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Dynamics of Blowfly Populations

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ABSTRACT

Blowflies have been recognised as useful biological experimental models for studies of population dynamics. These flies have received special attention because some species typically show an oscillatory behaviour, as reported for *Lucilia cuprina* by A. J. Nicholson. About 30 years ago, four Old World species of blowflies of the genus *Chrysomya* were introduced to the Americas, where they apparently displaced native species. Laboratory experiments were combined with mathematical models in an attempt to better understand the population dynamics of blowflies in the context of this biological invasion. The application of mathematical modelling has revealed different patterns of oscillation for the native and the exotic species. Experiments focussed on interspecific interactions have also provided important results in the context of the dynamics of interactions between native and exotic species. This mini-review is an attempt to synthesise results centred on the dynamics of blowflies during recent years, focussing primarily on the connection between experiments and mathematical modelling and considering the biological invasion scenario.

Keywords: biological invasion, blowflies, *Chrysomya*, population dynamics

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INTRODUCTION

Blowflies are interesting insects because of their characteristics. They can act as vectors of pathogens and producers of myiasis (Harwood and James 1979; Guimarães and Papavero 1999), and can also serve as an alternative medical treatment by applying larval therapy procedures and to help to elucidate crimes if their larvae are used to estimate the post-mortem interval (Courtenay 1999; Amendt *et al.* 2004). With respect to biology and ecology, they also exhibit interesting aspects, which have attracted the attention of ecologists, mainly those interested in interspecific or trophic interactions. The larvae of different species of blowflies compete for food, and this behaviour does not rarely lead to resource scarcity and/or to other kind of interactions, as for example, intraguild predation (Polis *et al.* 1989; Faria *et al.* 1999; Rosa *et al.* 2006).

Population dynamics of blowflies has historically been placed among the principal examples of studies suitable for quantitative analysis, mainly investigations involving mathematical modelling. Nicholson (1954, 1957) developed long-term laboratory studies of the sheep blowfly *Lucilia cuprina*, focussed on the population dynamic effects of resource limitation at different life stages. His results, a time series showing quasi-cycles in a laboratory culture, have been widely cited in theoretical studies, as for example the classic paper by Gurney *et al.* (1980) entitled “Nicholson’s blowflies revisited”. In this mini-review I have focussed my attention on an interesting scenario of biological invasion by blowflies, showing how the combination of population theory and experimentation can reveal unexpected and important results in the context of invasion, colonisation, and establishment of flies in new geographical regions.

BIOLOGICAL INVASION: AN INTERESTING SCENARIO FOR BLOWFLY MODELLING

Four Old World blowfly species, *Chrysomya albiceps*, *C. rufifacies*, *C. megacephala*, and *C. putoria* were introduced into the Americas around 1975 and have become established (Guimarães *et al.* 1978). The introduction of these species has culminated with the decrease in abundance of native species, mainly *Cochliomyia macellaria* (Guimarães *et al.* 1978, 1979). *Lucilia eximia*, another native species, has also been impacted by the introduction of *Chrysomya* species, but to a lesser extent (Prado and Guimarães 1982; Madeira *et al.* 1989). Some studies have shown that the main causes of the species displacement are the interactions

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with the exotic species (Wells and Greenberg 1992a, 1992b, 1992c; Faria *et al.* 1999; Gião and Godoy 2007). Interspecific competition between native and exotic species, and facultative predation by *C. albiceps* and *C. rufifacies* are examples of interactions, which have been investigated in laboratory (Wells and Greenberg 1992a, 1992b, 1992c; Faria *et al.* 1999). Both interactions have been studied with experimental populations and the results show that the *Chrysomya* species significantly influence the survival of *C. macellaria*. This impact is certainly the result of the preference by *C. albiceps* on *C. macellaria* (Faria *et al.* 1999). Adults and larvae interactions has been also investigated in laboratory and there are evidences to conclude that adult female avoid lay eggs in substrates previously occupied by larvae from other species, mainly *C. albiceps* (Gião and Godoy 2007).

BIOLOGY, POPULATION DYNAMICS, AND POPULATION THEORY

In blowfly populations, adults search for substrates on which to feed and lay eggs (Gião and Godoy 2007). The ovipositional substrates are ephemeral, and the immatures hatched from eggs experience high levels of competition for limited resources (Atkinson and Shorrocks 1981; Rosa *et al.* 2004). The amount of food consumed by larvae will determine the size of adults, which is correlated with fecundity, that is, larger blowfly females lay more eggs than smaller ones (Goodbrod and Goff 1990). The experiments performed by Goodbrod and Goff (1990) show that in pure cultures, puparial and adult weights vary inversely with larval densities, with maximal weights and lengths obtained in cultures with 2 larvae/g food, and minimal found with 40 larvae/g food. Blowfly generations occupy patchy and discrete resources, and fecundity and survival of adults are dependent on density conditions that affect the larval stage (Godoy *et al.* 1997). Any attempt to understand the population dynamics of blowflies will have to take into account the delay effect on adult fecundity and survival of competition among immatures during the larval state. Evidences of density dependence in several life history traits, such as rate of development, mortality and larval weight, have been also reported by Goodbrod and Goff (1990).

Taking into account all these aspects, the modelling of blowfly population dynamics should consider discrete generations and density dependence at the immature stage, with a delayed effect on the survival and fecundity of adults. Prout and McChesney (1985) proposed a mathematical formulation that takes into account all these features. This model is based on a finite-difference equation that models the density-dependent dynamics of immatures, eggs, or larvae, in succeeding generations, n_{t+1} and n_t, as a function of the decrease in fecundity (F) and survival (S) with increasing density of immatures (n).

The model considers two density-dependent functions, survival and fecundity, both dependent on the density of immatures, n_t. The recursion between immatures in succeeding generations n_{t+1} and n_t can be written as:

$$n_{t+1} = \frac{1}{2} F(n_t) S(n_t) n_t, \tag{1}$$

where $F(n_t)$, fecundity, and $S(n_t)$, survival, are both decreasing functions of n_t and the factor ½ indicates that one-half of the survivors are females. The exponential function has been applied to the survival and fecundity data, respectively, as $S\, e^{-sn}$ and $F\, e^{-fn}$, with uppercase letters defining the intercept in the regression analysis, which describe maximum survival, S, or fecundity, F, and lowercase letters describing regression coefficients for survival, s, and fecundity, f. Both intercepts and coefficient values were obtained by exponential regression from the experimental blowfly populations (Godoy *et al.* 2001). The exponential function was used because it fits the blowfly data as well as or better than the linear and hyperbolic functions (Von Zuben *et al.* 1993; Godoy *et al.* 2001). Furthermore, the decrease in fecundity as a function of the density of immatures can be viewed biologically as a Poisson process that is described by an exponential function (Rodriguez 1989). Applying the exponential functions to equation (1), the recursion equation describing changes in population numbers then reads

$$n_{t+1} = \frac{1}{2} F S e^{-(f+s)n_t} n_t, \tag{2}$$

Equation (1) is a nonlinear finite-difference equation whose dynamics can be deduced by the single eigenvalue calculated at the point of equilibrium (Luenberger 1979). The theoretical number of immatures at equilibrium (k) is given by $n_{t+1} = n_t = k$, and this condition occurs when

$$\frac{1}{2} F(k) S(k) = 1 \tag{3}$$

The general expression for the eigenvalue associated with equation (1) is given by the derivative of n_{t+1} with respect to n_t evaluated at k, which yields

$$\lambda = 1 + \frac{1}{2} k S(k) \left.\frac{dF(n_t)}{dn_t}\right|_{n_t = k} + \frac{1}{2} k F(k) \left.\frac{dS(n_t)}{dn_t}\right|_{n_t = k} \tag{4}$$

