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Allee Effect in Exotic and Introduced Blowflies

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Abstract

We combined two models to investigate the theoretical dynamics of five exotic and native blowfly species in response to the Allee effect by using demographic parameters estimated from experimental populations. Most of the results suggest stabilization of dynamic behavior in response to the Allee effect. However, the results depended on the magnitude of the demographic parameters of each species, and also indicated chaotic fluctuations and limit cycles. The results are discussed in the context of larval aggregation, an important biological process for blowflies, which naturally incorporates the Allee effect.

Introduction

Larval aggregation is an important biological mechanism that takes place during the initial period of development in blowflies (Goodbrod & Goff 1990, Reis *et al* 1999). After the eggs hatch, first-instar larvae tend to remain aggregated inside the food substrate, in order to increase the efficiency of the feeding process by secreting saliva and proteolytic enzymes (Goodbrod & Goff 1990, Reis *et al* 1999). These enzymes act together with bacteria present in the food substrate to decompose food (Hobson 1932, Mackerras 1933, Mackerras & Freney 1933, Goodbrod & Goff 1990).

This process is essential to create initial conditions for the larvae to exploit food, and has direct implications for the survival and fecundity of the species (Goodbrod & Goff 1990, Gião & Godoy 2007). It is a specific case of the Allee effect, because it requires a minimum number of larvae to decompose the food substrate and make the population viable (Wertheim *et al* 2002).

The Allee effect can be understood as a positive relationship between fitness and density of conspecifics, providing advantages to the individual (Stephens *et al* 1999). It reflects the mechanism of isolation, resulting in a benefit of aggregation, since for some densities the positive-density dependence dominates, but for other densities it does not (Stephens *et al* 1999). For example, the Allee effect may operate in mating systems, not only of obligate co-operators but also of other species (Boukal & Berec 2002). In these systems, the spatial distribution generally determines the number of females that males can monopolize (Allee 1931, 1938, Boukal & Berec 2002). Other studies have discussed the diversity of mechanisms of the Allee effect (Amarasekare 1998, Dennis 1989, Courchamp *et al* 1999), including beneficial effects such as mitigation of predation, antipredator vigilance, social thermoregulation, reduction of inbreeding, and exploitation of resources (Stephens *et al* 1999, Liebhold & Tobin 2008).

The exotic blowfly species (Diptera: Calliphoridae) *Chrysomya albiceps* (Wiedemann 1819), *C. megacephala* (Fabricius 1794), and *C. putoria* (Wiedemann 1830) were introduced into Brazil about 30 years ago, and have displaced native species such as *Cochliomyia macellaria* (Fabricius 1775) and, to a lesser extent, *Lucilia eximia* (Wiedemann 1819) (Guimarães *et al* 1978, Silva *et al* 2003). This episode has motivated several studies on the population dynamics of introduced and native blowfly species, in an attempt to better understand their ecological patterns of fluctuation as well as the potential impact of biological invasion on the structure of the local fauna (Reis *et al* 1996, Serra *et al* 2007). The most recent studies include investigations of population dynamics by connecting laboratory experiments with mathematical models, focusing on density dependence, spatial structure, and stochasticity (Castanho *et al* 2006, Serra *et al* 2007).

Blowfly populations have been investigated with experiments and mathematical modelling since the classical studies on resource limitation carried out by Nicholson (1954, 1957) and revisited by Gurney *et al* (1980). The results obtained by Nicholson (1954, 1957) have been regularly analyzed because of the cyclic tendency found in the blowfly populations. The causes of cycles in insect populations have received considerable attention from ecologists and entomologists because they are often associated with density-dependent mechanisms (Hassell 1975, Muller 1986). A density-dependent mathematical model developed by Prout & McChesney (1985) to study population dynamics in experimental populations of *Drosophila melanogaster* has been successfully employed in studies of blowfly population dynamics (Godoy *et al* 2001, Godoy 2007, Serra *et al* 2007).

The model has raised important points in the context of blowfly biological invasions. The analysis indicates that the exotic species introduced into the Americas from the Old World exhibit dynamic behavior described by a two-point limit cycle, characterized by a fluctuation between two points. The native species show a monotonic stable equilibrium, described by a constant population size (Godoy *et al* 2001, Silva *et al* 2003).

