

[ARTIGO RETRATADO] Diffusion Model Applied to Postfeeding Larval Dispersal in Blowflies (Diptera: Calliphoridae)

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The article "Diffusion Model Applied to Postfeeding Larval Dispersal in Blowflies (Diptera: Calliphoridae)" published in *Memorias do Instituto do Oswaldo Cruz* 92(2):281-286, 1997, [dx.doi.org/10.1590](https://doi.org/10.1590), authored by RC Bassanezi, MBF Leite, WAC Godoy, CJ Von Zuben, FJ Von Zuben, and SF dos Reis has been retracted. We have been informed about the use of graphical figure presentation published in *Journal of Theoretical Biology* vol. 185(4):523-531 1997, and following a careful analysis of the content in both papers, we concluded that the figure presented in *Mem. Inst. Oswaldo Cruz* 92(2):281-286, 1997 constitutes plagiarism. Consequently, we decided to retract this paper.

Adeilton Alves Brandão,
Editor de Publicação

Diffusion Model Applied to Postfeeding Larval Dispersal in Blowflies (Diptera: Calliphoridae)

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This paper presents a diffusion model of larval dispersal specifically for particular aspects of postfeeding larval dispersal from the food source in blowflies. In these organisms the dispersal of immatures includes two groups of larvae: the actively migrating and those that have initiated the pupation process. The diffusion equation in one dimension was modified to incorporate a function which describes the process of larvae to become pupae. The analytical solution of this equation predicts oscillatory dispersal behaviors, which are observed in experimental populations of blowflies.

Key words: *Chrysomya megacephala*- *Chrysomya putoria* - diffusion model - larval dispersal - blowflies

Diffusion models have been extensively employed to investigate dispersal and have provided considerable insight into the dynamics of movement in space and time (Okubo 1980, 1982, 1983, Andow et al. 1993, Clobert et al. 1995). Diffusion models can be written in the simplest form as

$$\frac{\partial u}{\partial t} = D \nabla^2 u$$

where the operator ∇^2 is the Laplacian, t is time, $u(x,y,t)$ is the density in the spatial variables, D is the coefficient of diffusion, and ∇^2 is the Laplacian describing the net population growth and death. Whereas the diffusion equation is a general simplifying assumption for the dispersal process (Andow et al. 1993), which distinct behaviors are incorporated has turned diffusion a powerful tool (Holmes et al. 1994).

(1) has been variously modified to account animal movement toward external stimuli or movement driven by wind or water currents (Helland et al. 1984, Banks et al. 1988), to describe the combination of movement between directions of movement (Holmes 1993), and cases where organisms have a tendency to move away from conspecifics (Gurney & Nisbet 1975, see review in Holmes et al. 1994).

Most studies employing diffusion equations have described movement in adult animals (Andow et al. 1993), but this approach has seldom been used to study dispersal in immatures, whose dispersal has important consequences for the population and community dynamics and genetic structure of populations (de Jong 1979, Roughgarden et al. 1988, Gaines & Bertness 1993). However, the same theoretical results concerning diffusion in adults can be applied to study dispersal in immatures (Broadbent & Kendall 1953). In the present study a diffusion approach is employed to model the form of larval dispersal from the food source based on experimental data from three blowfly species, *Chrysomya megacephala*, *C. putoria*, and *Cochliomyia macellaria*. We take advantage of the flexibility of diffusion models to incorporate behavioral characteristics of dispersal in the larval stage. The model includes the classic diffusion and velocity terms and also a function which describes the process of larvae burying in the substrate to become pupae. The focus on these blowflies is

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motivated by the fact that the two *Chrysomya* species, which are native from the Old World and Australasia, are part of an ongoing invasion of the Americas (Guimarães et al. 1978, Baumgartner & Greenberg 1984). The invading flies have dispersed rapidly throughout the continent and have apparently caused the decline in population numbers of the native species, *C. macellaria* (Guimarães et al. 1979, Guimarães 1984, Greenberg & Szyska 1984).