If λ < 1, the equilibrium is linearly stable (Hofbauer and Sigmund 1988). The number of immatures at equilibrium (k) obtained from equation (3) is given by

$$k = \frac{\left(\ln \frac{FS}{2} \right)}{f + s} \tag{5}$$

The eigenvalue (λ) describing the stability at steady state is obtained from equation (3) as

$$\lambda = 1 - \frac{1}{2} k F f e^{-fk} S(k) - \frac{1}{2} k S s e^{-sk} F(k) \tag{6}$$

The Prout and McChesney model has been intensively employed to investigate the dynamics of blowflies in Brazil under different ecological aspects, such as equilibrium stability, metapopulation, and stochastic dynamics (Von Zuben *et al.* 1993; Reis *et al.* 1996; Godoy *et al.* 1997, 2001; Silva *et al.* 2003; Castanho *et al.* 2006; Serra *et al.* 2007). Then, the population dynamics of *Chrysomya megacephala*, *C. putoria*, *C. albiceps*, *C. macellaria*, and *L. eximia* have been investigated by combining laboratory experiments and the Prout and McChesney model to investigate the system.

LABORATORY EXPERIMENTS FOCUSSED ON POPULATION DYNAMICS

The experiments usually employed to investigate the population dynamics of blowflies are motivated by ecological processes that normally take place on discrete substrates, which exhibit specific conditions to permit the insects to experience strong intraspecific competition for food. Exploitative intraspecific competition among immatures, which is known to occur under natural conditions (de Jong 1976; Lomnicki 1988) has been established in the laboratory by setting up larval densities, developing in a fixed amount of artificial media (Leal *et al.* 1982), ranging from 200 to 2,000 larvae per vial. This range of densities is generally suitable to simulate intraspecific competition process in blowflies, because it produces decreases in demographic parameters as a function of density (Godoy *et al.* 1993; Von Zuben *et al.* 1993). Fecundity was measured by counting the number of eggs per female, and expressed as the mean daily egg output (Godoy *et al.* 2001), which is based on the length of the gonotrophic cycle of *Chrysomya* species at 25°C (Avancini and Prado 1986; Linhares 1988). Survival was estimated as the number of adults emerging from each vial (Godoy *et al.* 2001).

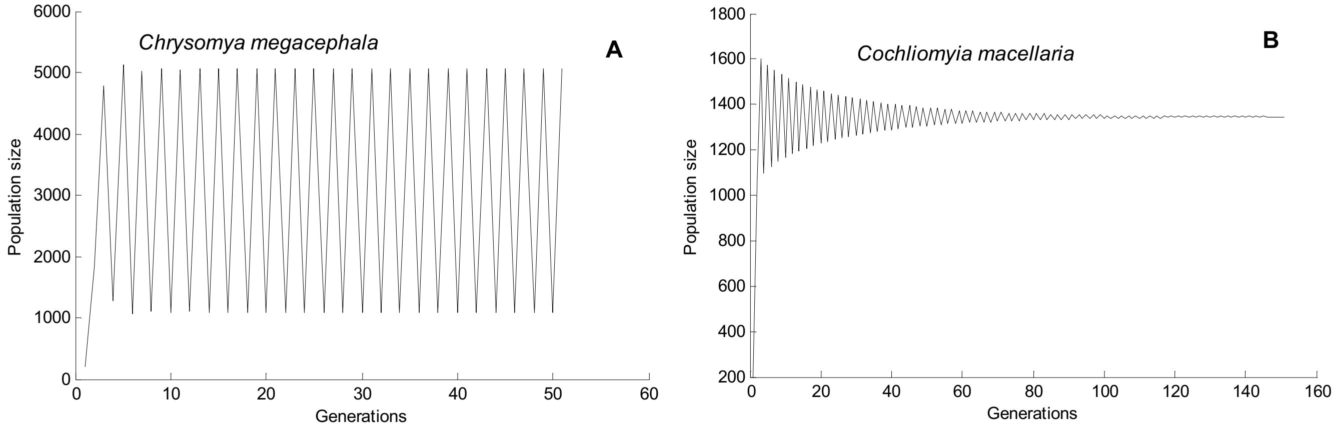

Fig. 1 Recursion for successive generations for the number of immatures in, *C. megacephala* (**A**) and *Cochliomyia macellaria* (**B**). Reprinted from **Reis SF, Teixeira MA, Von Zuben FJ, Godoy WAC, Von Zuben CJ** (1996) *Journal of Medical Entomology* **33**, 537-544, Fig. 2, with kind permission from the Entomological Society of America.

SPATIO-TEMPORAL PATTERNS OF DYNAMIC BEHAVIOUR IN EXOTIC AND NATIVE BLOWFLIES

The application of the Prout and McChesney model to investigate blowfly population dynamics resulted in a two-point limit cycle (**Fig. 1A**) for the exotic species, *C. albiceps*, *C. megacephala*, and *C. putoria* (Godoy *et al.* 2001). For the native species *C. macellaria* and *L. eximia*, a monotonic stable equilibrium was found (**Fig. 1B**). The results obtained in these studies are closely related to the demographic parameters, fecundity and survival, which are functions of the larval densities.

The approach cited above addresses important questions in the context of biological invasions, such as the arrival and establishment of *Chrysomya* species in the Americas and the concomitant decline in population sizes of *C. macellaria* and *L. eximia*. The dynamic behaviour exhibited by the exotic species is more complex than that of the native species. It is possible that this result explains, at least in part, the success of the *Chrysomya* species during the biological invasion. Species that exhibit cyclic or chaotic dynamics show higher demographic parameter values, such as fecundity and survival, than do species that exhibit a stable equilibrium (Godoy *et al.* 2001).

Survival and fecundity are essential parameters for demography, and certainly are strongly associated with the abundance of animal populations (Ebert 1999). Currently, the *Chrysomya* species are the most frequent blowflies found in several localities of South America (Souza and Linhares 1997; Carvalho and Linhares 2001; Centeno *et al.* 2002; Carvalho *et al.* 2004) and this fact confirms their ability to invade and successfully colonise new environments.

