.01$) than the linear ($r^2 = 0.81$, $P < 0.01$) in response to a decrease in mortality among immature stages, confirming the non-linear association between mortality and trajectory of life stages.

The histogram shown in Fig 1 describes the theoretical *C. albiceps* stage distribution over a hundred generations. A strong non-linear trend can be seen in the decrease of the bars. The density-dependence test shows that the



Fig 1 Life-stage distribution in *Chrysomya albiceps* obtained from the Matrix model, with survival and fecundity estimated in the laboratory.

most susceptible period between life stages to density dependence is from egg to first instar ($\chi^2 = 10.87$, $df = 1$, $P < 0.05$).

The simulations using the Matrix model produced seven graphs showing the fluctuations for each life stage over 300 generations (Fig 2). The largest population sizes were found for the estimates from egg to first instar, and the highest abundance through the generations were followed by dramatic decreases, produced in response

to density dependence (Fig 2).

Following the decreases, the population sizes remained at low levels over several generations. Introduction of the cannibalism term into the matrix model, using laboratory estimates obtained by Faria et al (2004a), produced no qualitative change in the dynamic behavior for all life stages (Fig 2). Only an arbitrary reduction of survival in this study to 0.5 produced oscillations, tending to periodicity with double peaks (Fig 3). The

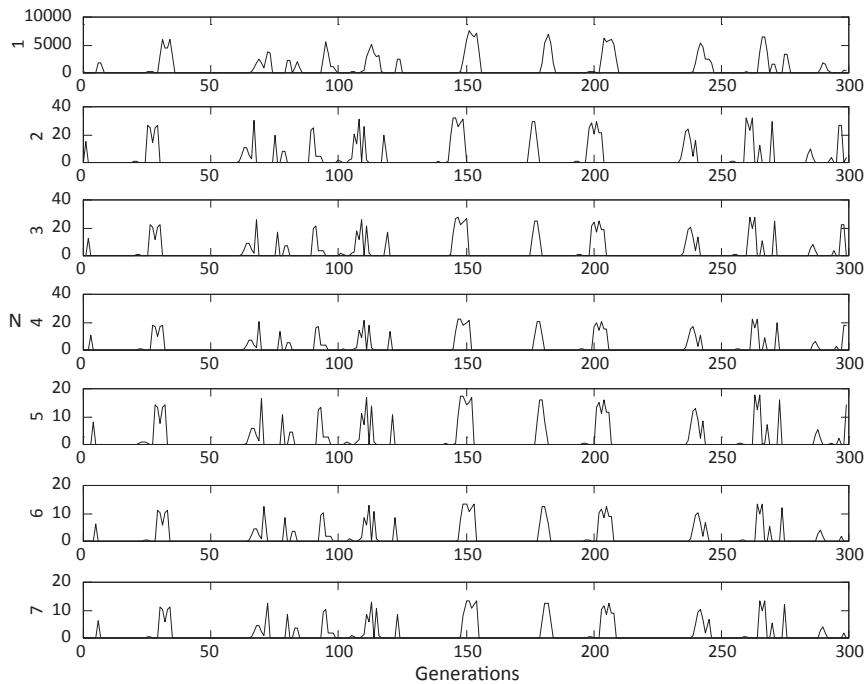


Fig 2 Population dynamics of *Chrysomya albiceps* life stages (1-7) produced by the Matrix model, with survival and fecundity estimated in the laboratory. $F = 281$; $EL1 = 0.88$, including density dependence; $L2L3 = 0.86$, cannibalism by L3 on L2; $L3P = 0.81$; $SPA = 0.79$; $SAA = 0.77$.