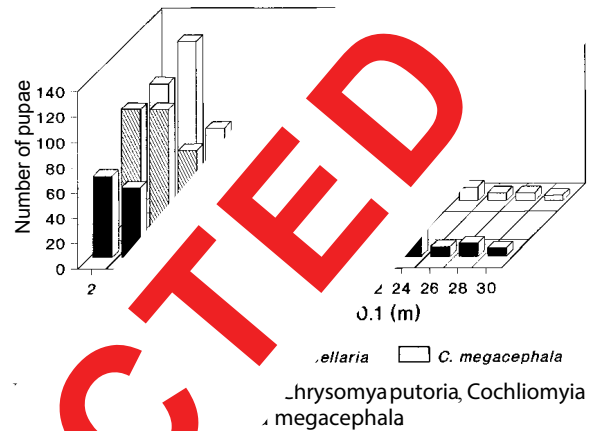
MATERIALS AND METHODS

The process of larval migration from the food source was investigated in laboratory populations of *C. megacephala*, *C. putoria* and *C. macellaria*. Laboratory colonies were founded from specimens collected in the vicinities of the Universidade Estadual de Campinas, SP, Brasil, and these individuals were considered the parental generation. Adult flies were maintained at 25±1°C in cages (30×30×48 cm) covered with nylon and were fed water and sugar ad libitum. Eggs were obtained by providing females with fresh beef liver. Newly hatched larvae, the F₁ generation, were transferred to vials (7.2 cm diameter, 13.8 cm height), containing 100 g of rearing media (Leal et al. 1982). Horizontal dispersal of full grown larvae was separately monitored for each species, deposited in vials at one end of a cardboard box (3.0×12 cm height, 30 cm wide), covered with shavings, 5cm depth at the bottom. Distance travelled was quantified (in cm) as the distance from the starting point at the release point to the point where they buried. Larval dispersal was run, with the larvae in each replicate: *C. macellaria*, 119; *C. putoria*, 119; *C. megacephala*, 119.

Larval dispersal of postfeeding larvae from the food source in calliphoridae, *C. putoria*, and *C. megacephala*. Individuals that are actually dispersed from the site where they begin to bury the food source. Because of this characteristic, larval dispersal can only be investigated after the larvae have pupated. For each species, 100 individuals had pupated in the cardboard box. The number of pupae observed in each 2 cm interval from the release point at one end of the cardboard box. Individual dispersal distances were then measured as the distance travelled by the postfeeding larvae from the point of release to the site of pupation.

The number of pupae found at each interval was plotted against distance travelled by the larvae and the overall pattern that emerges from this data set is similar for the three species in that they

did not move far from the food source, and the number of larvae dispersing decreases with distance (Fig. 1). Nevertheless the two invading species differ remarkably from the native species in the shape of dispersal. In *C. megacephala* and *C. putoria*, the shape of dispersal shows dampened oscillations, whereas in the native species, *C. macellaria*, the number of larvae apparently declines monotonically.



The diffusion model developed takes into account both dispersing individuals and those that have already buried, and is described in one-dimensional space and time as:

$$\frac{\partial c(x,t)}{\partial t} = D \frac{\partial^2 c(x,t)}{\partial x^2} + a \frac{\partial c(x,t)}{\partial x} - h(x,t), \tag{2}$$

where $c(x,t)$ is the concentration of larvae on surface, x is the one-dimensional spatial coordinate, t is time, D is the diffusion coefficient representing the random movement of the larvae and a is a coefficient of proportionality describing the velocity which is taken to be characteristic of each species. The first two terms in equation (2) describe the movement of larvae in the surface of the substrate. The last term in equation (2) is of particular importance in the context of larval migration because it is a function describing the rate of burying of the larvae.

As an approximation to the shape of spread of larvae shown in Fig. 1, the process of larval burying in the substrate is considered to decline exponentially with the distance dispersed by the larvae and to be directly proportional to the difference in concentration of the larvae. These assumptions then lead to

$$h(x,t) = k \left[c_0 \frac{(x^* - x)}{x^*} e^{-\alpha x} - c(x,t) \right] \text{ for } t \in t^* \text{ and } x \in x^*, \tag{3}$$

where k is a constant of proportionality, c_0 is proportional to the initial concentration of larvae, x^* is the maximum distance travelled by the larvae, and t^* indexes the end of dispersal when no larvae remain in the surface. Notice that $c(x,t) \geq 0$ and $h(x,t) \geq 0$ for $t \in t^*$. On the other hand, $t > t^*$, $c(x,t) = h(x,t) = 0$.