Spatial structure was also studied in blowflies, by combining the Prout and McChesney model with the formalism of coupled map lattices (Bascompte and Solé 1994). Spatial structure was incorporated as a lattice of discrete points, with the populations arranged on the nodes of this square lattice. The populations on each node were linked with dispersal to the four nearest neighbours (Godoy *et al.* 1997). The combination yielded an equation written as:

$$n_{t+1}(i,j)=\frac{1}{2}F^{*}S^{*}e^{-(f+s)n_t(i,j)}n_t(i,j)+D\nabla^2 n_t(r) \qquad (7)$$

where D is the diffusion rate that indexes dispersal as the fraction of the population in each node, (i,j), which is exchanged. The geometry of the diffusion among points in the lattice is defined as

$$\nabla^2 n_t(r) = n_t(\mathrm{i}+1,j) + n_t(i,j-1) + n_t(i,j+1) - 4\,n_t(i,j) \qquad (8)$$

The term $D\nabla^2 n_t(r)$ gives the diffusion effect, i.e., the effect of individual dispersal to the four adjacent nodes, and those that immigrate from these nodes. The principal result found was that the *Chrysomya* blowfly species exhibited one-point equilibrium as a diffusive dispersal effect Godoy *et al.* 1997). The analysis showed that the stabilising effect produced by the migration between patches places exotic and native blowfly species in the same equilibrium, a stable equilibrium. Certainly, migration decreases the number of individuals in the population, producing negative delayed effects in terms of fecundity for the next generation, and for this reason it is a stabilising influence (Godoy *et al.* 1997).

INTRODUCING UNCERTAINTY INTO MODELS

Unpredictable variations in population numbers are expected to occur in animal populations. The persistence of populations, including blowflies, may be strongly influenced by environmental and demographic stochasticity (Castanho *et al.* 2006; Serra *et al.* 2007). The deterministic approach employed to investigate the population dynamics of blowflies (Reis *et al.* 1996; Godoy *et al.* 1997, 2001) has revealed some interesting points, which show different patterns of dynamic behaviour. However, this dimension is not completely suitable to project trends in terms of local extinction, except in cases involving deterministic chaos.

Two approaches have been exploited to assess the uncertainty, by using the model proposed by Prout and McChesney (1985). The first approach is focussed on blowfly coupled population dynamics, applying fuzzy subsets to model the population trajectory of two blowfly species, analysing fecundity, survival, and migration in populations from different environments, classified as hostile, slightly unfavourable, and favourable (Castanho *et al.* 2006).

Some issues in modelling applied to population dynamics and risks of extinction require advanced mathematical approaches, principally because populations tend to fluctuate as a function of their variability in demographic parameters (Gotelli 2001; Godoy and Costa 2005). However, some specific systems are not suitable to produce a mathematical model directly, but are suitable to describe processes in linguistic terms (Barros *et al.* 2000).

Linguistic observations can be transformed into mathematical components, in order to analyse dynamic behaviour patterns and susceptibility to local or global extinction (Dubois and Prade 1998; Castanho *et al.* 2006). Fuzzy logic is the most effective approach to transform linguistic data into mathematical formulas and vice versa. Indeed, Dubois and Prade (1998) stated that the real power of fuzzy logic lies in its ability to combine modelling (constructing a function that accurately mimics given data) and abstracting knowledge from the data.

Combining Prout and McChesney (1985) with coupled population equations (Roughgarden 1998), which give a migration dimension (*m*) between two patches, with *m* describing the fraction of migrant individuals and *1- m* the non-migration fraction, yields:

$$n_{1,t+1} = [(1-m_1)\tfrac{1}{2}F_1^{*}S_1^{*}e^{-(f+s)n_t}n_t + m_2\tfrac{1}{2}F_2^{*}S_2^{*}e^{-(f+s)n_t}n_t] \qquad (9)$$

$$n_{2,t+1} = [m_1\tfrac{1}{2}F_1^{*}S_1^{*}e^{-(f+s)n_t}n_t + (1-m_2)\tfrac{1}{2}F_2^{*}S_2^{*}e^{-(f+s)n_t}n_t]$$

The parameters *F*, *S* and *m* are known for their density dependence, associated with resource availability and environmental factors (Prout and McChesney 1985; Godoy *et al.* 1997). Hence, in this study they were considered linguistic variables, and were therefore estimated using fuzzy rules. Nine rules have been created according to different conditions, such as hostile, slightly unfavourable, and favourable environments. The fuzzy rules were established following the Mandani fuzzy inference (Castanho *et al.* 2006) and incorporate a set of premises written as “if” and “then”.

In this study, they were described as: *if* the population is small (large or medium) and the environment is favourable (slightly unfavourable or hostile), *then* survival is high (low or moderate), fecundity is high (low or moderate), and migration is low (moderate or high). The main results of the blowfly population fuzzy study by Castanho *et al.* (2006) suggest different possibilities in terms of dynamic behaviour produced by migration in coupled populations among hostile, slightly unfavourable, and favourable environments (**Figs. 2, 3**).

In **Fig. 2A** and **2B**, the bilateral is compared to unilateral migration in *C. albiceps* populations, from a hostile to a slightly unfavourable environment. For both cases, the equilibrium is the same, a monotonic stable equilibrium, but bilateral migration (**Fig. 2B**) avoids local extinction. However, populations migrating from a slightly unfavourable to a favourable environment exhibit no extinction (**Fig. 2C, 2D**). *Chrysomya albiceps* populations also exhibit qualitative differences, characterised by a two-point limit cycle and out-of-phase oscillations, when the bilateral migration is from favourable to slightly unfavourable environments (**Fig. 3**). The results suggest that different environmental conditions for two populations, may induce the appearance of more complex dynamic behaviours. In conclusion, environmental heterogeneity can play an important role in blowfly metapopulation systems. In other words, populations produced in environments of different qualities may induce different results with respect to population dynamics, including out-of-phase oscillations, behaviour indicative of improved likelihood of population persistence (Godoy and Costa 2005; Serra *et al.* 2007).

The second approach is centred on the incorporation of demographic stochasticity into the equation (9), by allowing variability between maximum and minimum values of fecundity, survival, and migration (Serra *et al.* 2007). The objective of the study was to explore the stochastic population dynamics in five blowfly species, *C. albiceps*, *C. megacephala*, *C. putoria*, *C. macellaria*, and *L. eximia*, by combining the Prout and McChesney model with the two-patch metapopulation model employed in the first approach (equation 9).

