

Stochastic dynamics of *Musca domestica* (Diptera: Muscidae) and *Chrysomya putoria* (Diptera: Calliphoridae)

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Abstract: We analysed the stochastic dynamics of *Musca domestica* L. (Muscidae) and *Chrysomya putoria* (Wiedemann) (Calliphoridae), 2 important dipteran species that are pests of poultry housing. The study is an attempt to examine demographic attributes of each species and compare ecological patterns of fluctuation, by combining empiricism with ecological modelling. The results of the ecological simulations suggest differences between the 2 species with respect to susceptibility to local extinction. *Musca domestica* is a species with a better population performance than that of *C. putoria*, mainly with respect to its survival. *Chrysomya putoria* is apparently more prone to extinction than is *M. domestica* and with stochastic fecundity exhibited fluctuations trending to cyclic oscillations, differing clearly from *M. domestica*. A reverse result was observed in *M. domestica*. With stochastic survival it was more prone to exhibit cycling than was *C. putoria*. These results are important to the implementation of population-control programs, mainly emphasising the implications of biological invasions and colonisation of new areas by exotic species.

Key words: Stochastic dynamics, *Musca domestica*, *Chrysomya putoria*, demographics

INTRODUCTION

Musca domestica (L.) (Muscidae) and *Chrysomya putoria* (Wiedemann) (Calliphoridae) are successful species in many parts of the world, because of their short life cycles and high growth rates (Krafsur *et al.*, 1985; Axtell and Arends, 1990). They are among the main pests in poultry farms, cause myiasis and transmit pathogens to animals and when they are synanthropic, to humans (Greenberg, 1973; Burg and Axtell, 1984; Guimaraes, 1985; Mendes and Linhares, 1993; Guimaraes and Papavero, 1999).

Several studies have shown that fly larvae developing in substrates such as dung or carrion are subject to intraspecific competition, with adverse effects upon their fitness and dramatic consequences for their population dynamics (Ives and May, 1985; Von Zuben *et al.*, 1993; Serra *et al.*, 2007). Dynamic behaviour is an important component for the assessment of relevant demographic aspects (Bulmer, 1994). However, this behaviour usually depends on factors such as growth rate, expressed directly or indirectly by fecundity and survival, but associated with carrying capacity (Lande, 1993; Uchmanski, 1999; Godoy *et al.*, 2001). The

values of demographic parameters may exhibit high variation among different species and populations and the causes of variation are usually diverse and depend upon the environment and/or biological attributes of each organism (Serra *et al.*, 2007).

The objective of this study was to examine the stochastic dynamics of *M. domestica* and *C. putoria*, in an attempt to contribute to the understanding of the population dynamics of both species, considering stochasticity in 2 important demographic parameters, fecundity and survival, combining laboratory experiments with ecological modelling. Then the present study presents an ecological analysis with mathematical modelling, in demographic parameters that are important for the persistence of the exotic species *C. putoria* and the cosmopolitan *M. domestica*, aiming to examine patterns of dynamic behaviour that are essential for population-control programs in flies.

MATERIALS AND METHODS

Fly collection and experiments: Adults of *M. domestica* and *C. putoria* were collected in natural environments from Botucatu, state of Sao Paulo, Brazil, using raw

Table 1: Mean daily fecundity and percentage survival of *Musca domestica* and *Chrysomya putoria* at different larval densities

Density	<i>Musca domestica</i>				<i>Chrysomya putoria</i>			
	Fecundity		Survival		Fecundity		Survival	
	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$
100	20	11.4±0.88	2	85.5±0.2	90	18.74±3.45	4	73.25±3.86
200	20	10.3±1.55	2	71.5±0.2	90	17.16±2.27	4	70.12±5.08
300	20	8.55±0.82	2	51.5±0.2	90	16.80±4.88	4	39.66±5.47
400	20	8±0.72	2	43±0.4	90	15.72±3.13	4	40.12±5.21
500	20	6.25±1.01	2	42±0.4	90	17.23±3.34	4	44.70±5.29
600	20	5.45±0.88	2	42±0.2	90	15.46±3.11	3	45.05±8.44
700	20	4.5±1.1	2	41.5±0.3	90	12.99±3.04	3	52.95±2.06
800	20	4.05±0.88	2	43.5±0.4	90	10.91±2.45	3	52.41±1.82
900	20	3.4±0.99	2	42±0.14	90	11.57±3.05	3	38.92±3.52
1000	20	3.35±0.98	2	40.5±0.4	90	12.66±3.53	2	25.10±4.24
1100	-	-	-	-	60	9.78±3.42	2	20.95±3.66
1200	-	-	-	-	60	8.63±2.35	2	19.41±2.24
1300	-	-	-	-	30	8.20±2.80	1	25.38
1400	-	-	-	-	30	7.39±1.80	1	9.35
1500	-	-	-	-	30	8.27±1.98	1	10.93
1600	-	-	-	-	30	7.52±1.25	1	7.18
1700	-	-	-	-	30	8.01±1.79	1	13.64
1800	-	-	-	-	30	8.69±1.63	1	18.00
1900	-	-	-	-	30	6.54±1.66	1	7.94
2000	-	-	-	-	30	6.78±1.58	1	4.65