The concentration of buried larvae at any point in time, $c^*(x,t)$, is given by

$$c^*(x,t) = \int_0^t h(x,\tau) d\tau \quad (4)$$

Using equation (3) in equation (4) we obtain

$$c^*(x,t) = \frac{kc_0}{x^*} (x^* - x) t e^{-rx} - k \int_0^t c(x,\tau) d\tau \quad \text{for } t \in t^* \text{ and } x \in x^* \quad (5)$$

When $t > t^*$, there are no larvae left in the substrate. In this case,

$$c^*(x,t^*) = \frac{kc_0}{x^*} (x^* - x) t^* e^{-rx} - k \int_0^{t^*} c(x,\tau) d\tau, \quad x \in x^* \quad (6)$$

describes the end of the process of larval dispersal as a result of all larvae having buried in the substrate, which implies

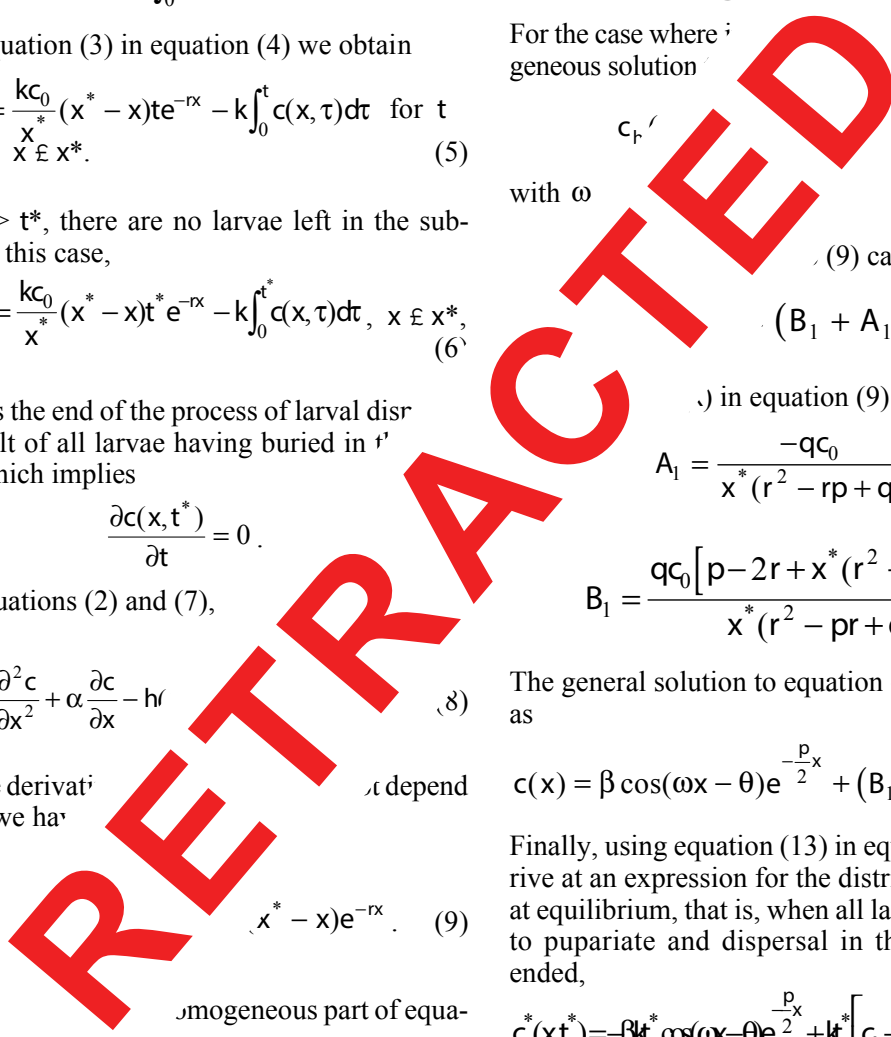
$$\frac{\partial c(x,t^*)}{\partial t} = 0.$$

From equations (2) and (7),

$$D \frac{\partial^2 c}{\partial x^2} + \alpha \frac{\partial c}{\partial x} - hc = 0 \quad (8)$$

Since the derivatives of c depend on time we have

$$\frac{d^2 c}{dx^2} + \alpha \frac{dc}{dx} - hc = 0, \quad x \in x^* \quad (9)$$



homogeneous part of equation (9)

$$= Ae^{\lambda_1 x} + Be^{\lambda_2 x},$$

where λ_i are given by the characteristic

$$\lambda_i = \frac{-p \pm \sqrt{p^2 - 4q}}{2}, \quad i = 1, 2,$$

where $p = \alpha/D$ and $q = k/D$. The real parts of λ_1 and λ_2 are always negative, yielding solutions with exponential decay. The case $p^2 \leq 4q$ is relevant for the understanding of the pattern of dispersal be-

cause the associated complex roots λ_1 and λ_2 describe the damped oscillations observed in our experiments of larval dispersal (Fig. 1). The discriminant in the characteristic equation establishes a relationship between the coefficients α (diffusion, D), the velocity of dispersal, a , and the constant of proportionality k , as follows.

