Quantitative and qualitative dynamics of exotic and native blowflies (Diptera: Calliphoridae) with migrations among municipalities

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Abstract: The population dynamics of blowflies (Diptera: Calliphoridae) has been investigated in studies combining different mathematical formalisms, with estimates of demographic parameters and spatial models. However, these applications are limited to laboratory data only. In this study, we investigated the population dynamics of three species of blowflies [*Chrysomya albiceps* (Wiedemann), *Chrysomya megacephala* (F.) and *Lucilia eximia* (Wiedemann)] in a mathematical model that includes parameters estimated in the laboratory and population sizes estimated from field collections, in order to simulate the dynamics of local migration. The model combines experimental estimates of fecundity and survival with abundance data obtained in field collections, to analyze comparatively the population dynamics of the three blowfly species, taking into account the theoretical movement by individuals among municipalities with different urbanization profiles. The ecological patterns of oscillation observed depended on the municipality only for *C. albiceps*, a species with special demographic characteristics that are probably associated with predatory and cannibalistic behaviors. The bifurcation diagrams showed that intermediate migration rates stabilize populations. Although the proposed model considers only six municipalities in a closed system, the study was able to show different impacts of local migration on the quantitative and qualitative population behaviors, by using different connectivity levels arising from the different distances among areas.

Introduction

Ecological modeling has been used to show population oscillations or persistence patterns of insects in both the laboratory and the field (Desharnais 2005). Population models extract information from laboratory experiments in order to investigate specific ecological aspects that are important for conservation and pest control (Yurk and Powell 2010). Field studies are important to supply models with data describing more realistic situations, in order to confirm patterns obtained in the laboratory or to compare results by using analytical tools (Petrovskii et al. 2012). Dynamic behavior of insects has been assessed by using models that explore the association between stability and magnitude of demographic parameter values, resulting in complex patterns in response to population growth (Desharnais 2005). Particularly, population dynamics has been strongly linked to laboratory ecology by the use of models, which have been particularly useful for understanding development, persistence, life history, foraging, demography, nonlinear dynamics, evolutionary dynamics and parasitism (Burd and Howard 2005, Desharnais 2005, Yurk and Powell 2010). Modeling focused on field studies has more recently been emphasizing swarm systems, foraging environment, epidemics and insect outbreaks (Fuller et al. 2012, Granovskiy et al. 2012, Hamann and Schmickl 2012).

Mathematical modeling of insect population dynamics provides interesting insights into comparative dynamics, because demographic parameters of exotic species generally exhibit larger differences in magnitude than those of native species (Godoy et al. 2001). These differences may drive dynamic behaviors, resulting in different spatio-temporal patterns. Generally, simple dynamics, characterized by monotonic equilibrium, is established when the magnitude of growth rates is low, compared to complex dynamics, which are characterized by periodic cycles or chaos (Desharnais 2005). Historically, blowflies (Diptera: Calliphoridae) have been cited as important examples of insects that exhibit complex cycles in the laboratory (Gurney et al. 1980). This type of behavior has also been observed in flour beetles, for which

the population dynamics have been intensively studied for successive years (Costantino et al. 2005).

The above-mentioned examples describe theoretical ecological patterns very well, taking into account the trajectory of time series. Time series make it possible to determine the tendencies and/or sensitivity of population parameters, but always consider only one dimension, time. In recent years, ecologists have been concerned about the kind of population behavior that could be expected if another dimension, space, is taken into account. Space can be interpreted as the movement of insects among patches (Okubo and Levin 2001). Perhaps the movement among patches is strongly dependent on connectivity. Connectivity, which is the degree to which populations are able to or prevented from moving among patches (Rösch et al. 2013), has been viewed as a major factor capable of determining species distributions (Moilanen and Hanski 2001). Extinction-colonization dynamics is probably strongly associated with connectivity (Moilanen and Nieminen 2002).

In insects, the spatial structure has been identified as a stabilizing factor in single-species population dynamics. However, little is known about possible synergic effects of the combination of demography and local migration, since demographic factors may be responsible for spatio-temporal variations (Reigada et al. 2013).