Previous investigations on the abundance of exotic and native blowfly species in the Americas reveals that if on the one hand, exotic species have successfully expanded their geographic area, on the other hand, native species have become much less abundant in all areas surveyed (Baumgartner & Greenberg 1984, Moura *et al* 1997, Centeno *et al* 2002, Carvalho *et al* 2004). These observations indicate that the demographic attributes of the several species are strongly influenced by interaction mechanisms.

In spite of the importance of these findings, an important point about the invasion has received no attention until now. The colonization process in blowflies differs according to areas and species, i.e., the four introduced species have reached different places, at different times, and with very different abundances (Guimarães *et al* 1978, Souza & Linhares 1997, Tomberlin *et al* 2001, Wolff *et al* 2001, Rosati & VanLaerhoven 2007). The most interesting example is the invasion of Central and North America by *C. rufifacies* and the introduction of *C. albiceps* into South America (Wells & Sperling 1999). The two species are ecologically similar, but have not overlapped in the same areas (Wells & Sperling 1999). Even among the species introduced into South America, their distribution and colonization differ among areas (Prado & Guimarães 1982, Carvalho *et al* 2000).

There is no specific study yet designed to investigate the causes of these differences, but there is evidence indicating that they may be associated with ecological factors governed by density dependence, such as demography, and interactions (Wells & Sperling 1999, Godoy *et al* 2001). Density dependence is a very influential mechanism in populations and acts on life-history parameters in insects (Muller 1986). The theoretical structure of the model employed in the previous studies includes negative density-dependence and delay effects (Prout & McChesney 1985). However, the Allee effect, recognized as a positive density-dependent effect, is not incorporated into this formulation yet.

Fowler & Ruxton (2002) exploited the Hassell model, including the Allee effect, and assumed that the contribution of an individual to the next generation is given by the Hassell function multiplied by an Allee effect. The Hassell function describes the effect of population size on individual reproductive output, by considering the reproductive potential in the absence of competition, the population size associated with the carrying capacity of the habitat, and the strength and form of competition (Hassell 1975). The authors demonstrated the changes that population dynamics could undergo when a factor representing an Allee effect is introduced.

The Allee effect has conventionally been investigated in an attempt to analyze low densities of endangered species (Tobin *et al* 2009). However, exotic species are generally at low density during an invasion process, the conditions in which the Allee effect takes place (Tobin *et al* 2009). The mathematical modeling scenario previously studied in blowflies indicates that exotic species exhibit high demographic values, tending to exhibit cyclic dynamics, and native species trend toward stability (Godoy *et al* 2001, Serra *et al* 2007).

In the present study, we used the Prout & McChesney model combined with the Fowler & Ruxton Allee-effect component to investigate the theoretical dynamic behavior of five native and exotic blowfly species, *L. eximia*, *C. macellaria*, *C. megacephala*, *C. albiceps*, and *C. putoria*. We believe that the Allee effect may impact the distribution of insects living in ephemeral substrates such as carcasses, influencing their ecological patterns of dynamic behavior important to their persistence.

Our main concern about this point is, could the Allee effect significantly influence the blowfly population dynamics, stabilizing or not populations of both exotic and native species? Native blowfly species in Brazil have apparently shown strong resistance to biological invasion since the exotic species introduction, in spite of their decline in population numbers (Serra *et al* 2007). This population performance could be associated with the stability previously mentioned.

The primary objective of this study was to investigate the theoretical influence of the Allee effect on the quantitative and qualitative behavior of native and exotic blowfly species. Secondly, we were interested to know how fecundity and survival can change the stability of population in association with different magnitudes of the Allee effect.

Material and Methods

Mathematical models

A mathematical model developed by Prout & McChesney (1985), combined with the model of Fowler & Ruxton (2002), was used to show how the theoretical variation of the strength of the Allee effect can influence the dynamic behavior of *L. eximia*, *C. macellaria*, *C. albiceps*, *C. megacephala*, and *C. putoria*. The Prout & McChesney (1985) model is based on a finite difference equation that models population dynamics, taking into account the number of immatures, eggs, or larvae in succeeding generations, n_{t+1} and n_t. The model also incorporates two density-dependent processes, fecundity (F) and survival (S), as a function of the density of immatures, n_t, which were estimated from experimental populations (Table 1). The

Table 1 Mean daily fecundity and survival of blowfly larvae at different densities