If $p^2 \leq 4q$ we have that

$$\frac{\alpha^2}{D} \leq 4k \quad (10)$$

For the case where $p^2 \leq 4q$, the general homogeneous solution can be written as

$$c(x) = \beta \cos(\omega x - \theta) e^{-rx} + (B_1 + A_1 x) e^{-rx} \quad (11)$$

with ω

where ω can be found as

$$\omega = \sqrt{4q - p^2} \quad (12)$$

where θ in equation (9) we obtain

$$A_1 = \frac{-qc_0}{x^* (r^2 - rp + q)}$$

$$B_1 = \frac{qc_0 [p - 2r + x^* (r^2 - pr + q)]}{x^* (r^2 - pr + q)^2}$$

The general solution to equation (8) is thus found as

$$c(x) = \beta \cos(\omega x - \theta) e^{-rx/2} + (B_1 + A_1 x) e^{-rx} \quad (13)$$

Finally, using equation (13) in equation (6) we arrive at an expression for the distribution of larvae at equilibrium, that is, when all larvae have buried to pupariate and dispersal in the substrate has ended,

$$c^*(x,t^*) = \beta k^* \cos(\omega x - \theta) e^{-rx/2} + k^* \left[c_0 - B_1 - \left(A_1 + \frac{c_0}{x^*} \right) x \right] e^{-rx} \quad (14)$$

DISCUSSION

Insects whose immature stages migrate from the food source in search of pupation sites, characterize a particular system with two populations; one of actively migrating larvae and the other of larvae burying to pupate. The process of larval dispersal is completed when all larvae have buried and no larvae remain dispersing in the substrate. These fundamental aspects were taken into account in our model by adding to the diffusion equation a

function, $h(x,t)$, describing the process of larval burying in the substrate. This function involves biologically important parameters such as the initial concentration of larvae, the maximum distance travelled by the larvae during dispersal and the time taken for dispersal to occur. The form of this function was inferred from the experimental data presented here that suggests that the decrease of the number of pupae with distance from the source is exponential.

The diffusion equation incorporating the burying function yielded an analytical solution (equation 14), which describes the equilibrium distribution of larvae buried in the substrate. This analytical solution was used to compare the dispersal behavior predicted by the diffusion model with the observed data for *C. megacephala*, *C. putoria*, and *C. macellaria*. Equation 14 was fitted to the data using a nonlinear regression whose details are described in the Appendix. Fig. 2 shows the fit of equation 14 to the dispersal data for the three species and demonstrates that the equilibrium distribution given by the diffusion model is consistent with the observed pattern of larval dispersal in the blowflies analyzed here. In other words, the diffusion equation incorporating the burying function seems to account for both the oscillatory and monotonic decrease in the number of pupae with increasing distance from the food source. The oscillatory behavior of dispersal as indicated by equation (10) is apparently the outcome of the interaction between the velocity (a^2), the movement of larvae in these blowflies, the diffusion coefficient (D), and the constant of proportionality (α) at which larvae bury in

Diffusion model was used to address ecological dispersal (Murray 1989, Puccia & Levins 1985) have been particularly useful in adult insects (Kareiva & Case 1993). Nevertheless the dispersal behavior of immature stages, where two groups of larvae are present, those that are actively dispersing and those that have already buried in the substrate, is a first approximation to the complex problem of larval dispersal, which involves factors acting at the individual level such as minimum weight necessary for pupation (Ulyett 1950) and those intervening at the population and community levels including the timing and the velocity with which larvae leave the substrate (Peschke et al. 1987, Blackith & Blackith 1990), the spatio-temporal patterning of predation and parasitism (Norris 1959, Putman 1977, Peschke