Stochastic fecundity, survival, and migration were investigated by permitting random variations between prede-

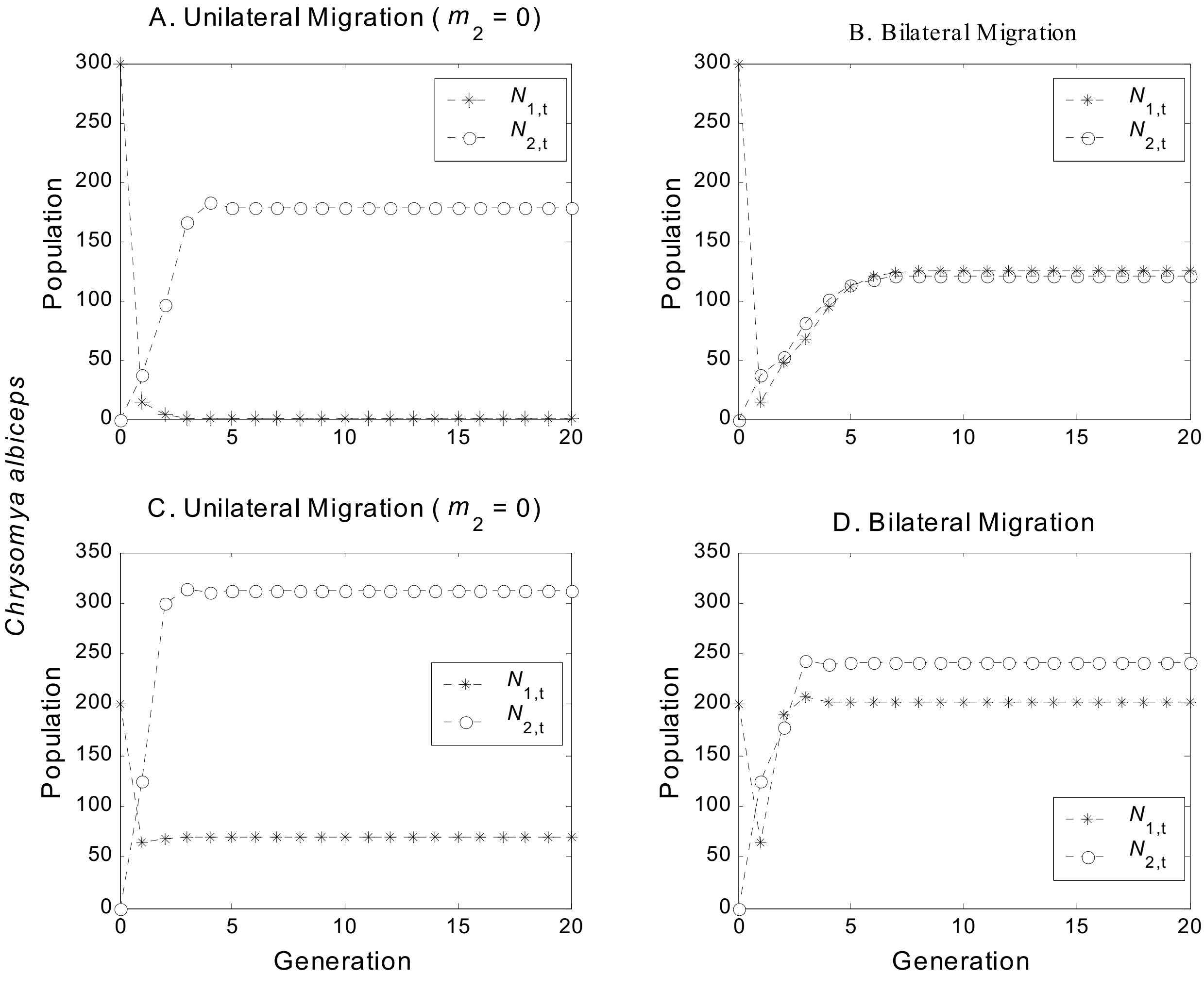

Fig. 2 Recursion for 20 generations from hostile to slightly hostile environments (**A** and **B**), recursion for 20 generations from slightly unfavourable to favourable environments (**C** and **D**). Reprinted from **Castanho MJP, Magnago KF, Bassanezi RC, Godoy WAC** (2006) *Biological Research* **39**, 341-352, Figs. 5 and 6, with kind permission from Sociedad de Biología de Chile.

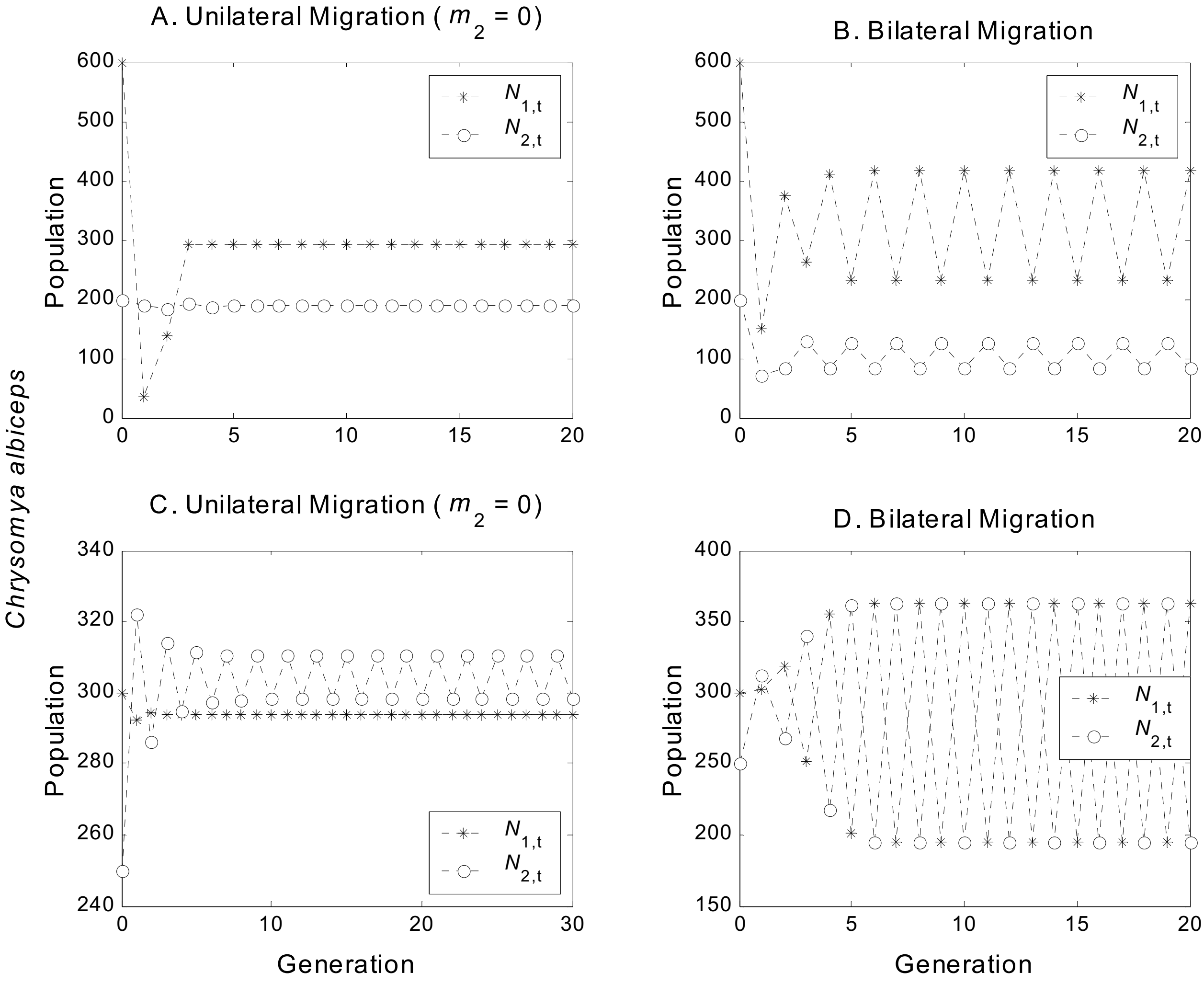

Fig. 3 Recursion for 20 generations from favourable to slightly unfavourable environments (**A** and **B**). Recursion for 20 generations between favourable environments (**C** and **D**). Reprinted from **Castanho MJP, Magnago KF, Bassanezi RC, Godoy WAC** (2006) *Biological Research* **39**, 341-352, Figs. 5 and 6, with kind permission from Sociedad de Biología de Chile.