Blowflies, apart from being extensively studied because they are important vectors of pathogens and causative agents of myiasis, and are useful in maggot debridement therapy and for estimating the minimum postmortem interval (Godoy 2007, Moretti and Godoy 2013), provide a valuable opportunity to assess demographic changes in response to competition for food in time and space. Nicholson (1954, 1957) experimentally studied population tendencies over time, revealing unpredictable ecological patterns of blowfly oscillations. Biological invasions by blowflies from the Old World to the New World have been documented over the last four decades, possibly in response to greater connectivity among continents (Coutinho et al. 2012).

However, particularly in Brazil, the scenario of this invasion has been changing in a singular way. The prevalence of species has changed over the last decades, inverting their abundance status. This is especially clear for the exotic species *Chrysomya megacephala* (F.) and the native species *Lucilia eximia* (Wiedemann), which have been changing their prevalence, apparently changing habits and exhibiting new preferences for areas. Certainly, the dynamics in time and dynamics in space are interdependent to some extent. The stabilizing effect of space on the population dynamics of blowflies has been investigated in studies that combine different mathematical formalisms by employing population growth and lattice models (Godoy et al. 1997, 2001, Serra et al. 2007). However, these applications are limited to laboratory data. Different areas may influence the demography of insects, mainly in highly heterogeneous environments. For insects, which are able to change habitats and migrate among urban, farm and forest environments, the urban habitat may

exert a significant influence on the population dynamics (Rubio et al. 2012). Habitat quality and the impact of natural enemies might profoundly affect metapopulation dynamics and the viability of local populations (Choutt et al. 2011).

The objective of this study was to propose a mathematical model that combines the use of demographic parameters estimated in the laboratory and abundance data obtained in field collections to analyze comparatively the population dynamics of three species of blowflies [*Chrysomya albiceps* (Wiedemann), *Chrysomya megacephala* (F.) and *Lucilia eximia* (Wiedemann)], taking into account the theoretical movement by individuals among municipalities with different urbanization profiles. The stabilizing influence of local migration was investigated algebraically, and the different results were discussed in light of the dynamic equilibrium theory, in order to compare the different ecological patterns of population behavior on the basis of the field and laboratory parameters.

Materials and methods

Some parts of the methods described here are similar to those used by Moretti et al. (2011) and Moretti and Godoy (2013), but are repeated here for the sake of clarity and convenience.

Study sites

The collections were carried out in rural, urban, and forest environments in six municipalities in São Paulo State, southeastern Brazil: Artur Nogueira (22°34'22''S, 47°10'22''W), Campinas (22°53'20''S, 47°04'40''W), Cosmópolis (22°38'45''S, 47°11'46''W), Jundiaí (23°11'11''S, 46°53'03''W), Mogi Guaçu (22°22'20''S, 46°56'32''W) and Paulínia (22°45'40''S, 47°09'15''W). Figure 1 shows the location of the municipalities and the distances between them. We chose these six municipalities because they are representative of the different public-sanitation conditions existing in the state of São Paulo.
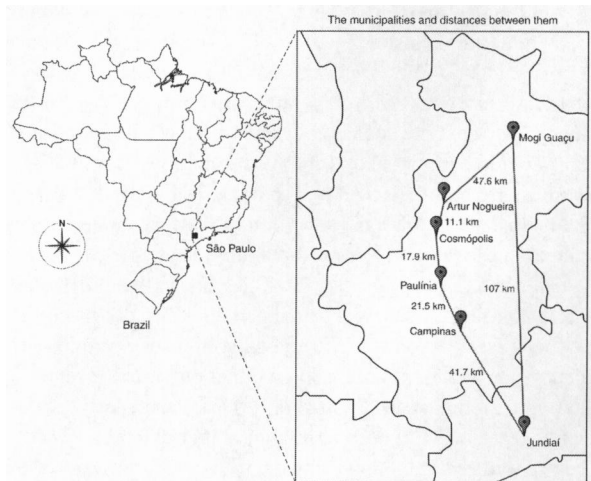

Figure 1. Location of the municipalities and the distances between them (adapted from Moretti et al. 2011).

Table 1. Mean survival and fecundity rates for each species (*Lucilia eximia*, *Chrysomya albiceps* and *Chrysomya megacephala*) and larval densities (adapted from Godoy et al. 1997, Godoy et al. 2001, Serra et al. 2007).