	Survival		Fecundity		
Density	n	Mean	n	Mean	Sd
L. eximia					
100	2	91.5	32	6.53	1.11
200	2	84	32	7.03	1.58
400	2	59	32	6.14	1.21
600	2	38	31	5.29	0.55
800	2	36	32	4.05	0.71
C. macellaria					
200	2	62.75	43	18.47	2.66
400	2	58.12	44	15.43	2.15
600	2	50.25	40	13.66	1.85
800	2	30.25	41	12.23	1.18
1000	2	36.7	44	10.84	1.64
1200	2	16.45	31	9.05	1.59
1400	1	21.42	8	10.85	0.84
1600	1	14.56	9	10.38	0.69
1800	1	16.77	29	7.23	1.56
2000	1	12.25	15	9.65	1.33
C. albiceps					
100	2	54	25	26.46	4.13
200	2	34	54	21.02	2.96
400	2	12	29	19.24	2.97
600	2	7.2	17	15.91	3.15
800	2	6.9	22	13.63	2.87
1000	2	2	10	8.57	2.43
C. megacephala					
200	2	66.5	47	21.79	3.62
400	2	55.1	52	20.4	3.63
600	2	30	31	17.76	3.81
800	2	34.94	58	13.84	3.21
1000	2	27	43	13.28	2.76
1200	2	23.24	53	10	3.06
1400	1	4.28	11	7.16	1.45
1600	1	4.06	11	7.65	2.11
1800	1	4.55	19	9.07	2.13
2000	1	10.3	18	9.65	1.62
C. putoria					
200	2	66.75	60	17.7	2.11
400	2	44	59	15.49	3.12
600	2	49.91	59	15.92	2.47
800	2	51.37	59	10.97	2.33
1000	2	25.1	57	13.07	3.1
1200	2	19.41	60	8.64	2.36
1400	1	9.35	30	7.39	1.8
1600	1	7.18	30	7.53	1.26
1800	1	18	29	8.82	1.51
2000	1	4.65	30	6.79	1.58

n (survival): number of vials examined.
n (fecundity): number of females dissected.

recursion is expressed by the non-linear finite difference equation

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

where F^* and S^* are the intercepts in the exponential regression analysis of fecundity and survival as a function of larval density (Table 2). These parameters describe the theoretical values for maximum fecundity and survival respectively. The factor ½ indicates that only half of the population consists of adult females that contribute eggs to the next generation. The values of *f* and *s* are regression coefficients that estimate the slope of fecundity and survival on the density of immatures (Table 2).

Table 2 Parameters for the regression analysis of fecundity and survival on larval densities

Lucilia eximia	Fecundity	Survival
Intercept in *y*	9.08	1
Regression coefficient	0.01	0.0014
t value	17.3	0.94
r^2	0.65	0.92
Anova	296.64	115.71
Cochliomyia macellaria	Fecundity	Survival
Intercept in *y*	18.33	0.788
Regression coefficient	0.000477	0.000985
t value	25.05*	9.57*
r^2	0.67	0.86
Anova	628*	92*
Chrysomya albiceps	Fecundity	Survival
Intercept in *y*	27.11	0.565
Regression coefficient	1×10^{-3}	3×10^{-3}
t value	18.36*	5.48*
r^2	0.68	0.75
Anova	337*	30*
Chrysomya megacephala	Fecundity	Survival
Intercept in *y*	23.49	0.916
Regression coefficient	0.000624	0.00148
t value	21.64*	6.78*
r^2	0.58	0.76
Anova	468*	46*
Chrysomya putoria	Fecundity	Survival
Intercept in *y*	19.32	0.970
Regression coefficient	0.000569	0.00135
t value	26.44*	8.3*
r^2	0.60	0.83
Anova	699*	69*

*P < 0.001

The exponential function was used because it fits the blowfly data as well as or better than linear and hyperbolic functions (Godoy *et al* 1993, Von Zuben *et al* 1993). In addition, linear regression produces steeper slopes (in absolute magnitude) that in turn produce larger eigenvalues, which do not accurately describe the model dynamics at carrying capacity (Mueller 1986). 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).

A component of fitness that increases with population size, termed the Allee effect (Fowler & Ruxton 2002), is expressed by

$$G(N_t) = \left(1 - A\exp\left(\frac{-an_t}{\gamma}\right)\right), \qquad (2)$$

where *A* and *γ* are positive constants, and *A* is restricted to [0,1]. In this specific formulation, it was assumed that *A* is a strength parameter of the Allee effect and *γ* is the population subject to the Allee effect. Parameter *a* is a coefficient to scale the population size to the carrying capacity. In a blowfly context, *A = 0* means no Allee effect, i.e., the larval density of blowflies is above a minimum necessary to make the population viable. With *A = 1* the larval population is not able to become adults.