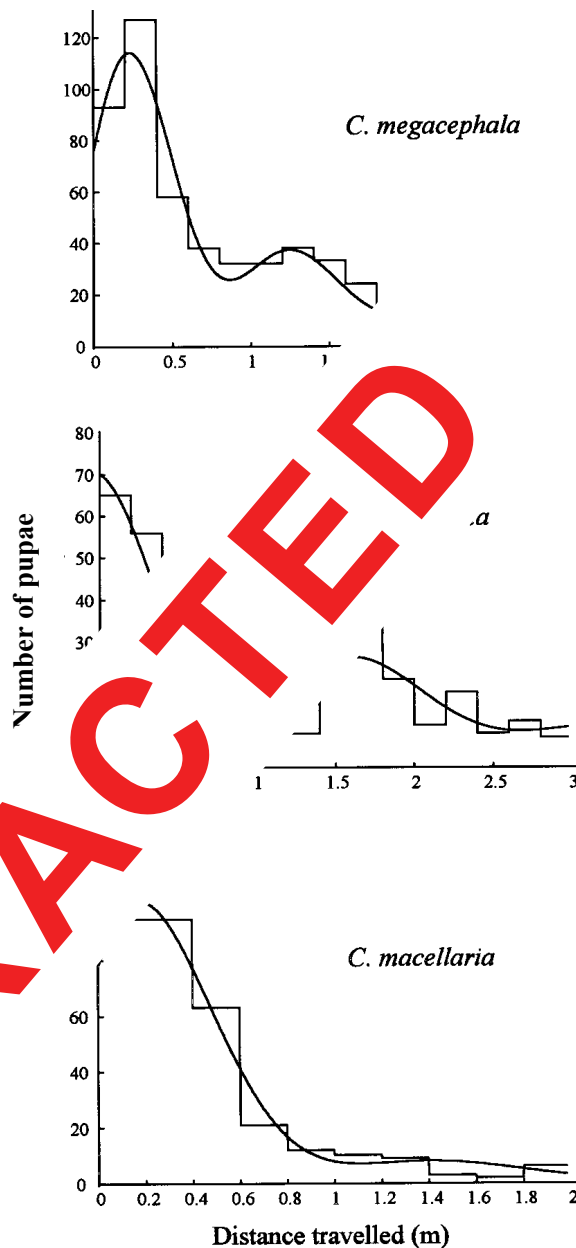


Fig. 2: fit of the diffusion model to dispersal data for *Chrysomya megacephala*, *Chrysomya putoria*, and *Cochliomyia macellaria*. The histograms are based on number of pupae plotted against distance travelled in meters and the curve fitted to the data is based on the solution of the diffusion equation (equation 14).

et al. 1987, Sereno & Neves 1993), the physical makeup of the substrate, and the availability of suitable places to pupate (Kneidel 1984).

The application of diffusion theory has a rich tradition of illuminating mechanisms and processes in population biology (Kareiva 1983), and we believe that the approach presented here follows this tradition. As in other studies (e.g. Kareiva 1983,

Possingham & Roughgarden 1990), simplifying assumptions were made such as the invariance of diffusion coefficients with space, time, and larval density. Nevertheless, the primary purpose of the model presented here was to develop a framework to analyze dispersal of immature insects living in carrion or other ephemeral substrates. The simple passive diffusion model approach taken here does include two relevant features in that it explicitly accounts for the dispersing life-stage and assumes that the dispersal distances are limited, which is commonly regarded as a limitation in diffusion models such as those applied to the dispersal of adult insects (Andow et al. 1993). We believe that the model presented here may prove a useful tool to explore the diffusion dispersal dynamics of organisms such as blowflies and other diptera where the same phase of the dispersing cycle in immatures has two stages, i.e., one actively moving and the other burying in the substrate.