L. eximia				
Density	Replicates	Mean survival	n	Mean fecundity
100	2	0.9150	32	6.53
200	2	0.8400	32	7.03
400	2	0.5900	32	6.14
600	2	0.3800	31	5.29
800	2	0.3600	32	4.05
C. albiceps				
Density	Replicates	Mean survival	n	Mean fecundity
100	2	0.5400	25	26.46
200	2	0.3400	54	21.02
400	2	0.1200	29	19.24
600	2	0.0720	17	15.91
800	2	0.0690	22	13.63
1,000	2	0.0200	10	10.00
C. megacephala				
Density	Replicates	Mean survival	n	Mean fecundity
200	2	0.6650	47	21.79
400	2	0.5510	52	20.40
600	2	0.3000	31	17.76
800	2	0.3494	58	13.84
1,000	2	0.2700	43	13.28
1,200	2	0.2324	53	10.00
1,400	1	0.0428	11	7.16
1,600	1	0.0406	11	7.65
1,800	1	0.0455	19	9.07
2,000	1	0.1030	18	9.65

The rural areas in these municipalities are homogeneous, with moderate agricultural activity and livestock farming, and a few scattered houses. Most of the urban sites have modest commercial activity, except Campinas (1,080,113 inhabitants and an area of 795 km^2) and Jundiaí (370,126 inhabitants and an area of 431 km^2) (IBGE 2012), the two largest cities monitored, which have very high levels of urbanization, dense housing and intense commerce. Finally, the forest sites are mainly remnant woodland patches with similar phytophysiognomic features, except Campinas, where the forest area is a 250-ha mesophilic semideciduous Atlantic Forest fragment (Morellato and Leitão Filho 1995) surrounded by human dwellings (Moretti et al. 2011).

All these cities have the same type of weather according to the Köppen climate classification: Cwa, a subtropical climate, with cool dry winters (temperatures below 18°C) and warm humid summers (with the mean temperature in the warmest month above 22°C), as generally occurs in the State of São Paulo, mainly in the central and eastern regions, at altitudes between 500 and 700 m (Setzer 1966).

Field and laboratory procedures to obtain abundance data

Monthly collections were made from September 2006 through October 2007. Each of the environments in each municipality was monitored using six traps per month, two for each kind of bait, totalling 18 traps per municipality/month and 1,512 sample units during the entire study (18 traps × 6 cities × 14 months of collection). Baits composed of 12 g of one of the following: fish (sardines), beef liver, or chicken gizzards were employed, after being allowed to putrefy for approximately 48 h at room temperature. The carrion traps were installed approximately 15 m apart at the collection sites. Each trap was made of two 2.0-liter plastic soft-drink bottles, each approximately 30 cm in height and 10 cm in diameter. The bottoms of both bottles were removed to allow one to fit into the other and to allow insects to enter through the bottom opening of the lower bottle, which was painted black. The cap of the lower bottle was also removed, so its top end was open. Each bait was placed at the top end of the lower bottle with a small metal hook, and was replaced in the traps every 24 h.

Each trap was suspended by a cord from a tree branch, approximately 180 cm above the ground. The traps remained exposed at the study site for a period of 72 h, after which all insects trapped in the upper bottle were collected, taken to the laboratory, and killed by freezing at -20°C, until later identification. The carrion-baited trap was illustrated by Moretti et al. (2011) and Moretti and Godoy (2013). Part of the collected material was mounted and deposited in the ESALQ Entomological Museum, Department of Entomology and Acarology, ESALQ/USP, Piracicaba, São Paulo, Brazil. The remaining specimens were preserved in 70% ethanol.

Demographic parameter values obtained in laboratory

Fecundity and survival were estimated in the laboratory by employing experiments to simulate the variation of these parameters as a function of intraspecific competition for food. Increasing larval densities were set up to estimate the influence of competition for food on fecundity and survival. A detailed description of these procedures was provided by Godoy et al. (1997, 2001). The mean survival and fecundity

Table 2. Total abundance of *Chrysomya albiceps*, *Chrysomya megacephala* and *Lucilia eximia* per municipality during the collection period.