The new equation, including both the Allee effect and the demographic functions *F* and *S*, is given by

$$n_{t+1} = \frac{1}{2} F^* S^* e^{-(f+s)^{n_t}} n_t \left(1 - A\exp\left(-an_t/\gamma\right)\right) \qquad (3).$$

Using Matlab 7.0 (Hanselman & Littlefield 1997), simulations were run based on bifurcation theory (May & Oster 1976). Then, the results obtained were analyzed by bifurcation diagrams. A bifurcation diagram is a way of summarizing ranges of dynamic behaviors, since it describes locations and stability properties of periodic states (Vandermeer & Goldberg 2003). The variation of parameters may cause qualitative changes in populations, which can be viewed as different patterns of fluctuation or stability.

In bifurcation diagrams, the horizontal axis gives the parameter value (*A* in the current study) and the vertical axis represents the magnitudes of the steady state of the equation. Bifurcations represent new steady states (Vandermeer & Goldberg 2003). Two stable branches indicate the existence of a stable period 2 orbit, four stable branches a period 4 orbit, and so on. In the simulations we used the values obtained from Table 2, which were statistically estimated from data acquired in laboratory experiments (Table 1).

Experiments

Laboratory populations of *L. eximia*, *C. macellaria*, *C. albiceps*, *C. megacephala*, and *C. putoria* were founded from specimens collected from the Campus of the Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. Adult flies were maintained at 25 ± 1°C in cages (30 x 30 x 48 cm) covered with nylon, and were fed water and sugar *ad libitum*.

Eggs were obtained by providing females with fresh beef liver. Larval densities (Table 1) were established using newly hatched larvae in 50 g of rearing medium prepared according to Leal *et al* (1982), with two replicates. Fecundity was estimated by randomly removing 30 females per replicate and counting the number of eggs per female. Survival was estimated as the number of adults emerging from each vial. The data presented in Table 1 were obtained from an experimental setting of increasing larval densities designed to estimate fecundity and survival as decreasing functions of the density.

With the results obtained from the experiments, exponential regressions were performed in order to analyze the decreasing functions of density, survival, and fecundity, and to obtain the parameters to be used in the Prout equation. The estimates of the parameters resulted in two theoretical values for fecundity (F) and survival (S). These values are the intercept of the regression. The regression coefficients (s) and (f) estimate the variation of survival and fecundity, respectively, as a function of density. The results of this analysis are shown in Table 2. It is important to emphasize that the F and S estimates were obtained in laboratory experiments designed to study intraspecific competition without considering the Allee effect. Then, the densities used in the experiments were suitable only to provide negative density-dependence. The Allee effect was taken into account only during simulations run with the combination between Prout & McChesney (1985) and Fowler & Ruxton (2002) models.

In order to investigate the magnitude of parameter values required to exhibit different dynamic behaviors, such as stable equilibrium, cycles, and unpredictable oscillations, arbitrary values of F and S were used in the simulations. The values were employed taking into account the maximum and minimum boundaries of survival and fecundity observed in natural populations (Ullyett 1950, Reigada & Godoy 2005, Gião & Godoy 2006, Riback & Godoy 2008). This procedure allowed us to determine the critical values for a change of equilibrium in each species. The constants a and γ were the same values employed by Fowler & Ruxton (2002), $\gamma = 1$ and $a = 0.005$.

The values used by Fowler & Ruxton (2002) guaranteed values that would produce chaotic dynamics in the equivalent Hassell model. Hence, a gradual introduction of these components resulted in stabilization of the dynamics, a typical result found with an influence from the Allee effect. An evaluation of the sensitivity in all parametrical space of the Fowler & Ruxton parameters (γ and a) was performed in order to understand how this can extrapolate into qualitative changes in the equilibrium dynamics of experimental populations of the five blowfly species, and consequently what are the consequences for the population viability.

The sensitivity analysis was conducted by employing the bifurcation theory following the procedures indicated by May & Oster (1976), with results indicating no qualitative change in all parametrical space of γ and a, and viability for all blowfly species. The results found guarantee that the Fowler & Ruxton (2002) parameter values applied to γ and a in this study do not influence qualitatively the dynamic behaviors observed in the current study and the quantitative changes observed do not drive the blowfly populations to extinction.