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REFERENCES

- Andow DA, Kareiva PM, Levin SA, Okubo T. Spread of invading organisms: patterns and processes. p. 219-242. In KC Kim, BA McPherson (eds), *Biology of insect pests* John Wiley & Sons, New York.
- Banks HT, Kareiva PM, Zia L. 1990. Studies of insect dispersal using transport equations. *Environ Biol Insect* 21: 105-111.
- Baumgartner DL, Greenberg M. *Chrysomya* (Diptera: Calliphoridae). *J Med Ent* 21: 105-111.
- Blackith RE, Blackith RL. 1979. Dispersions of small corpses. *Environ Biol Insect* 10: 460-465.
- Broadbent SR, Krombein PK. 1980. A random walk of *Trichostema*. *Biometrika* 9: 460-465.
- Christie I. 1980. Modeling of one-dimensional spread of gypsy moth. *Environ Biol Insect* 11: 234.
- de Souza J. 1980. The influence of the distribution of food on the dynamics of a population. *Zool* 29: 33-51.
- de Souza J. 1994. The dynamics of juvenile blowflies: field ecologists must integrate. *Ecol-Entomol* 19: 2435.
- de Souza J, Zyska ML. 1984. Immature stages and biology of fifteen species of Peruvian Calliphoridae (Diptera). *Ann Ent Soc Amer* 77: 488-517.
- Guimarães JH. 1984. Considerações gerais sobre moscas do gênero *Chrysomya* no Brasil. *Agroquímica* 24: 8-12.
- Guimarães JH, Prado AP, Linhares AX. 1978. Three newly introduced blowfly species in Southern Brazil (Diptera: Calliphoridae). *Revta bras Ent* 22: 53-60.
- Guimarães JH, Prado AP, Buralli GM. 1979. Dispersal and distribution of three newly introduced species of *Chrysomya* Robineau-Desvoidy in Brazil (Diptera: Calliphoridae). *Revta bras Ent* 23: 245-255.
- Gurney WSC, Nisbet RM. 1975. The regulation of inhomogeneous populations. *J theor Biol* 52: 441-457.
- Helland IS, Hoff JM, Anderbrant G. 1990. Attraction of bark beetles (Coleoptera: Scolytidae) to a pheromone trap: experiment and mathematical modeling. *Ecol* 10: 723-752.
- Holmes EE. 1993. Are diffusion models a good comparison with telegraph models? *Nat* 142: 403-419.
- Holmes EE, Lewis MA. 1993. Partial differential equations and population dynamics. *SIAM Rev* 35: 36-62.
- Ives AR. 1991. The effect of carrion on blowfly competition. *Environ Biol Insect* 12: 94.
- Kareiva PM. 1990. Mathematical analysis of dispersal: quantifying the influence of dispersal on population dynamics. *Environ Biol Insect* 11: 1-10.
- Krombein PK. 1980. Movement in herbivorous insects: a diffusive diffusion model to mark-recapture experiments. *Oecologia* 57: 322-327.
- Krombein PK, Bouslog AA. 1980. Competition and disturbance in carrion-breeding Diptera. *J Anim Ecol* 49: 1-10.
- Lo AP, Antunes AJ. 1982. Rearing the larva of the blowfly *Chrysomya chloropyga* (Wiedemann) (Diptera, Calliphoridae) on oligidic diets. *Rev bras Entomol* 1: 41-44.
- May JD. 1989. *Mathematical biology*. Springer-Verlag, Berlin, 787 pp.
- Norris KR. 1959. The ecology of sheep blowflies in Australia, p. 514-544. In A Keast, RL Crocker, CS Christian (eds), *Biogeography and ecology in Australia*. Volume 8. Junk, The Hague.
- Okubo A. 1980. *Diffusion and ecological problems: Mathematical models* Springer-Verlag, New York, 245 pp.
- Peschke K, Krapp D, Fuldner D. 1987. Ecological separation, functional relationships, and limiting resources in a carrion insect community. *Zool Jahr Syst* 114: 241-265.
- Possingham HP, Roughgarden J. 1990. Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* 71: 973-985.
- Prout T, McChesney F. 1985. Competition among immatures affects their adult fertility: population dynamics. *Am Nat* 126: 521-558.
- Putman RJ. 1977. Dynamics of the blowfly, *Calliphora erythrocephala* within carrion. *J Anim Ecol* 46: 853-866.
- Roughgarden J, Gaines SD, Possingham HP. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460-1466.
- Sereno FTPS, Neves DP. 1993. Ocorrência natural de microhimenópteros parasitoides de pupas de moscas em aviário. *An Soc Ent Bras* 22: 527-533.
- Uilyett GC. 1950. Competition for food and allied phenomena in sheep-blowfly populations. *Phil Trans R Soc London B* 234: 77-174.