Table 2: Parameters of regression analysis of fecundity and survival on larval densities of *Musca domestica* and *Chrysomya putoria*

Parameters and statistics	<i>Musca domestica</i>	<i>Chrysomya putoria</i>
Intercept (F*)	11.7±0.14	19.47±0.288
Regression coefficient (f)	0.00056±0.0000322	0.000594±0.0000152
t-value	122	38.94
r ²	0.6	0.55
ANOVA	304	1516
Intercept (S*)	0.67±0.06	0.82±0.0686
Regression coefficient (s)	0.00079±0.000138	0.00116±0.0000876
t-value	4.71*	13.26*
r ²	0.64	0.8
ANOVA	32.5*	176*

*p<0.001

bovine liver as bait and a fly net. The specimens were transported alive to the laboratory where they were anaesthetised in a low temperature and then were identified morphologically based on Carvalho and Mello-Patiu (2008).

The flies were kept in separate cages (30×30×30 cm) with nylon screens on the sides to allow ventilation, in a climate chamber with a 12 h photoperiod, at 25±1 °C and 70±10% relative humidity. The flies were fed raw bovine liver, sugar and water to allow the complete development of the gonotrophic cycle (Linhares, 1988). Raw ground beef was used as the medium for oviposition. The eggs were removed from the substrate by means of a fine brush and were transferred to plastic vials (6×8 cm) containing an artificial larval diet that consisted of casein, agar, brewer's yeast, powdered whole milk and water (Leal *et al.*, 1982).

The experiments were performed using the F₂ generation, which is the progeny of one generation that had completed its life cycle in the laboratory. Intraspecific

competition among larvae, since the first instar, was established in the laboratory by setting 10 larval densities for *M. domestica* and 20 for *C. putoria* (Table 1). Larval densities were set to simulate exploitative competition among immatures, which is known to occur under natural conditions (Lomnicki, 1988). Survival was estimated as the number of adults emerging from each vial. Fecundity was measured by counting the number of eggs per female, expressed as the mean daily egg output based on the length of the gonotrophic cycle.

Ecological modelling: Prout and McChesney (1985) developed a mathematical model applied to investigate the population dynamics of *Drosophila melanogaster* (Meigen) (Diptera: Drosophilidae). The model is described by a difference equation that models the dynamics, taking into account the number of immatures in succeeding generations. The equation incorporates the variation of fecundity and survival as functions of the density of immature individuals. The recursion can be written as:

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

where Fecundity (F) and Survival (S) are decreasing functions of n_t. The factor ½ indicates that only half of the population is adult females, which contribute eggs to next generation. An exponential function was used because it fitted the blowfly data as well as or better than linear and hyperbolic functions in previous studies (Table 2). The parameters F and S were allowed to oscillate between the maximum and minimum mean values of overall densities

(Table 1). The function rand (Matlab 5.0) was employed to simulate the stochastic dynamics for fecundity and survival of *M. domestica* and *C. putoria*, with uniform distribution, in order to ensure that all the values between the established bounds had the same chance of occurrence. For each species and stochastic parameter, 1,000 simulations were run (Hanselman and Littlefield, 1997).

RESULTS AND DISCUSSION

Stochastic fecundity produced similar results for *M. domestica* and *C. putoria* (Fig. 1). The minimum value obtained by the estimates for both species was around 300 individuals, suggesting that random values of fecundity have practically the same chance of reaching

population sizes of this magnitude for both species. On the other hand, for stochastic survival, *C. putoria* clearly exhibited values closer to zero than did *M. domestica* (Fig. 2). In addition, even under the stochastic effect of fecundity on *C. putoria*, it exhibited fluctuations trending to cyclic oscillations, differing clearly from *M. domestica*. An interesting result occurred for survival, which suggests a reverse result if compared to the previous one, i.e., *M. domestica* was more prone to exhibit cycling than was *C. putoria* (Fig. 2).