Results

Bifurcation diagrams obtained from experimentally estimated parameters

Lucilia eximia and *C. macellaria* exhibited a monotonic stable equilibrium within the entire parametric space of A, with *L. eximia* trending to extinction for values of A higher than 0.8 (Fig 1a, b). *Chrysomya albiceps* showed a two-point limit cycle for initial values of A, and a stable equilibrium above 0.15 (Fig 1c). *Chrysomya megacephala* and *C. putoria* exhibited a two-point limit cycle during the entire parametric space of A (Fig 1d, e).

Bifurcation diagrams obtained from varying parameters (native species)

The neighborhood of fecundity and survival was investigated by varying parameter values in the simulations, in order to determine what demographic values are necessary to find the exact point of bifurcation, taking into account the Allee effect. For high values of fecundity in *L. eximia*, twice the experimentally obtained value, the bifurcation diagram showed a two-point limit cycle for the initial values of A and a stabilizing effect for values of A higher than 0.25 (Fig 2a). A very slight increase of fecundity in *C. macellaria*, from 18.33 to 18.65, was sufficient to show the bifurcation point, where the two-point limit cycle changed to stable equilibrium (Fig 2b). A decrease in survival from the estimate value of 1 (100% survival) produced stable equilibrium, but an increase in the survival of *C. macellaria* from 0.78 to 0.8 was also sufficient to show the bifurcation, trending to stability for A values closer to 1 (Fig 2c).

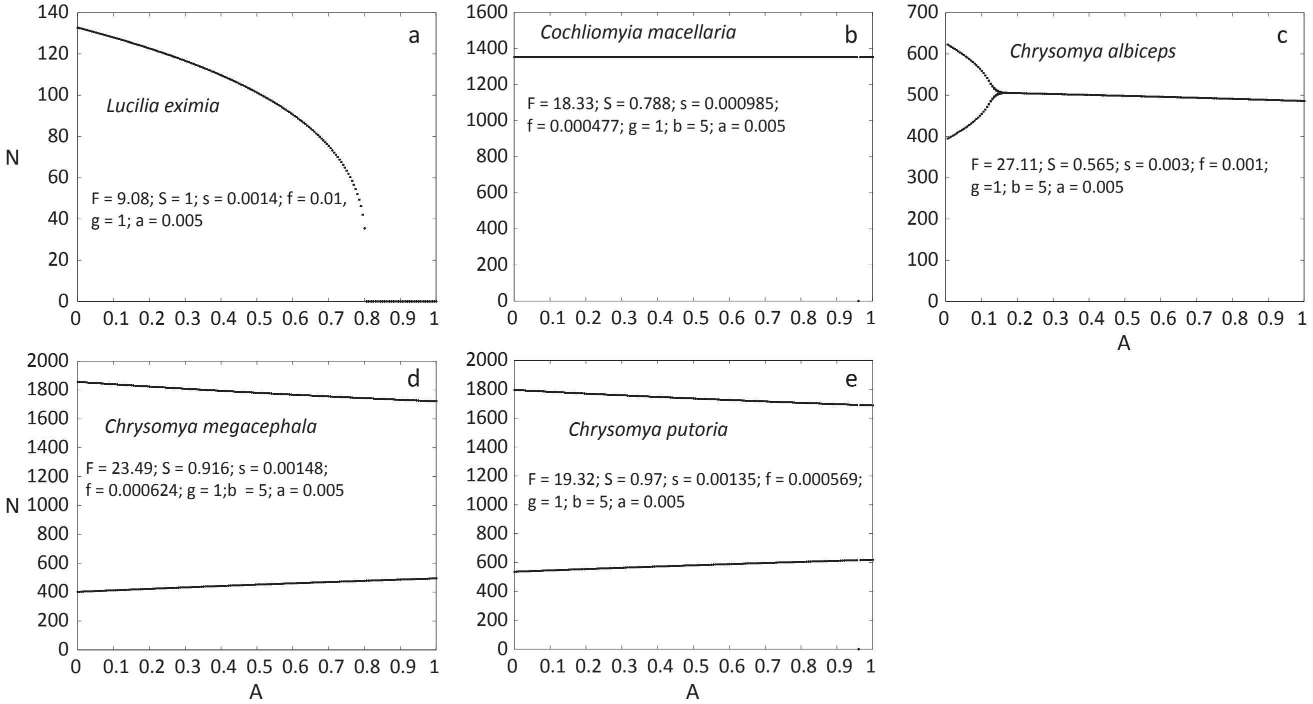

Fig 1 Bifurcation diagrams for experimentally obtained values, with the parametric space of *A* (Allee effect) for a) *Lucilia eximia*; b) *Cochliomyia macellari*a; c) *Chrysomya albiceps*; d) *Chrysomya megacephala*; e) *Chrysomya putoria*.