Species	Municipalities					
	Artur Nogueira	Campinas	Cosmópolis	Jundiaí	Mogi-Guaçu	Paulínia
C. albiceps	1,290	1,781	1,022	368	531	488
C. megacephala	518	687	872	324	411	404
L. eximia	781	486	437	521	340	325

rates for *L. eximia*, *C. albiceps* and *C. megacephala* at different larval densities obtained in these studies are provided in Table 1.

Mathematical modeling

In order to model fly dynamics, Prout and McChesney (1985) developed a discrete-time mathematical model, which was subsequently used in blowfly ecology by Von Zuben et al. (1993) and Godoy et al. (2001). This model includes density dependence, and assumes that the population size at generation $t+1$ depends on the reproductive capability of the surviving females at generation t. Therefore, the main parameters of the model are fecundity (egg production) and survival, expressed as functions of the density. The sex ratio is considered to be 1:1, so the females account for half of the population. The model is written as:

$$N_{t+1} = G(N_t) = \frac{1}{2} F(N_t) S(N_t) N_t , \qquad (1)$$

where N_t is the number of individuals at generation t, and $F(N_t)$ and $S(N_t)$ are the functions that describe the fecundity and survival rates, respectively. These functions, which depend on the larval density, are described as an exponential decline (Silva et al. 2003), written as:

$$F(N_t) = P\exp\{-pN_t\} , \qquad (2)$$

$$S(N_t) = Q\exp\{-qN_t\} , \qquad (3)$$

where P and Q describe the maximum fecundity and survival rates, respectively, and p and q are coefficients related to the rate of decline of the exponential curves.

In this study, we consider several sites whose local dynamics will be described by model (1), supplemented by migration functions in order to reproduce the dynamics that might occur in a closed system, composed by six municipalities located in São Paulo State, Brazil. The new model is:

$$N_{t+1}^{(i)} = \left(1 - \sum_{j \neq i} m_{ij}\right) G_i(N_t^{(i)}) + \sum_{j \neq i} m_{ji} G_j(N_t^{(j)}); \qquad (4)$$

$i = 1, 2, ..., 6; j = 1, 2, ..., 6,$

$$m_{ij} = M_i \frac{\exp\left(-\frac{d_{ij}}{\alpha}\right)}{\sum_{j \neq i} \exp\left(-\frac{d_{ij}}{\alpha}\right)}, 0 \leq M_i \leq 1, \qquad (5)$$

where the superscript i denotes the site, G_i is the growth func-

tion with site-dependent parameters, m_{ij} is the migration rate from municipality i to municipality j, m_{ji} is the migration rate from municipality j to municipality i, α is the range of flight, M_i (the values of which are assumed to be independent of site i) is the likelihood of migrating away from site i, and d_{ij} is the shortest distance between municipality i and municipality j. When α decreases, the migration rates shift toward closer sites, as

$$\lim_{\alpha \to 0^+} m_{ij} = M_i \text{ if } d_{ij} < d_{ik} \text{ for all } k \neq j,$$

$$\lim_{\alpha \to 0^+} m_{ij} = 0 \text{ otherwise.}$$

Conversely, when α increases substantially, the migration rates are determined only by the likelihood of migrating, as

$$\lim_{\alpha \to \infty} m_{ij} = \frac{M_i}{6} .$$

The coefficients of $F(N_t)$ and $S(N_t)$ were estimated by Godoy et al. (2001), who used data from laboratory experiments. Studying the equilibrium of the Prout model by setting $N_{t+1} = N_t = u^*$, it follows that:

$$u^* = \frac{1}{2} F(u^*) S(u^*) u^* ,$$

$$u^* = \frac{1}{2} PQ\exp\{-(p+q)u^*\} u^* .$$

By isolating $(p + q)$, the following is obtained:

$$(p+q) = \ln\left(\frac{PQ}{2}\right)\frac{1}{u^*} .$$

In this study, only the values for P and Q, the maximum fecundity and survival rates, were obtained from the experiments by Godoy et al. (2001). By setting u^* equal to the sampling average for each municipality, different $(p + q)$ values are obtained for each species and each municipality. By taking that estimate from the Prout model without immigration, we are effectively assuming that total migration, that is, immigration minus emigration, is zero in each municipality. While this is not true in general nor is it expected from observational data, it is nonetheless a good approximation for the average population over many generations.