termined demographic boundary values (maximum and minimum of all densities) based on experimental data (Godoy *et al.* 2001; Serra *et al.* 2007). The migration rate (*m*) was allowed to fluctuate between 0.4 and 0.6. These limits for migration were chosen in order to investigate the effects of high migration rates in a stochastic context on the population dynamics of introduced and native blowflies. They also were the most suitable to show synchrony between local populations, since several simulations were run considering all possible combinations between 0.1 and 1, with intervals of 0.1.

Lucilia eximia and *Chrysomya albiceps* are the species, which are most susceptible to the risk of local extinction. *Cochliomyia macellaria*, *C. megacephala*, and *C. putoria*, according to the simulations, are subject to lower risks of extinction than are the other species (Serra *et al.* 2007). Simultaneous analysis of stochastic fecundity and survival indicates an increase in extinction risk for all species. Nevertheless, when stochastic fecundity, survival, and migration are simulated together, the coupled populations appear synchronised in all five species (Serra *et al.* 2007).

Lucilia eximia shows low population sizes and oscillations of low amplitude. This is an interesting result, because low-amplitude oscillations tend to push populations toward stability. The abundance of *L. eximia* in Brazil is low but relatively stable year-round (Moura *et al.* 1997). This corroborates, at least in part, the results found in the simulations. The good performance observed for *C. macellaria* is also interesting, because this species has been negatively affected by the introduction of *Chrysomya* species (Guimarães *et al.* 1979). However, the design of the Prout and McChesney model, to analyse single species without considering interspecific interactions, may explain this finding. On the other hand, *C. macellaria* has withstood the effects of a biological invasion for about 30 years, despite its low abundance (Carvalho *et al.* 2000). This finding confirms the persistence of this species even under stressful conditions.

The results obtained with *C. albiceps* are surprising, because the simulations indicate low survival, principally when compared to other *Chrysomya* species and *C. macellaria*. This species exhibits several characteristics that could contribute to a good performance in terms of persistence (Faria *et al.* 1999; Godoy *et al.* 2001; Rosa *et al.* 2004). However, we believe that *C. albiceps* is only successful in the presence of other blowfly species (Faria *et al.* 1999), because its larvae predate upon other species, such as, *C. macellaria*, *C. megacephala* and *C. putoria* (Faria *et al.* 1999); this habit strongly influences its survival (Rosa *et al.* 2006). Recently, Rosa *et al.* (2004) investigated the influence of food abundance, larval density and interspecific interactions with *C. megacephala* and *C. macellaria* on the survival of *C. albiceps* and observed that it exhibits higher survival in mixed compared to pure cultures, suggesting that larval predation offers more advantages than competition for food.

The synchronous behaviour observed has important implications for local and global persistence. Synchrony is an important factor because it is directly related to the likelihood of global extinction (Heino *et al.* 1997). The more spatially synchronous is a metapopulation, the shorter is its expected persistence time. If all local populations fluctuate in unison, then when one becomes extinct, all of the others are likely to suffer the same fate; if spatial synchrony is low, some local populations are likely to be abundant and can serve to replace extinct populations (Heino *et al.* 1997). The results obtained by Serra *et al.* (2007) suggest that the synchrony observed is associated with pre-established migration limits, because this result was not found between other limits.

EVALUATING POST-FEEDING LARVAL DISPERSAL IN BLOWFLIES

A recent review of postfeeding larval dispersal in blowflies focussed on the process of larval dispersal and its implications for forensic entomology, describing how aspects such as dispersal of immatures, burial behaviour, and competition among species usually influence the population dynamics of blowflies (Gomes *et al.* 2006). The dispersal models presented in this review are supported by several previous studies that described larval migration in detail, based on investigations performed from 1950 to 2005 (Gomes *et al.* 2006).

The foundation for the mathematical modelling of post-feeding larval dispersal in blowflies comes from the biology of species, which has been intensively studied in the laboratory (Levot *et al.* 1979; Godoy *et al.* 1995; Gomes *et al.* 2006). In the life history of the immature stage of blowflies, at least two stages, eggs and larvae, are extremely important. In the case of both, there are essential biological processes involved. After the eggs hatch, the larvae may experience strong intra- and interspecific competition (Levot *et al.* 1979; Rosa *et al.* 2004). Those larvae which have already attained the weight necessary for pupation, begin to disperse outside the food substrate in search of sites for burying (Levot *et al.* 1979; Greenberg 1990).

The initial idea to study the process of larval dispersal was proposed by Von Zuben *et al.* (1996), who employed a diffusion approach to describe the movements of postfeeding larva. The equation used for this description can be written as:

$$\frac{\partial c(x,t)}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + \alpha\frac{\partial c}{\partial x} - h(x,t) \qquad (10)$$

In this equation, *c*(*x*,*t*) gives the concentration of larvae at any given location (*x*) and time *t*, *D* is the diffusion coefficient representing migration of larvae, and *α* is a coefficient of proportionality describing the velocity which may be taken to be characteristic of any given species. The first two terms describe the dynamics of larvae actively dispersing on the soil.

The function *h*(*x*,*t*) is included in the diffusion model to describe the process of larval burying in the soil. This model was applied to describe the larval dispersal of *C. megacephala*, *C. putoria*, and *C. macellaria* (Bassanezi *et al.* 1997) by fitting theoretical curves based on the solution of the diffusion equation (equation 10) to larvae distribution data (**Fig. 4**). The different oscillations produced over the larval dispersal of blowflies (**Fig. 4**), considered as a consequence of larval crowding, were analysed with a model which considers two immature populations of blowflies, one of larvae dispersing on the soil, and the other of larvae that burrow in the soil to pupate.