Bifurcation diagrams obtained from varying parameters (exotic species)

Increasing the fecundity of *C. albiceps* from 27.11 to 48, it was possible to observe a bifurcation diagram containing two- and four-point limit cycles (Fig 2d). The same result was obtained by changing survival from 0.56 to 1 (Fig 2e). The increase of fecundity in *C. megacephala* and *C. putoria* produced destabilizing effects for increasing values of *A*, with results indicating a succession of bifurcations leading to unpredictable fluctuations, alternating with periodicity windows (Fig 2f, h). Nevertheless, *C. putoria* showed periodic behaviors at the parametric extremes of *A*, differing from *C. megacephala*, which showed periodicity only for initial values of *A*.

Because the survival values of *C. megacephala* and *C. putoria* were very close to 1 (0.91 and 0.97 respectively), an increase in survival would produce no qualitative change in the dynamic behavior of the two species. Otherwise, a decrease in survival in *C. megacephala* and *C. putoria* produced a monotonic stable equilibrium (Fig 2g, i), leading both species to the same result obtained for *C albiceps* in the simulations with experimental data.

Discussion

In *L. eximia* and *C. macellaria*, only the arbitrary increase in fecundity resulted in the appearance of two behaviors, a two-point limit cycle and a stable equilibrium. This result can be explained by considering the values of λ for both species, which are more distant from 1 compared to the values found for *C. albiceps* (Reis *et al* 1996, Silva *et al* 2003). The λ value has a critical change when it is equal to 1, i.e., when λ is lower than 1 the result is a monotonic stable equilibrium, but if λ is higher than 1 the result is a limit cycle (Prout & McChesney 1985). *Lucilia eximia* requires at least twice its estimated value to exhibit changes, since its experimentally obtained fecundity was very low. Nevertheless, natural populations of this species show fecundity values significantly higher than the numbers found in laboratory, justifying the arbitrary change in the simulations (Gião & Godoy 2006).

Cochliomyia macellaria had been previously recognized as a species capable of exhibiting only a monotonic stable equilibrium, but in our simulations it requires only a slight change in the fecundity (*F*) value to exhibit the two-point limit cycle, i.e. from *F* = 18.33 to *F* = 18.65. This result was found because although *λ* is less than 1, it is very close to 1, differing from *C. albiceps*, a species that exhibits *λ* slightly higher than 1 (Reis *et al* 1996, Godoy *et al* 2001).

By using the experimentally obtained demographic values, only *C. albiceps* showed more than one type of dynamic behavior, i.e., a two-point limit cycle and a stable equilibrium. This result could be understood as a response to its eigenvalue (λ), which is very close to 1, but higher than 1 (Godoy *et al* 2001), making the species prone to changes in terms of equilibrium. This result suggests that the Allee effect was responsible for the