Results and discussion

Table 2 shows the abundance of *C. albiceps*, *C. megacephala* and *L. eximia* per municipality of collection. The results suggest that *C. albiceps* had its largest population
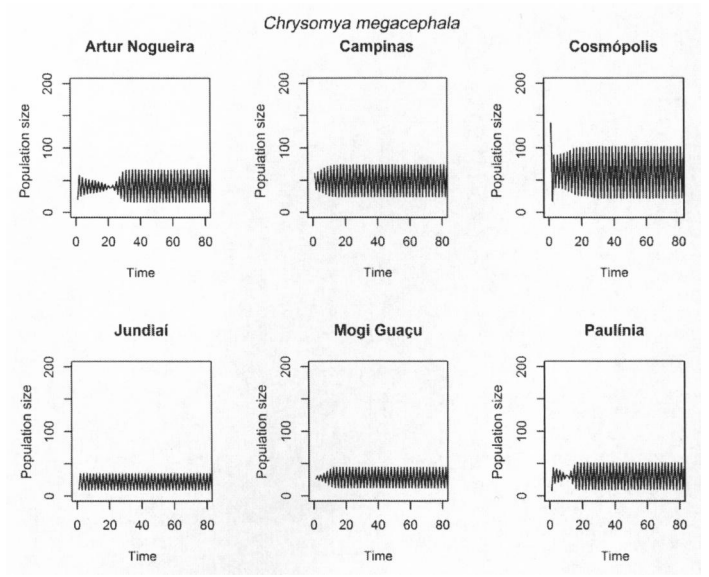
Figure 2. Recurrence obtained from equation (4) showing the population dynamics of *Chrysomya megacephala* in different municipalities.
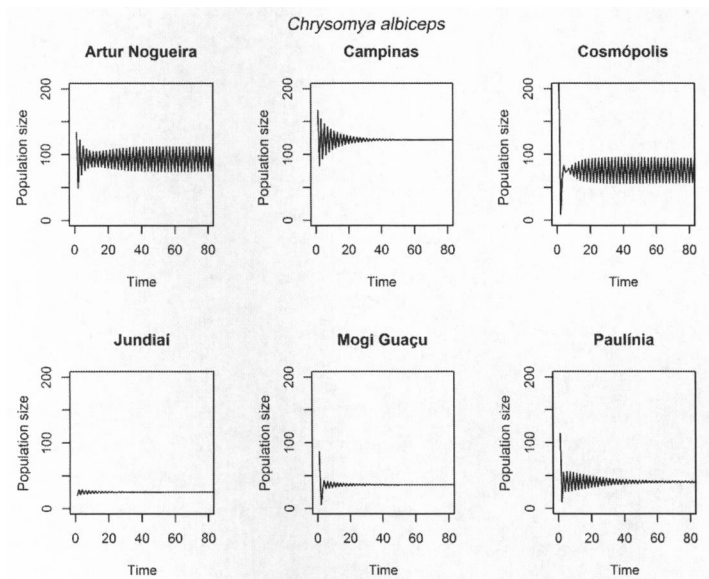
Figure 3. Recurrence obtained from equation (4) showing the population dynamics of *Chrysomya albiceps* in different municipalities.
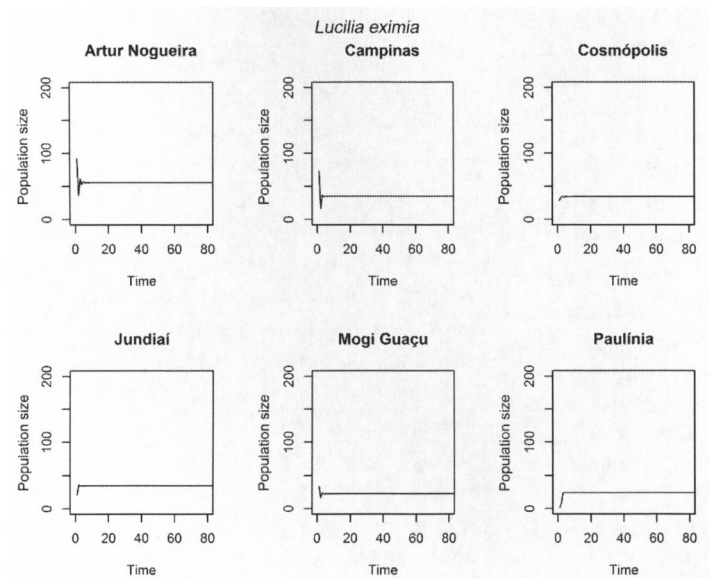
Figure 4. Recurrence obtained from equation (4) showing the population dynamics of *Lucilia eximia* in different municipalities.