This type of process can be modelled by non-local interaction equations (Murray 1990), that consider that the rate of change in density, *n*(*x*,*t*), at position *x* at a time *t* depends on the influence of *n*(*x'*,*t*) at all other positions in space, denoted by *x'*. The model that describes the larval dispersal depending on the neighbouring of *n*(*x'*,*t*) exerted on *n*(*x*,*t*) can be written as

$$\frac{\partial n}{\partial t}(x,t) = f(n) + \int_{-x}^{x} w(x-x')n(x',t)dx' \qquad (11)$$

In this equation *w*(*x-x'*) is the kernel function that quantifies the non-local interaction in space variable, and *f*(*n*) is the usual source term employed in reaction diffusion approaches. Numerical solutions of integro-partial differential equations indicate that changes in the parameter that governs the non-local interaction between dispersing and buried larvae induce oscillations in the final horizontal distribution of pupae (**Fig. 5**). The results suggest that the greater the neighbourhood influence acting to inhibit pupation, the greater the frequency of waves of dispersing larvae (Boldrini *et al.* 1997). These waves determined the oscillation in pupal frequencies as a function of the distance from the food source. Thus, the neighbourhood influence seems to influence the determination of the form of horizontal frequency distribution of pupae in the native and exotic blow-

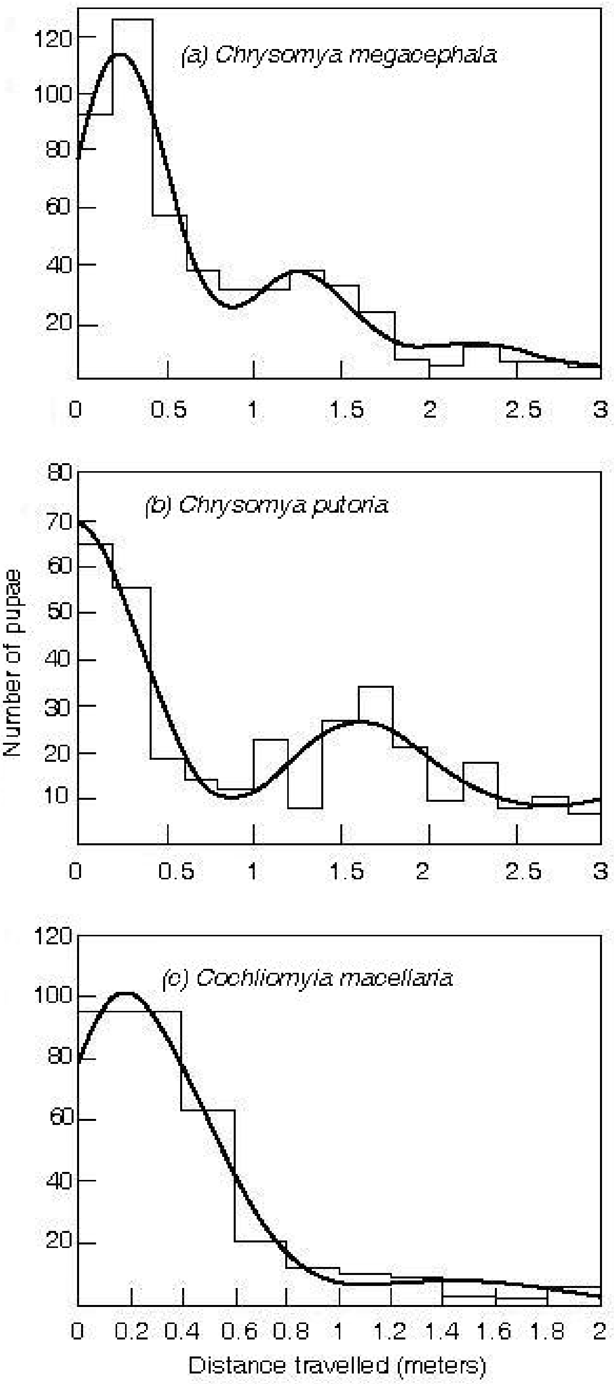

Fig. 4 Histogram of the experimental data for the number of buried pupae as a function of distance travelled as a result of larval dispersal from the food source in three blowfly species. The curve fitted to the data is based on the solution of the diffusion equation (equation 10). Reprinted from **Boldrini JL, Bassanezi RC, Moretti AC, Von Zuben FJ, Godoy WAC, Von Zuben CJ, Reis SF** (1997) *Journal of Theoretical Biology* **185**, 523-531, Figs. 1 and 2, with kind permission from Elsevier.

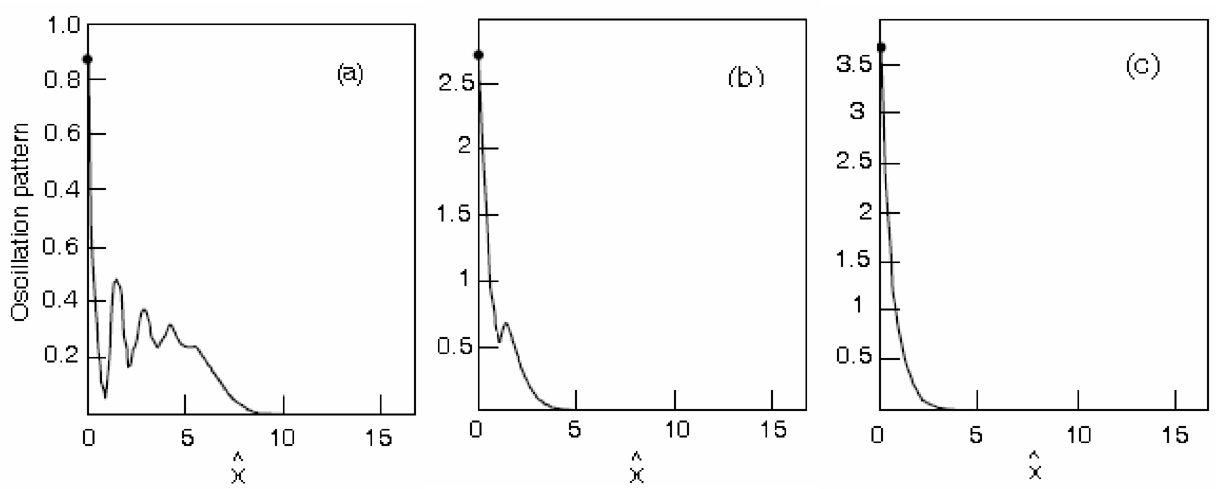

Fig. 5 Theoretical dispersal pattern obtained from numerical experiments of equation 11 for decreasing values of the neighbourhood coefficient, with $\bar{x}$ describing the theoretical position of larvae of (a) *C. megacephala*, (b) *C. putoria*, and (c) *C. macellaria*. Reprinted from **Boldrini JL, Bassanezi RC, Moretti AC, Von Zuben FJ, Godoy WAC, Von Zuben CJ, Reis SF** (1997) *Journal of Theoretical Biology* **185**, 523-531, Figs. 1 and 2, with kind permission from Elsevier.

fly species, as seen in **Fig. 4**.