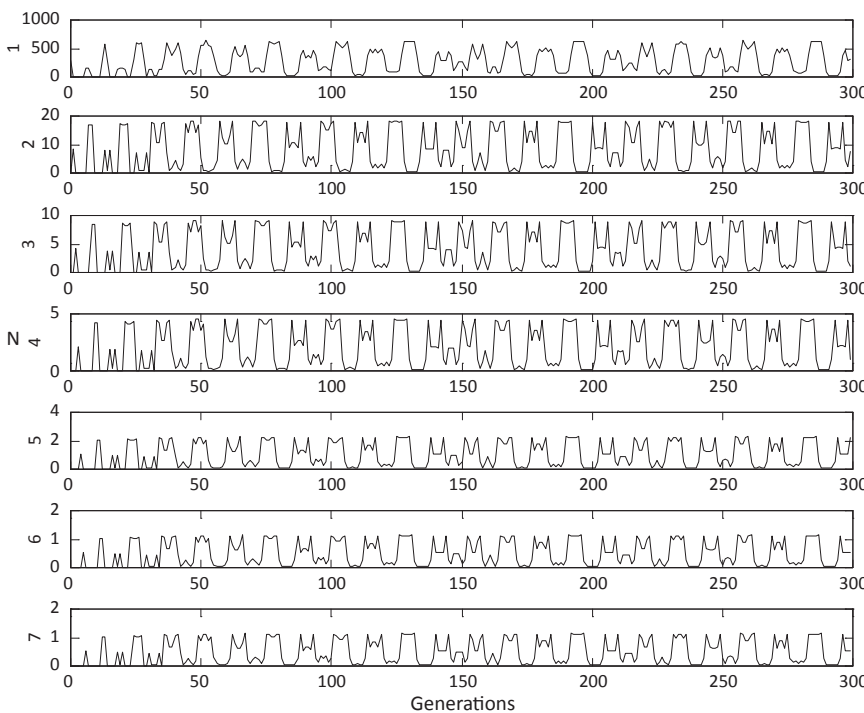


Fig 3 Population dynamics of *Chrysomya albiceps* life stages (1-7) produced by the Matrix model, with survival set to 0.5 in all life stages. $F = 281$; $EL1 = 0.5$, including density dependence; $L2L3 = 0.5$, cannibalism by L3 on L2; $L3P = 0.5$; $SPA = 0.5$; $SAA = 0.5$.

bifurcation diagram shows that low values of survival lead the population to a stable equilibrium, and survival higher than 0.45 produces unpredictable oscillations

(Fig 4). The bifurcation diagram for cannibalism suggests unpredictable oscillations over the entire parametric space, except for values higher than 0.85 (Fig 5).

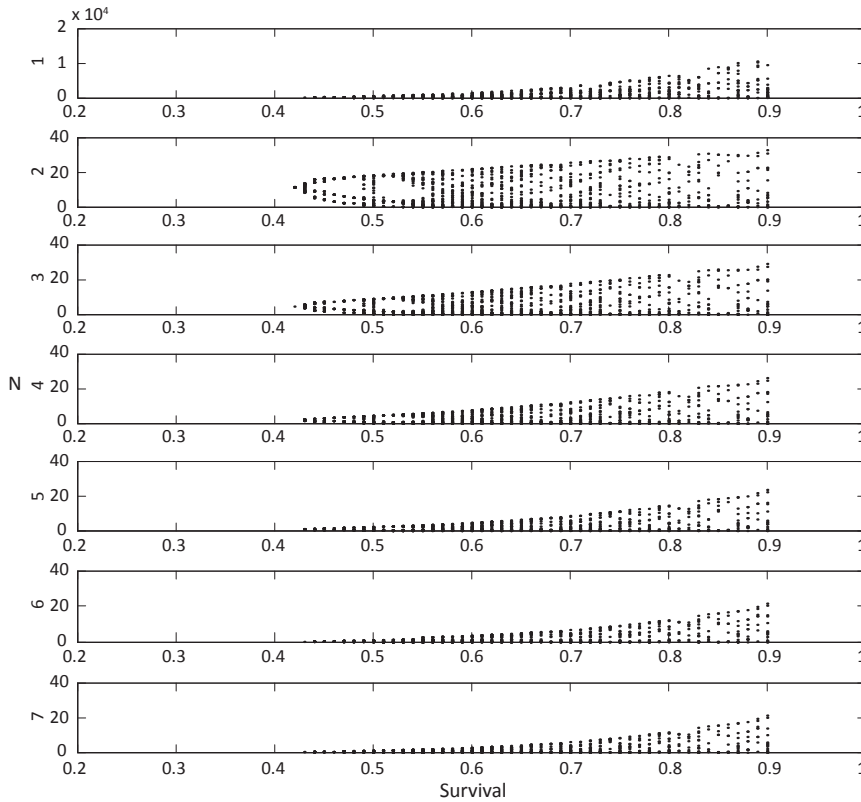


Fig 4 Bifurcation diagram analyzing the parametric space of survival in *Chrysomya albiceps*. F = 281; EL1 = including density dependence (-0.01); L2L3 = cannibalism by L3 on L2 (-0.01335).