Table 3. Estimates of the parameters of the model for *Chrysomya albiceps* in the different municipalities.

Parameter	Estimate					
	AN	CAM	COS	JUN	MOG	PAU
N_0	134	167	223	20	87	114
u^*	92.14	127.21	73.00	26.29	37.93	34.86
P	27.11					
Q	0.5650					
$(p + q)$	0.0258	0.0187	0.0325	0.0904	0.0626	0.0682
α	1.80					
M_i	0.10					

Table 4. Estimates of the parameters of the model for *Chrysomya megacephala* in the different municipalities.

Parameter	Estimate					
	AN	CAM	COS	JUN	MOG	PAU
N_0	20	61	138	10	26	8
u^*	37.00	49.07	62.29	23.14	29.36	28.86
P	23.49					
Q	0.9160					
$(p + q)$	0.0642	0.0484	0.0381	0.1027	0.0809	0.0823
α	1.80					
M_i	0.10					

Table 5. Estimates of the parameters of the model for *Lucilia eximia* in the different municipalities.

Parameter	Estimate					
	AN	CAM	COS	JUN	MOG	PAU
N_0	92	73	29	21	34	2
u^*	55.79	34.71	31.21	37.21	24.29	23.21
P	9.08					
Q	1.00					
$(p + q)$	0.0271	0.0436	0.0485	0.0407	0.0623	0.0652
α	1.80					
M_i	0.10					

N_0: abundance on the first month of collection; u^*: sampling average; P: maximum fecundity; Q: survival rate; $(p + q)$: refer to the text; α: range of flight in km, estimated from Coutinho et al. (2012); M_i: proneness to migrate away from site i (illustrative value used in figures 2, 3 and 4, not obtained from data); AN: Artur Nogueira; CAM: Campinas; COS: Cosmópolis; JUN: Jundiaí; MOG: Mogi Guaçu; PAU: Paulínia.

in Campinas and its smallest in Jundiaí. *C. megacephala* had its largest population in Cosmópolis and its smallest also in Jundiaí. *L. eximia* had its largest population in Artur Nogueira and its smallest in Paulínia.

The oscillation patterns obtained by simulating the recurrence from equation (4) indicate that *C. megacephala* showed periodic fluctuations in all the municipalities (Fig. 2). The stability of *C. albiceps* depended on the municipality, as the pattern obtained for three of them (Campinas, Jundiaí and Mogi Guaçu) is a stable equilibrium (Fig. 3). *L. eximia* showed only stable equilibrium patterns (Fig. 4). *C. megacephala* and *L. eximia* showed the same patterns regardless of the municipality, with the main differences being in the peak sizes (*C. megacephala*) and population size (*L. eximia*).

The estimates for the parameters used in the model for *C. albiceps*, *C. megacephala* and *L. eximia* in the different municipalities are shown in Tables 3, 4 and 5, respectively. The different types of temporal patterns found for *C. albiceps* suggest that they can be related to their respective parameter values, as previously observed in other studies (Godoy et al. 2001). It is possible that the apparent special demographic condition of *C. albiceps* is connected with its different strategies to obtain food, for example its cannibal behavior in the larval stage, as well as its intraguild predator habit (Faria et al. 2007). In a study on oviposition behavior, *L. eximia*

avoided laying eggs in patches where *C. albiceps* larvae had been present previously (Gião and Godoy 2007), indicating the existence of interaction between the two species. Previous laboratory estimates of survival rates for *C. albiceps* are very low compared to those for other blowfly species (Godoy et al. 2001), probably leading the species to search for compensatory perpetuation strategies.