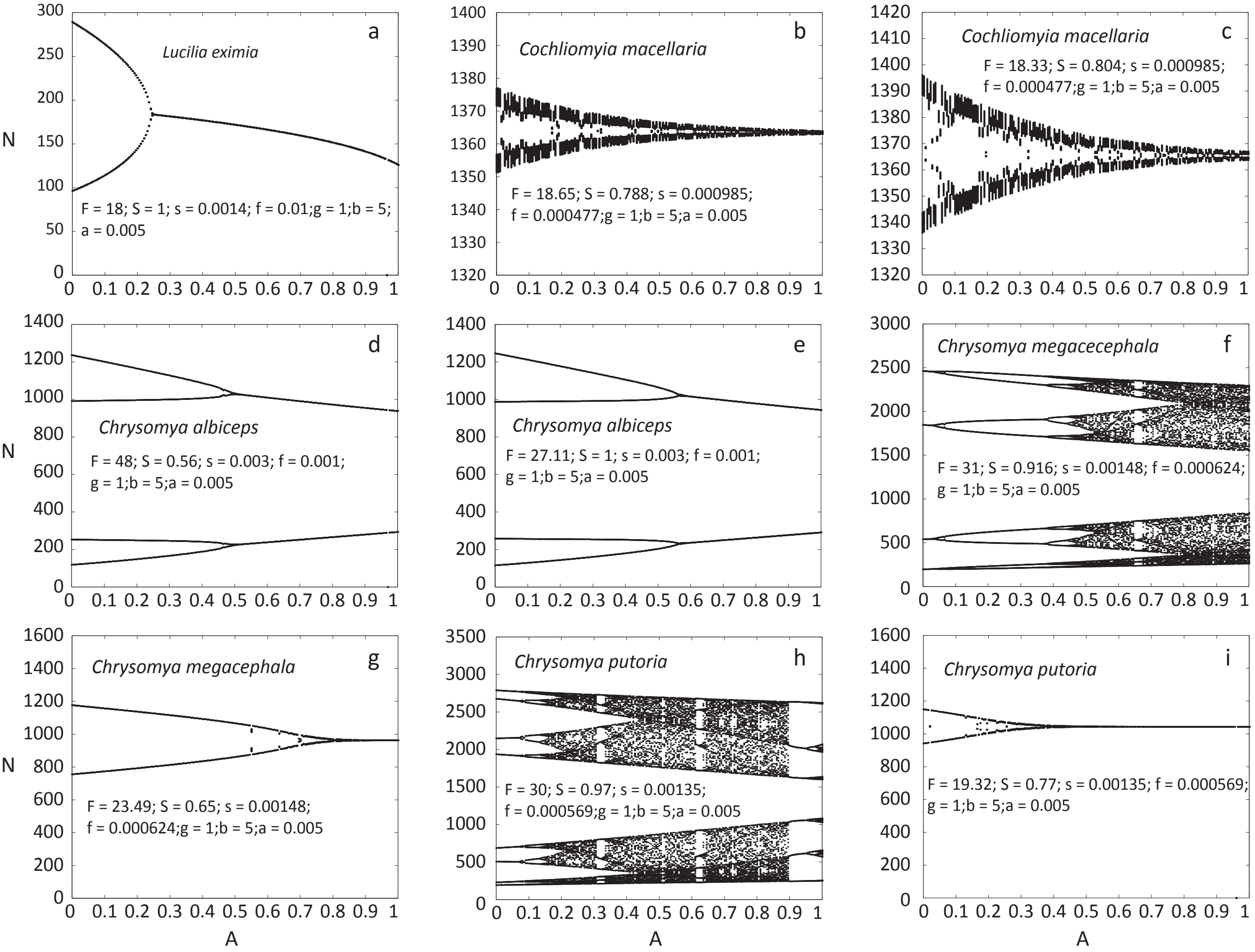

Fig 2 Bifurcation diagrams for arbitrarily set values, with the parametric space of *A* (Allee effect) for a) *Lucilia eximia*; b, c) *Cochliomyia macellaria*; d, e) *Chrysomya albiceps*; f, g) *Chrysomya megacephala*; h, i) *Chrysomya putoria*.

change in λ and consequently for the appearance of the two different equilibria. These findings make sense if the results are compared to the previous studies by Godoy *et al* (2001), where only one type of dynamic behavior was found.

Chrysomya albiceps differs from the other species in several respects. It is cannibal and predator during larval stage, and its predatory habit has strongly influenced the current Brazilian necrophagous fauna (Faria *et al* 1999). Its strategy to obtain food is probably different from the other blowflies, in response to larval habits, which could affect the larval aggregation process, making the species more prone to the Allee effect than other species (Faria *et al* 2007). The survival of *C. albiceps* was probably influenced by cannibalism. This habit is certainly the reason for the difference between its survival pattern and the other blowfly species. Cannibalistic behavior could explain, at least in part, the poor performance of *C. albiceps* for intraspecific densities.

The variation of fecundity in *C. albiceps*, i.e. the increase in fecundity, resulted in only two types of behavior, differing from *C. megacephala* and *C. putoria*, which showed a cascade of bifurcations. There is a very interesting point here. The changes in fecundity resulted in different patterns of bifurcation for *C. albiceps* and the other two *Chrysomya* species. In *C. albiceps*, cycles appeared first, subsequently trending to stability. For *C. megacephala* and *C. putoria* the result was the reverse, starting with periodic cycles, but changing to more complex cycles and chaos, including the occurrence of periodicity windows. Thus, for *C. albiceps* the increase of the Allee effect is a stabilizing strength, but for *C. megacephala* and *C. putoria* it is not.