Apparently, the influence of neighbourhood on *C. macellaria* is weaker than on *C. megacephala* and *C. putoria*, because the waves produced in the larvae distribution are different (Boldrini *et al.* 1997). These results are probably associated with the larval aggregation processes inherent in each species. Godoy *et al.* (1996) estimated larval aggregation over blowfly dispersal process based on the parameter *k* in the negative binomial distribution, usually employed to measure aggregation (Ludwig and Reynolds 1988). *Cochliomyia macellaria* exhibited the lowest larval aggregation level, compared with the exotic species *C. megacephala* and *C. putoria* (Godoy *et al.* 1996). This may be related to the smaller neighbourhood size exhibited by the species, described by a monotonically decaying dispersal (Boldrini *et al.* 1997).

INTERSPECIFIC INTERACTIONS AND PERSPECTIVES FOR MATHEMATICAL MODELLING

Interspecific interactions in biological populations are complex processes, consisting of challenging opportunities for mathematical modelling (Kot 2001). Two central questions motivate the implementation of modelling in interspecific interactions: what determines whether populations of different species can coexist? Do the details of feeding relationships, i.e., who is predator or prey, matter? As noted in previous sections of this review, mathematical models involve a set of assumptions about an ecological system, expressed in mathematical language.

However, the formulation of the assumptions depends on previous background knowledge of the system, which requires exhaustive investigations (Kareiva 1989). Blowfly communities are complex systems that involve the use of ephemeral substrates, which constantly receive different species. The composition of the blowfly fauna in carcasses is usually influenced by several physical and biological factors (Varatharajan and Sen 2000; Grassberger *et al.* 2003). Physical factors are related to environmental conditions, such as temperature, humidity, rain, and type of soil. Biological factors include demographic parameters associated with intra- and interspecific interactions.

Interspecific and even trophic interactions can take place during three stages of the life cycle in blowflies: larval, postfeeding, or adult. In all cases, the faunal composition may be markedly changed, depending on the interaction strength (Grassberger *et al.* 2003). The number of eggs or larvae in carrion frequently exceeds its carrying capacity (Kneidel 1984a, 1984b), and often leads to intra- and interspecific interactions such as competition for food, cannibalism, or predation, with consequences for adult fitness and community structure (Atkinson and Shorrocks 1981; Kneidel 1984b; Faria *et al.* 1999, 2004c).

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 (Ullyett 1950; Goodbrod and Goff 1990). For *C. albiceps* and *C. rufifacies* (Macquart), 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 (Ullyett 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. rufifacies* show such behaviour during the larval stage (Wells and Greenberg 1992a, 1992b, 1992c; Faria *et al.* 1999).

Facultative predation by species of *Chrysomya* (Robineau-Desvoidy) was classified as intraguild predation (IGP) by Polis *et al.* (1989); they suggested that IGP can promote faster growth and earlier metamorphosis in these flies. Intraguild predation is usually categorised 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 is distinguished from traditional concepts of competition by the immediate energy gains for the predator, and differs from classic predation because the act reduces potential exploitation competition (Polis *et al.* 1989).

The specific predatory habit of *C. albiceps* has been investigated through choice experiments designed to analyse larval predation rates and prey choice (Faria *et al.* 1999; Faria and Godoy 2001). *Chrysomya albiceps* attacks *C. macellaria* more often than *C. megacephala* and *C. putoria* (Faria *et al.* 1999). However, in the absence of *C. macellaria*, it attacks *C. putoria* more often than *C. megacephala* (Faria and Godoy 2001). Wells and Kurahashi (1997) also carried out a study in which *C. rufifacies* larvae were paired individually with *C. macellaria* and *C. megacephala*. Under these circumstances, *C. macellaria* larvae were killed at a higher rate than were *C. megacephala* larvae.

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*. The flexibility of *C. albiceps* in choosing larvae suggests that the predatory behaviour of this species can change as a function of prey availability, including other species not yet attacked. In a natural setting, the coexistence of different blowfly species in the same substrate is not uncommon (Kneidel 1984a, 1984b; Wells and Greenberg 1994), and such a situation would provide *C. albiceps* larvae with a choice of prey.

The predation by third-instar larvae of *C. albiceps* on first-, second- and third-instar larvae of *C. megacephala* and *C. macellaria* was also evaluated in no-choice experiments, in order to compare the vulnerability of larval instars to predation. With first- and second-instar prey, the highest predation rate by *C. albiceps* was on *C. megacephala* (Faria *et al*. 2004a). For third-instar prey, the highest predation rate was on *C. macellaria*. With second-instar prey, there was complete predation on *C. megacephala* within 90 min, whereas in *C. macellaria* only 55% of the larvae were eaten by 90 min (Faria *et al*. 2004a).

For third-instar prey, most predation on *C. macellaria* (80%) occurred within 90 min, whereas in *C. megacephala* only 35% of the larvae were eaten in the same time period (Faria *et al*. 2004a). These results indicate that the preference for prey depends to some extent on the instar. Different predation rates by *C. rufifacies* on *C. macellaria* have been described, with the third instar being most frequently attacked (Wells and Greenberg 1992a). *Chrysomya rufifacies* has also shown predatory behaviour only in the third instar; whereas *C. macellaria* may be attacked in both the second and third instar (Wells and Greenberg 1992a).

All these results have been observed during the larval interactions and prior to the larval burying. However, larvae are expected to leave the substrate, looking for a suitable place for pupation when the food is scarce (Godoy *et al*. 1995). Certainly, this behaviour is influenced by the presence of different species, competitors, prey, or predators. This aspect has been investigated by Andrade *et al*. (2002) and Reigada and Godoy (2005), with laboratory experiments.

Postfeeding larval interspecific interactions

Attacks occur more often within the carcass, but may also occur outside, during larval dispersal (Andrade *et al*. 2002). In this stage, the larvae may be at risk of predation, parasitisation and desiccation (Legner 1977; Peschke *et al*. 1987). Recently, Andrade *et al*. (2002) investigated larval dispersal associated with predation in experimental populations of *C. albiceps* and *C. macellaria* in single- and double-species combinations. For double species, the number of recovered larvae of *C. albiceps* was similar to the number initially released. However, the number of recovered larvae of *C. macellaria* was significantly smaller than the initially released number (Andrade *et al*. 2002). The results showed that *C. albiceps* attacks *C. macellaria* larvae during the larval dispersal processes.

The influence of larval predation on the dispersal of *C. albiceps* and *C. megacephala* single and double species was also investigated, in order to study simultaneously larval predation and patterns of larval frequency distribution. The results showed that *C. albiceps* attacks *C. megacephala* larvae during dispersal and maintains an aggregated pattern close to the release point, in single and double species. *Chrysomya megacephala* single species exhibited the same pattern, but in double species this changed to a random distribution (Reigada and Godoy 2005).