The bifurcation diagrams obtained for the likelihood of migrating (M_i parameters) show that, in some cases, high migration rates may lead to extinction (Figs. 5, 6 and 7). On the other hand, intermediate migration rates may act as a stabilizing factor (Figs. 5, 6 and 7). With a few exceptions, the most stable pattern is obtained at intermediate values, as an overall increase in the likelihood of migrating may lead populations in some patches to extinction, which may cause population overflow in other patches and subsequently less stability (Solé and Bascompte 2006). The species that show smaller oscillation spectra are those that are prone to reach stability (Fig. 7). In contrast, the species that oscillate more widely reach higher population levels, increasing their chances of colonizing new areas (Hanski 1999). These latter species may be forensically important, because they will be more abundant in a given area, and then will have higher chances of colonizing cadavers.
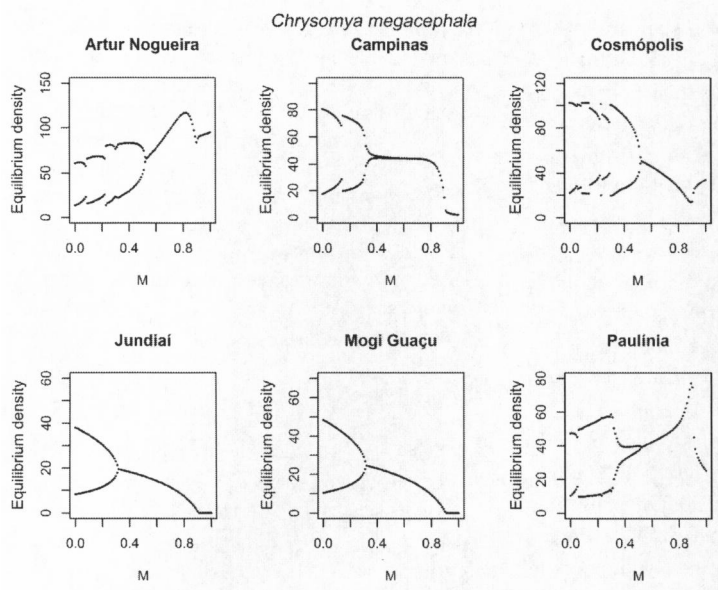
Chrysomya megacephala

Artur Nogueira — Equilibrium density vs M

Campinas — Equilibrium density vs M

Cosmópolis — Equilibrium density vs M

Jundiaí — Equilibrium density vs M

Mogi Guaçu — Equilibrium density vs M

Paulínia — Equilibrium density vs M

Figure 5. Bifurcation diagram for the likelihood of *Chrysomya megacephala* migrating away from each municipality (M).

Chrysomya albiceps

Artur Nogueira — Equilibrium density vs M

Campinas — Equilibrium density vs M

Cosmópolis — Equilibrium density vs M

Jundiaí — Equilibrium density vs M

Mogi Guaçu — Equilibrium density vs M

Paulínia — Equilibrium density vs M

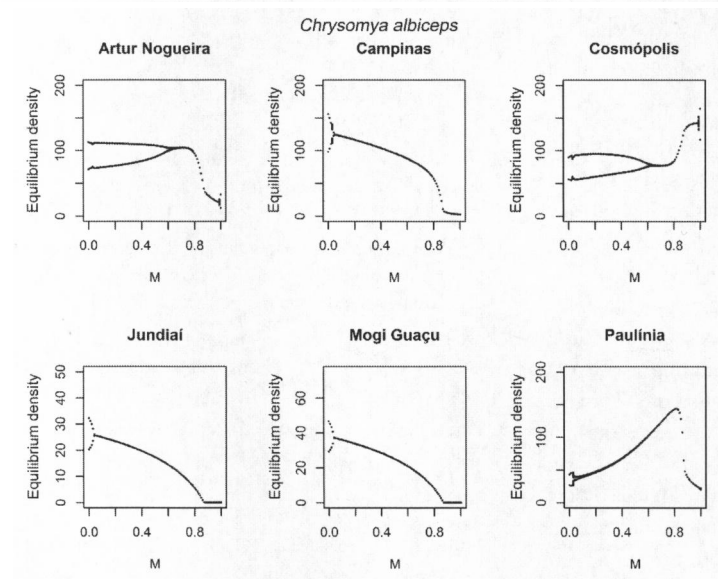**Figure 6.** Bifurcation diagram for the likelihood of *Chrysomya albiceps* migrating away from each municipality (M).