These results probably reflect the differences among these species with respect to demographic parameter values. However, the differences can only be observed by analyzing the combination of the two mathematical models. In spite of their biological differences, *C. albiceps* seems closer to *L. eximia* and *C. macellaria* than the other *Chrysomya* species, at least in terms of susceptibility to changes from cyclic to stable behavior. Two levels of stability were observed by Godoy *et al* (2001), with implications for the equilibrium dynamics of these species. High fecundity and survival values led to eigenvalues higher than 1.3, exhibited by *C. megacephala* and *C. putoria*, and low fecundity and survival values led to eigenvalues lower than 1.3, exhibited by *L. eximia*, *C. macellaria*, and *C. albiceps* (Godoy *et al* 2001). The combination found between high and low demographic values, associated with different values of *A* (Allee effect), may result in different patterns of bifurcation, explaining the results observed for exotic and native blowflies in this report. For survival, all species underwent a stabilizing effect with increasing values of this parameter, showing a monotonic stable equilibrium.

Although the laboratory data do not wholly reproduce the parameter values in natural populations, the results found represent a good approach for the blowfly system. In addition, the results from previous studies designed to investigate the variation of demographic parameters in natural populations of blowflies show a spectrum of parameter values compatible with the numbers used in this study (Reigada & Godoy 2005, Gião & Godoy 2006, Riback & Godoy 2008).

Blowflies are insects that easily exhibit cyclic fluctuations (Nicholson 1954, 1957, Von Zuben *et al* 1993), a behavior characterized by demographic parameter values of high magnitude (Edelstein-Keshet 1988). Unfortunately there is no comparable long-term study focusing on real-world observations of population patterns. However, the spectrum of oscillations in natural populations of exotics is probably wider than native species because of the magnitude of their survival and fecundity in natural conditions (Ullyett 1950, Reigada & Godoy 2005, Gião & Godoy 2006, Riback & Godoy 2008).

In a previous study, Godoy *et al* (1996) showed that the succession of increases both in fecundity and survival results in destabilizing the population equilibrium. On the other hand, several studies have shown that the Allee effect influences populations with a stabilizing effect on their dynamics (Scheuring 1999, Fowler & Ruxton 2002). It was clear in our study that the Allee effect may invert tendencies toward both stabilizing and destabilizing populations, and this depends on the magnitude of and combinations among demographic parameters.

The inversions caused by the Allee effect address questions of fundamental importance in the context of biological invasions, since the ability of invader organisms to colonize new niches depends essentially on the magnitude of their demographic parameters and the strength of the Allee effect. On the other hand, for native species, the presence of other species that share the same resources may cause serious population declines, decreasing population sizes and increasing the possibility of local extinction (Reis *et al* 1996, Serra *et al* 2007).

In blowflies, the level of larval aggregation is directly associated with the females' oviposition behavior. Blowfly females usually lay eggs in batches of 100-300, frequently among eggs of several different species (Smith 1986). The larval distribution in carcasses depends on the dispersal of the females, and can have implications for their population dynamics (De Jong 1976, Blackith & Blackith 1990, Turchin 1998). However, the initial larval density, the factor that is subject to the Allee effect, also depends on the existing assemblage of blowfly species, because the previous presence of some species, as for example the predatory larvae of *C. albiceps*, significantly influences the diversity and abundance of blowflies (Gião & Godoy 2007). Hence, for blowflies, the Allee effect depends on a set of factors important to the larval aggregation, such as: carrion size, attractiveness of substrates, ovarian development stage in females, and number of eggs laid.

The strategies of exploiting food resources differ significantly in blowflies (Goodbrood & Goff 1990, Godoy *et al* 1996, Faria *et al* 1999). Intra- and interspecific interactions in blowflies have been investigated, and have suggested different larval aggregation patterns, probably associated with the type of food item and the stage of larval development (Reis *et al* 1999, Gião & Godoy 2007). We believe that the blowfly system deserves special attention, considering all these aspects, in an attempt to analyze which exogenous and endogenous forces might explain the inter- and intraspecific variability in terms of population dynamics of exotic and native blowfly species.

We have shown that the differences in terms of population behavior found among blowfly species play an important role in determining dynamics, resulting in clear population patterns. Several studies have documented the causes of Allee effects and their association with biological invasions (Taylor & Hastings 2005). For invader insects such as *Chrysomya* species, the colonization and trophic interactions could be subject to different mechanisms of an Allee effect (Tobin *et al* 2009). In conclusion, our results show clearly that the Allee effect may stabilize or destabilize the dynamic behavior of blowflies, depending on the parametric space of demographic parameters.

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