Appendix

Nonlinear Parametric Regression to Estimate the Parameters of Equation (14)

The parameters presented in equation (14) can be grouped and renamed to produce the following nonlinear regression model:

$$c^*(x, t^*) = a_1 \cos(a_2 x - a_3) e^{-a_4 x} + (a_5 + a_6 x) e^{-a_7 x}.$$

For the three species *C. megacephala*, *C. putoria* and *C. macellaria*, the objective is to determine the corresponding set of parameters $\{a_1, \dots, a_7\}$ from the experimental data (x_i, y_i) , $i=1, \dots, N$. Here, x (the explanatory variable) denotes the distance travelled, y (the response variable) denotes the corresponding number of buried larvae, and N is the number of discrete distances considered (Fig. 1).

The set of parameters $\{a_1, \dots, a_7\}$ can be estimated through nonlinear parametric regression, generally described as the minimization of the mean square error:

$$\min_{a_1, \dots, a_7} \frac{1}{2} \sum_{i=1}^N (c^*(x_i, t^*) - y_i)^2 = \min_{a_1, \dots, a_7} J(a_1, \dots, a_7).$$

Denoting the gradient of $J(\cdot)$, the vector of derivative terms, by $\tilde{\nabla} J(\cdot)$, we have:

$$\nabla J(a_1, \dots, a_7) = \begin{bmatrix} \frac{\partial J}{\partial a_1} \\ \vdots \\ \frac{\partial J}{\partial a_7} \end{bmatrix} = \sum_{i=1}^N (c^*(x_i, t^*) - y_i) \begin{bmatrix} \frac{\partial c^*}{\partial a_1} \\ \vdots \\ \frac{\partial c^*}{\partial a_7} \end{bmatrix}$$

where

$$\begin{aligned} \frac{\partial c^*(x, t^*)}{\partial a_1} &= \cos(a_2 x - a_3) e^{-a_4 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_2} &= -x \sin(a_2 x - a_3) e^{-a_4 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_3} &= \sin(a_2 x - a_3) e^{-a_4 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_4} &= -x a_1 \cos(a_2 x - a_3) e^{-a_4 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_5} &= e^{-a_7 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_6} &= x e^{-a_7 x} \\ \frac{\partial c^*(x, t^*)}{\partial a_7} &= -x(a_5 + a_6 x) e^{-a_7 x} \end{aligned}$$

$$\frac{\partial c^*(x, t^*)}{\partial a_4} = -x a_1 \cos(a_2 x - a_3) e^{-a_4 x}$$

$$\frac{\partial c^*(x, t^*)}{\partial a_5} = e^{-a_7 x} \quad \frac{\partial c^*(x, t^*)}{\partial a_6} = x e^{-a_7 x}$$

$$\frac{\partial c^*(x, t^*)}{\partial a_7} = -x(a_5 + a_6 x) e^{-a_7 x}$$

We are now prepared to estimate the parameters $\{a_1, \dots, a_7\}$ through the following iterative algorithm:

Initialization: Set $\{a_1, \dots, a_7\}$ to some initial values $\{a_1^0, \dots, a_7^0\}$ and an arbitrary tolerance $\epsilon > 0$.

Step 1: Compute the gradient $\tilde{\nabla} J(a_1^0, \dots, a_7^0)$.

Step 2: Determine the step size α_k such that the new parameters $\{a_1^{old}, \dots, a_7^{old}\}$ are given by

$$a_i^{new} = a_i^{old} - \alpha_k \sigma \frac{\partial J}{\partial a_i}, \quad i = 1, \dots, 7,$$

$$J(a_1^{new}, \dots, a_7^{new}) < J(a_1^{old}, \dots, a_7^{old});$$

If $J(a_1^{new}, \dots, a_7^{new}) > \epsilon$, return to step 1.

When the algorithm converges, the application of the algorithm for each species gives:

C. megacephala: $a_1 = 60.0872$; $a_2 = 5.9472$; $a_3 = 1.8544$; $a_4 = 1.4474$; $a_5 = 93.2371$; $a_6 = 26.6265$; $a_7 = 1.1573$

C. putoria: $a_1 = 34.8800$; $a_2 = 3.6839$; $a_3 = 0.1634$; $a_4 = 0.9026$; $a_5 = 35.7570$; $a_6 = 13.9524$; $a_7 = 0.6872$

C. macellaria: $a_1 = 85.6961$; $a_2 = 4.6069$; $a_3 = 1.6826$; $a_4 = 2.3604$; $a_5 = 87.6527$; $a_6 = 17.6138$; $a_7 = 1.9009$