The results suggest that *M. domestica* is a species with a better population performance than that of *C. putoria*, mainly with respect to its survival. Although the set of densities differed between the 2 species, the highest density of *M. domestica* produced a very low fecundity, which was not observed in *C. putoria*

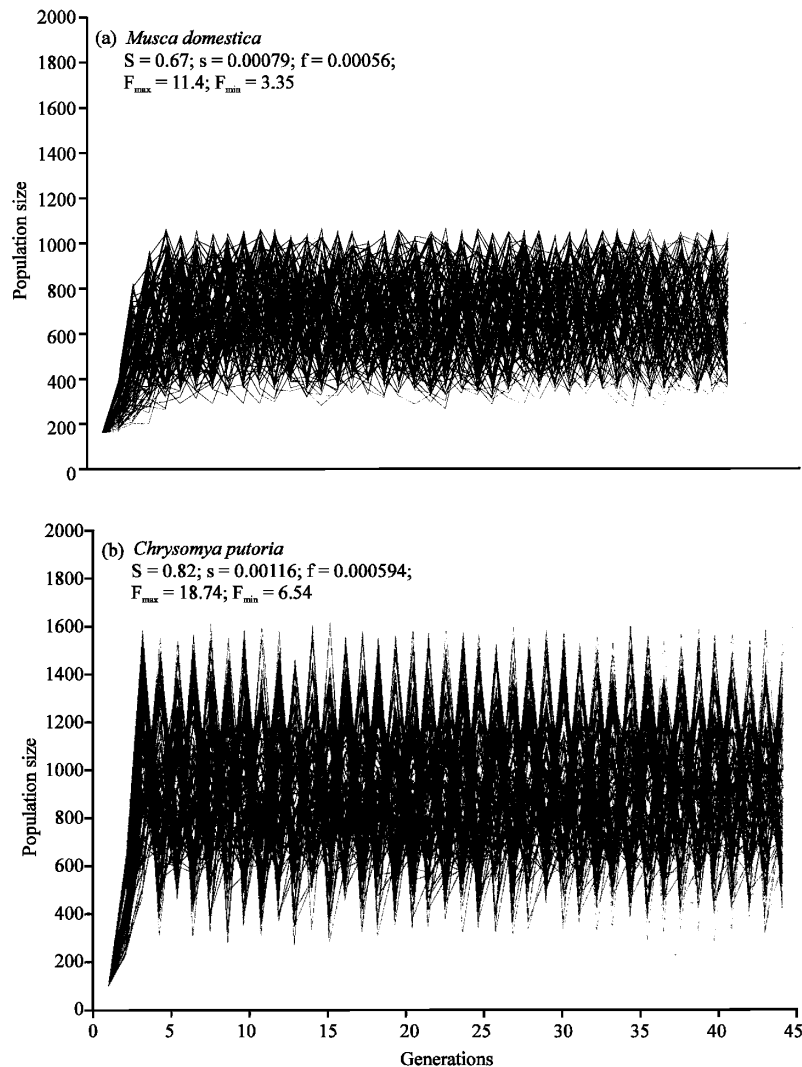


Fig. 1: Persistence in *Musca domestica* and in *Chrysomya putoria* with stochastic fecundity