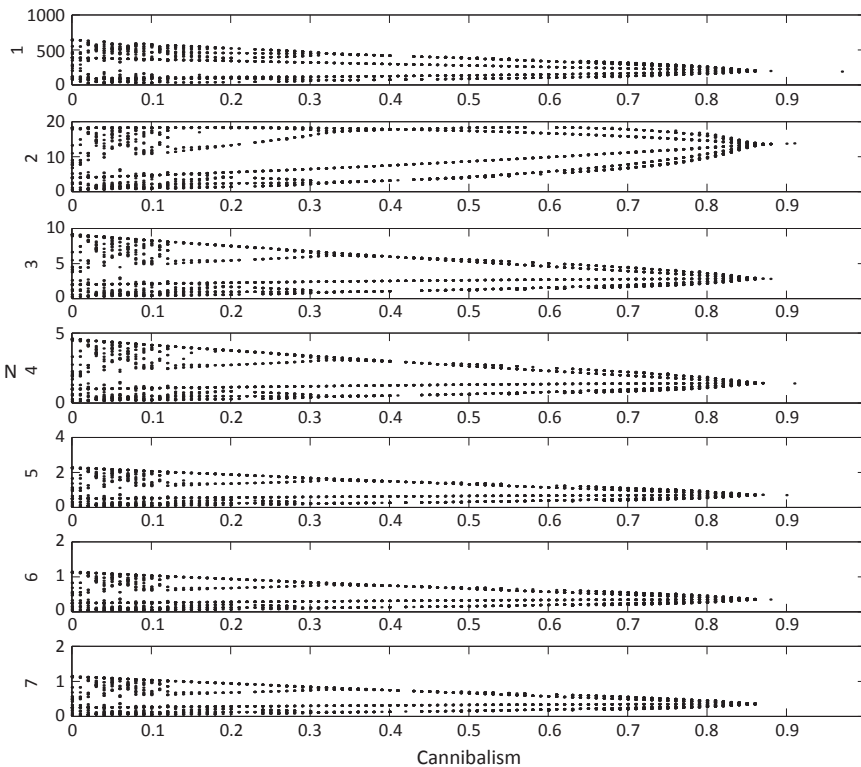


Fig 5 Bifurcation diagram analyzing the parametric space of cannibalism in *Chrysomya albiceps*, with survival set to 0.5 in all life stages. F = 281; EL1 = 0.5, including density dependence; L2L3 = 0.5; L3P = 0.5; SPA = 0.5; SAA = 0.5.

Discussion

The similarity among survival curves indicates that populations of *C. albiceps* always exhibit the same survival pattern among life stages, in which survival decreases with each stage. The most important mortality period was observed between the egg and the first instar, suggesting that the following instars are more resistant. The exponential function produced the best statistical fit in response to a decrease in mortality among immature stages. This result was the first suggestion of nonlinearity in the system.

Survival and fecundity have been investigated previously in blowflies, including *C. albiceps*, and show a significant exponential decrease as a function of larval densities (Reis *et al* 1996, Godoy *et al* 2001). However, these studies have considered no stage structure in their designs. In any event, demographic factors such as these usually exhibit strong associations with the population dynamics of blowfly species, often influencing the patterns of dynamic behavior and population persistence (Serra *et al* 2007).

The histogram time series suggests that a strong non-linear trend, characterized by the decrease of the bars, could take place during successive generations in *C. albiceps*. The density-dependence test indicates that the most susceptible period among life stages to density dependence is from egg to first instar. The density dependence observed in this life period has commonly been observed in experimental and natural blowfly populations, since during this time many adult flies are attracted to oviposition substrates in order to deposit a large number of eggs (Von Zuben *et al* 1996). A large number of larvae is commonly expected in carcasses, leading blowfly populations to compete for food in response to strong density dependence (Carvalho *et al* 2004, Serra *et al* 2007).