This type of interaction and the consequent distribution may have serious implications for the faunal structure of necrophagous flies, and consequently for forensic entomology. The abundance and coexistence of species are important data, because carcasses may be nearly monopolised by a single predator fly species such as *C. albiceps* (Grassberger *et al*. 2003). The level of larval aggregation is an important factor, because the distribution of larvae can influence the survival of the population. Predation of postfeeding larvae by coleopterans and attack by parasitoids occur primarily in the neighbourhood of the food source (Peschke *et al*. 1987) and can contribute to a reduction in fitness. It has been estimated that predation and parasitisation during the pre-adult stages, mainly pre-pupae and pupae, can increase mortality rates up to 60% in some blowfly species (Putman 1977). These results indicate that the postfeeding larval interactions are important events for the population dynamics of blowflies, and must be considered in modelling.

Functional response in blowflies

We have demonstrated the influence of predation on two important life stages of blowfly larvae. In both periods, i.e., larval interspecific interaction during feeding, and postfeeding larval interspecific interactions, the dynamics of predation by *C. albiceps* may influence the abundance and diversity of necrophagous dipteran fauna, depending on the rate of consumption of larvae, in addition to affecting its own development rate. This kind of relation, i.e., prey abundance and consumption by the predator, is usually termed the functional response.

The functional response provides information about basic mechanisms inherent in prey-predator dynamics (Lipcius and Hines 1986), and is an essential component of prey-predator models (Jeschke *et al*. 2002). The functional response can also determine whether a predator is able to regulate the density of its prey when the response depends on density (Murdoch and Oaten 1975). Usually, the functional response is most conveniently classified into three general types (Holling 1959), termed I, II, and III, which describe, respectively, linear, asymptotic, and sigmoid patterns. The functional response by *C. albiceps* on different prey species and larval instars of blowflies was analysed by Faria *et al*. (2004a, 2004b). The type II functional response was observed when second-instar larvae of *C. megacephala* and *C. macellaria* were consumed (Faria *et al*. 2004a, 2004b).

The asymptotic pattern observed in *C. albiceps* is a reflex of its predation dynamics, which depend essentially on the chance of encounter with other prey species and on the handling time, an important factor that can determine how rapidly the larva consumes its prey. The negative influence of *C. albiceps* on the abundance of other blowfly species has been frequently studied. The results of these investigations clearly suggest that this habit may be an important factor in the displacement of native species in the New World (Wells and Greenberg 1992a, 1992b, 1992c; Faria *et al*. 1999).

Adult interspecific interactions

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

There are few studies on ovipositional behaviour in species of Calliphoridae. The principal studies have focused on patch dynamics and distribution of dipterans in different food substrates (Hanski 1987; d'Almeida and Almeida 1998). The main reason to investigate this point is that ovipositional behaviour may indirectly affect individual fitness, population dynamics, and community structure (Blaustein 1999). The ovipositional behaviour of *C. albiceps*, *C. megacephala*, and *L. eximia* in response to the previous presence of larvae of different species, both predator and prey, was recently investigated (Gião and Godoy 2007).

All the species preferred substrates that had previously contained no larvae. However, *C. megacephala* and *L. eximia* avoided laying eggs principally in patches where *C. albiceps* larvae were already present (**Fig. 6**). It is possible that ovipositional avoidance occurred in response to the movement of *C. albiceps* larvae, which during the third larval instar move vigorously on the substrate searching for food or prey larvae (Faria *et al*. 1999; Reigada and Godoy

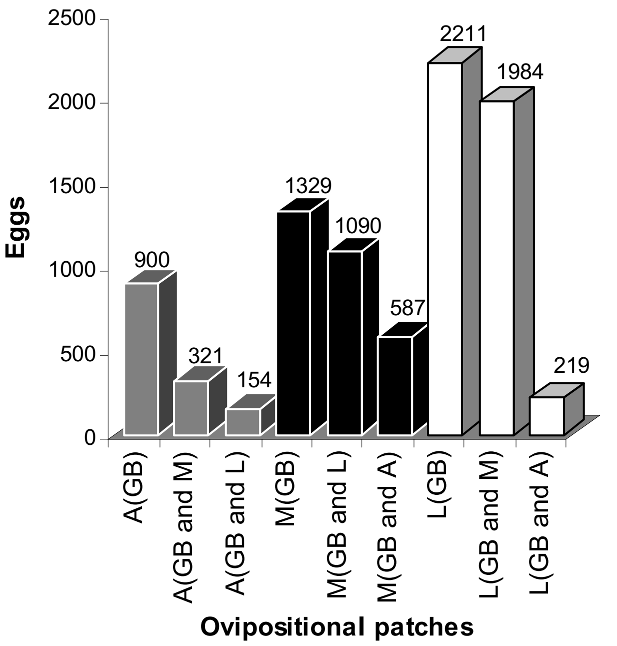

Fig. 6 Number of eggs laid by *C. albiceps* (A), *C. megacephala* (M), and *L. eximia* (L) in three different ovipositional patches. Reprinted from **Gião JZ, Godoy WAC** (2007) *Journal of Insect Behavior* **20**, 77-86, Fig. 2, with kind permission from Springer Science and Business Media.

2005). Hence, the results suggest that the previous presence of *C. albiceps* larvae can significantly influence the ovipositional behaviour of *L. eximia* and *C. megacephala*.

Several studies have investigated prey-predator interactions in Calliphoridae, but all the studies were designed to analyse larval interactions (Faria *et al.* 1999, 2004a, 2004b; Rosa *et al.* 2004; Reigada and Godoy 2005). Larval predation in blowflies frequently results in important consequences for community dynamics of necrophagous dipterans, because it may significantly influence the abundance of several species (Faria *et al.* 1999; Rosa *et al.* 2004). In addition, the necrophagous fauna composition appears to exhibit wide variations with respect to diversity, making interspecific interaction an important factor to be considered in forensic entomology (Grassberger *et al.* 2003). The focus of studies, evolving adult behaviour, makes an important contribution to the database applied to population ecology and forensic science, since the population potential for future generations essentially depends on the ovipositional behaviour of the flies.

CONCLUDING REMARKS

Laboratory studies focussed on blowfly interaction ecology are certainly much simpler than real systems in which the insects are inserted. However, they provide detailed information about the system, which may provide a useful background for the development of mathematical models. Prospective models and laboratory studies on interspecific dynamics of blowflies should establish that a laboratory community has inherent complexity, which if thoroughly analysed will be useful to ecologists.

When complexity is gradually incorporated into laboratory studies and models, it may indicate that assemblages of species may exhibit patterns that are on the one hand greater than the sum of their parts, and on the other can reveal patterns and dynamics not yet discovered. A blowfly community is a complex system, with many interactive processes acting at the same and at different trophic levels. This characteristic justifies implementing laboratory and mathematical frameworks capable of focussing on the blowfly system, because a natural complexity in terms of interspecific interactions has been observed, principally considering the intraguild predation exhibited by *Chrysomya* species (Faria *et al.* 1999; Rosa *et al.* 2004). We are pursuing this line because there is both empirical and theoretical evidence from previous investigations (Faria *et al.* 1999; Reigada and Godoy 2005; Gião and Godoy 2007; Serra *et al.* 2007) that shows great promise for studies of blowfly interactions from the perspective of intraguild predation (Polis *et al.* 1989).

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