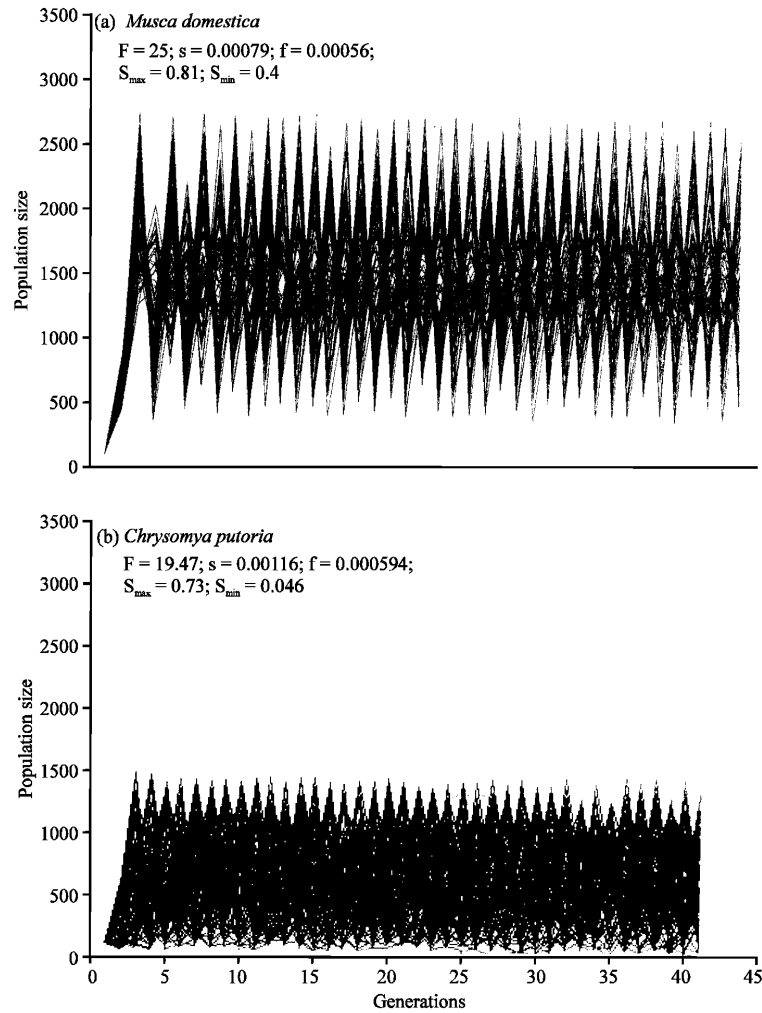


Fig. 2: Persistence in *Musca domestica* and in *Chrysomya putoria* with stochastic survival

(Table 1). In addition, the lowest survival value for *M. domestica* was much higher than for *C. putoria*, if the same density is compared (Table 1). *Musca domestica* and *C. putoria* have been investigated in the laboratory by using the Prout and McChesney (1985) model, but with deterministic emphasis (Godoy *et al.*, 1993; Tardelli *et al.*, 2004). The findings suggest that *M. domestica* exhibits a stable equilibrium and *C. putoria* a two-point limit cycle (Godoy *et al.*, 1993; Tardelli *et al.*, 2004). The results found by Tardelli *et al.* (2004) indicate that *M. domestica* is more prone to maintain a stable population size. On the other hand, the study by Godoy *et al.* (1993) suggested that *C. putoria* may exhibit oscillations. We do not know the exact reason that cyclic tendencies were obtained for both species in the current study. This result is probably a response to a combination of demographic values, which were probabilistically produced by a random-number generator. However, it is important to consider

these inversions in natural populations and their consequences for population dynamics of the fly species.

Population fluctuations and interactions in insects, particularly in blowflies, have been systematically studied since the classic studies by Nicholson (1935, 1957) until more-recent studies, which show interactive ecological aspects (Faria *et al.*, 1999; Godoy *et al.*, 2001; Godoy, 2007; Gao and Godoy, 2007). *Chrysomya putoria* is a species originating in Africa, but it was introduced to the Americas about 35 years ago together with *C. megacephala*, *C. albiceps* and *C. rufifacies* (Guimaraes *et al.*, 1978, 1979; Baumgartner and Greenberg, 1984). It has been considered a successful species, exhibiting characteristics of an invader and coloniser (Prado and Guimaraes, 1982). In addition, it has significantly influenced the abundance of the native species (Reis *et al.*, 1999) together with other exotic blowflies (Faria *et al.*, 1999; Rosa *et al.*, 2004; Faria *et al.*,

2007). In spite of this, *M. domestica* is a cosmopolitan species (Rossi and Godoy, 2006), an attribute which confirms the high ability of the insect to survive and persist under adverse conditions (Axtell and Arends, 1990).

Recently, Serra *et al.* (2007) investigated the stochastic dynamics of 5 blowfly species, by using a mathematical model with emphasis on local migration, concluding that *C. putoria* is one of the species which exhibits the best performance for local persistence. However, comparing its performance with *M. domestica* in the current study, it shows an inferior survival pattern. It is interesting to observe that immediately after the invasion by the *Chrysomya* species in Brazil, *C. putoria* exhibited a higher frequency in poultry housings than did *M. domestica* (Prado and Guimaraes, 1982). However, in recent years this scenario has changed and nowadays its abundance differs significantly among areas in Brazil (Mendes and Linhares, 1993; Carvalho *et al.*, 2000; Serbino and Godoy, 2007). It is possible that the invasion process by the *Chrysomya* species that began in Brazil 35 years ago has been causing changes in the muscoid faunal structure. In this sense, studies such as the present one show that demographic parameters influence significantly the population dynamics and persistence of fly species of economic importance. *Musca domestica* and *C. putoria* both have important ecological and demographic attributes that make them excellent biological models for studies on the population biology of pests.

CONCLUSION

The results found in this study have potential practical implications for the analysis of pest dynamics, mainly when the population performances of *M. domestica* and *C. putoria* are compared, taking into account the sensitivity of the survival and fecundity parameters to variation between maximum and minimum values. A tendency for population cycling was observed in *M. domestica* with stochastic survival and in *C. putoria* with stochastic fecundity. The simulations of stochastic survival suggest that *C. putoria* is more prone to local extinction than is *M. domestica*.

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