Lucilia eximia

Artur Nogueira — Equilibrium density vs M

Campinas — Equilibrium density vs M

Cosmópolis — Equilibrium density vs M

Jundiaí — Equilibrium density vs M

Mogi Guaçu — Equilibrium density vs M

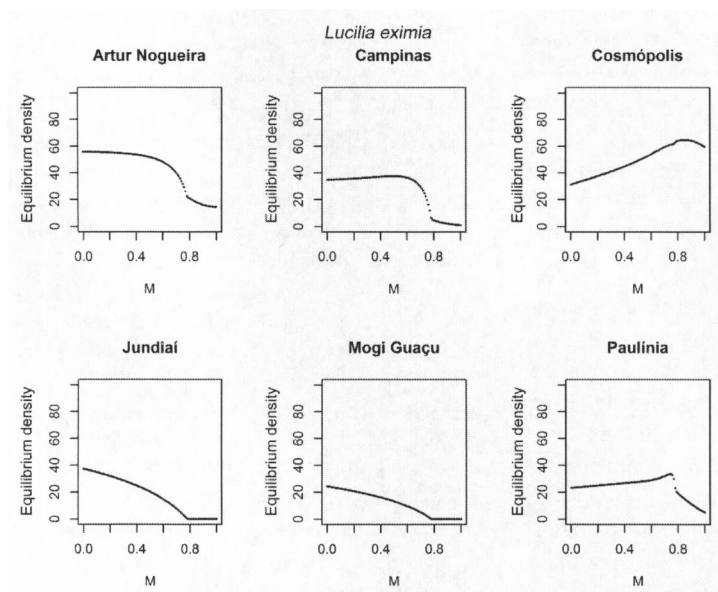**Paulínia** — Equilibrium density vs M

Figure 7. Bifurcation diagram for the likelihood of *Lucilia eximia* migrating away from each municipality (M).

Populations located in municipalities distant from each other will certainly show lower migration rates than those located close to each other, and this may lead to distinct faunistic patterns. Knowledge of such patterns is essential for mapping insect species of forensic importance for a given area. The changes in preference for areas shown by blowflies can be easily illustrated by *C. megacephala*. In the first years after its introduction into Brazil, this species was associated with decomposing organic matter and garbage dumps, mainly in urban areas (D'Almeida et al. 1991). However, *C. megacephala* was recently collected in larger numbers in forests (Souza and Von Zuben 2012) and in rural areas (Moretti and Godoy 2013) than in urban areas, also in investigations in São Paulo State. *L. eximia*, which seems to be especially adapted for colonizing small carcasses (Moretti and Godoy 2013), was formerly found mainly in rural and forest habitats in Brazil (Guimarães and Papavero 1999). However, Moretti and Godoy (2013) collected *L. eximia* in larger numbers in urban areas than in rural and forest ones, in São Paulo State. *C. albiceps* has apparently retained its synanthropic behavior since its introduction to Brazil, and continues to be mostly collected in urban areas (Moretti and Godoy 2013).

Migration between adjoining areas has been investigated in insects, particularly with mathematical models emphasizing the dynamics of hosts and parasitoids (Hassell et al. 1991). Among the limitations of models that only consider the recurrences through time is the normal behavior of populations to increase very rapidly, resulting in immediate dramatic declines that usually culminate in extinction. Spatially arranged models usually allow more possibilities, such as the global persistence of locally unstable populations (Hassell et al. 1991). The overall probability of persistence generally increases with the increase in the complexity and size of spatial arrays. Hassell et al. (1991) have shown that some ecological patterns important for population persistence, such as spiral waves, crystal lattices or chaotic variation, can only be obtained when spatial structure is taken into account. Migration may also trigger a rescue effect, when populations decline below critical points, increasing the extinction risk (Serra et al. 2007). These migration effects are more closely related to the idea of conservation biology, but they also should be considered an important factor in pest-management strategies because the level of economic damage can be changed significantly by considering the local migration of pests (Lima et al. 2009).

A limitation of our model is that it considers the six municipalities as a closed system, without considering possible in- and out-migration between the municipalities that we studied and those not included in the system. However, even with this limitation, the study was able to show different impacts of local migration on the quantitative and qualitative population behaviors. Another aspect is that the use of carrion-baited traps, although they are effective for comparing the abundances of necrophagous flies between sites, may bias the collection results (Hwang and Turner 2005).

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