The Matrix model produced seven graphs showing fluctuations apparently chaotic for each life stage over 300 generations. The dynamics of blowflies has historically been viewed as a good example of complex dynamics, characterized by time series with quasi-cycles or chaos observed in the laboratory (Gurney *et al* 1980, Godoy 2007). Nevertheless, these results seem to be essentially connected to demographic parameter values, such as survival and fecundity (Gurney *et al* 1980, Godoy *et al* 1996).

Up to now, the population dynamics of *C. albiceps* has been studied without considering age or stage structure (Godoy *et al* 2001, Serra *et al* 2007). Godoy *et al* (2001) investigated the population dynamics of *C. albiceps* by means of a mathematical model developed by Prout & McChesney (1985), which incorporates fecundity and survival as density-dependent demographic parameters in discrete time, and found a two-point limit cycle for

this species. The estimates of demographic parameters obtained in the laboratory by Godoy *et al* (2001) showed that *C. albiceps* is a species with high sensitivity to change in its dynamic equilibrium, exhibiting an eigenvalue close to the frontier between stable equilibrium and a limit cycle. This sensitivity could explain the result found in the current study, showing a tendency to change the dynamics in response to different values of demographic parameters.

The interesting point is that both the Prout & McChesney model and the matrix model here employed have the same function to describe the density dependence, i.e., exponential functions, but the dynamic behavior differed between the two formulations. The result obtained for *C. albiceps* with the Prout & McChesney model was a two-point limit cycle, and with the matrix model simulations unpredictable fluctuations were also observed. The difference could be explained by the magnitude of the survival. In the simulations with the Prout & McChesney model (Godoy *et al* 2001), the estimated survival (0.56) was clearly lower than in this study (minimum equal to 0.7).

The bifurcation diagram clearly indicates that low values of survival lead the population to a stable equilibrium. Then, the arbitrary decrease in survival among immature stages in the matrix model gave similar results, making the system more stable. Bifurcation analysis was previously performed by Godoy *et al* (1996) by using a density-dependent population growth model in exotic and native blowflies, with results also showing stability associated with low survival values. It is possible to conclude from these findings that the stability of blowfly populations is closely associated with their demography.

Introduction of the cannibalism term into the matrix model, using laboratory estimates obtained by Faria *et al* (2004a), produced no qualitative change in the dynamic behavior for all life stages. Cannibalism in *C. albiceps* is still a little-studied interaction, but there is clear evidence that it occurs in response to food scarcity (Faria *et al* 2004a, Rosa *et al* 2006). The simulation obtained with the bifurcation diagram for cannibalism indicated that apparently chaotic oscillations can occur. This result suggests that cannibalism is an important interaction for *C. albiceps* in spite of the low rate estimated by Faria *et al* (2004a).

Chrysomya albiceps is a blowfly species that exhibits attributes of organisms highly sensitive to intraspecific competition (Rosa *et al* 2006). This kind of behavior usually leads insects to show cannibalistic behavior (Costantino *et al* 1995, Rosa *et al* 2006). Although cannibalism has been regarded as of little ecological interest in animal populations (Elgar & Crespi 1992), it has more recently received significant attention by ecologists and entomologists (Cushing *et al* 2003) mainly

considering demographic and behavioral aspects in insect populations. There is strong experimental evidence indicating that *C. albiceps* shows a dramatic decline in the number of survivors under intraspecific competition (Rosa et al 2006). In this case, cannibalism could be also responsible for the stability found in response to low survival rates.

The current study showed through the simulations, that both survival and cannibalism are important parameters for species such as *C. albiceps* because of their ability to influence the dynamic behavior of species that exhibit high sensitivity to competition. In spite of the partial theoretical connotation of this study, most of simulations were performed by using real data obtained from laboratory. The simulations run with arbitrary values were motivated by a plausible ecological scenario commonly observed in the blowfly system, described by intense intraspecific competition, which takes place in ephemeral patches where there is food scarcity, as for example carcasses (Ives & May 1985). In any attempt to model a biological system, one must confront a tradeoff between simulations and realism. In this study, we attempted to retain what we feel are the most important aspects of the biology of *C. albiceps* in relation to its population dynamics, while keeping the model as simple as possible. The relatively small number of parameters in the matrix model allowed us to retain some generality and to probe the parameter space for insight into the dynamic properties of *C. albiceps* populations.

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