Population Dynamics of *Musca domestica* (Diptera: Muscidae): Experimental and Theoretical Studies at Different Temperatures

Carina Aparecida Tardelli[1], Wesley Augusto Conde Godoy[1*] and Paulo Fernando Arruda Mancera[2]

[1] *Departamento de Parasitologia; IB; UNESP; 18618-000; wgodoy@ibb.unesp.br; Botucatu - São Paulo - Brazil.*
[2] *Departamento de Bioestatística; IB; UNESP; C. P. 510; 18618-000; Botucatu - São Paulo - Brazil*

ABSTRACT

In the present study, the population dynamics of M. domestica *was evaluated at two different temperatures, 20 and 30^0 C. The dynamics was modeled using a density-dependent model of population growth. The temperatures investigated in this study produced no qualitative change in terms of dynamic behaviour, i. e. the population dynamics of* M. domestica *was characterized by a stable equilibrium at both temperatures. However, the steady state was influenced by the results obtained at different temperatures. The difference between the eigenvalues obtained at the two temperatures was probably the cause of the difference between the distinct steady states. The implications of these results for the population dynamics of* M. domestica *are discussed.*

Key words: Population dynamics, *Musca domestica*, density-dependent model, temperature

INTRODUCTION

Musca domestica is a species of worldwide distribution (Smith, 1986; Ferreira and Lacerda, 1993) and of medical and veterinary importance since it is a mechanical vector of several diseases (Harwood and James, 1979; Smith, 1986, Levine and Levine, 1991). The pathogens are transported on the fly's cuticle and proboscis, by regurgitation or through the feces (Greenberg, 1970, 1973). Cholera, typhoid fever, amebiasis and poliomyelitis are among the main diseases transmitted by *M. domestica* (Greenberg, 1970, 1973). The successful persistence of *M. domestica* in different regions of the world can be explained by at least two important factors, i.e., a short life cycle and a high growth rate (Ostrolenk and Welch 1942; Rutz and Axtell 1980; Krafsur et al. 1985, Axtell and Arends, 1990). The growth rate is generally influenced by environmental factors (Chapman and Goulson, 2000).

Temperature is an important environmental factor for *M. domestica* population growth, particularly in equatorial and tropical zones, where there is a high density of the species (Levine and Levine, 1991). Temperature has been considered to influence the life history of insects, including *M. domestica* (Chapman and Goulson, 2000). Although some studies have been designed to investigate population behaviour in response to temperature, they have

focused specifically on geographic variation, genetic divergence and natural selection (Anderson 1972; Huey et al., 1991; Partridge et al., 1994; Santos et al., 1997). In the present study we analyse the theoretical dynamics of *M. domestica* populations kept at two different temperatures, using a density-dependent mathematical model developed by Prout and McChesney (1985), with all parameters estimated in the laboratory.

MATERIAL AND METHODS

Specimens of *M. domestica* were collected in the vicinity of the UNESP campus, Botucatu, São Paulo State, Brazil. The adult flies were maintained in cages (30 cm x 30 cm x 30 cm) covered with nylon at 20 and 30 ± 1^0 C receiving water and sugar *ad libitum.* The experiment was performed using laboratory populations which were the progeny of one generation that had completed its life cycle in the laboratory. Exploitative intraspecific competition among immatures, which is known to occur under natural conditions (De Jong, 1976; Lomnicki, 1988), was established in the laboratory at the above temperatures by setting up six larval densities, 100, 200, 400, 600, 800 and 1000, with two replicates each, developing on 50 g of rodent diet. 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 average daily egg output based on the length of the gonotrophic cycle

of *Musca domestica,* which is estimated at 10 days (Harwood and James, 1979). The sample size was 20 females per vial. The following difference equation developed by Prout and McChesney (1985) considers the number of immatures, eggs or larvae, in succeeding generations, n_t and n_{t+1}, and incorporates the variation of the immature density. The model is written as

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

where F^* and S^* are the intercepts in the regression analysis of the fecundity and survival as a function of the larval density, respectively. These parameters respectively express the maximum value of fecundity and survival. In this model, half of the population consists of adult females contributing eggs to the next generation. The other two parameters, f and s, are regression coefficients that respectively estimate the slope of fecundity and survival on the density of immatures.
Rodriguez (1989) demonstrated that most biological phenomena could be viewed as a Poisson process, which involved a decrease described by an exponential function.
On this basis, there was a strong reason to use exponential regression, in addition to the fact that linear regression produces larger slopes in absolute magnitude resulting in large eingenvalues which did not accurately describe the dynamics at the carrying capacity (Mueller, 1986).

Table 1 - Mean daily fecundity and survival at ten larval densities at 20^0C.

Density	Fecundity (*) Number of eggs	Survival(%)** %
100	11.2 ± 1.36	66 ± 0.14
200	10.45 ± 0.99	58 ± 0.28
300	9.25 ± 0.96	58 ± 0.14
400	9.7 ± 1.21	46.5 ± 0.07
500	9 ± 1.25	35 ± 0.14
600	8 ± 1.29	44 ± 0.28
700	7.45 ± 0.95	45.5 ± 0.07
800	8.5 ± 1.35	25.5 ± 0.4
900	6.85 ± 0.74	35.5 ± 0.2
1000	6.55 ± 0.51	35 ± 0.07

* N = 20; ** N = 2

Table 2 - Parameters of regression analysis of fecundity and survival on larval densities at 20^0 C.

	Results
Maximum *F** value for fecundity	11.7
	0.14
Regression coefficient (*f*)	5.6×10^{-4}
	$\pm 3.22 \times 10^{-5}$
T value	122
r^2	60.0
Anova	304
Maximum *S** value for survival	0.67
	0.06
Regression coefficient (*s*)	7.9×10^{-4}
	$\pm 1.38 \times 10^{-4}$
T value	4.71
r^2	64
Anova	32.5

$P < 0.001$

Table 3 - Mean daily fecundity and survival at ten larval densities at 30^0C.

Density	Fecundity *	Survival(%)**
100	11.4 ± 0.88	81.5 ± 0.2
200	10.3 ± 1.55	71.5 ± 0.2
300	8.55 ± 0.82	51.5 ± 0.2
400	8 ± 0.72	43 ± 0.4
500	6.25 ± 1.01	42 ± 0.4
600	5.45 ± 0.88	42 ± 0.2
700	4.5 ± 1.1	41.5 ± 0.3
800	4.05 ± 0.88	43.5 ± 0.4
900	3.4 ± 0.99	42 ± 0.14
1000	3.35 ± 0.98	40.5 ± 0.4

* N = 20; ** N = 2

RESULTS

Tables 1 and 2 present the results obtained at 20°C, and Tables 3 and 4 the results obtained at 30°C. Tables 1 and 3 show that the fecundity and the survival of *M. domestica* decrease with increasing immature density. Tables 2 and 4 show exponential regression slopes for both fecundity and survival that are significantly different from zero (P < 0.001). Tables 2 and 4 also present the values of *F**, *S**, *f* and *s*, and then the difference equation (1) for the temperatures of 20°C and 30° C is respectively given by

$$n_{t+1} = \tfrac{1}{2}11.7e^{-0.00056\,n_t}\,0.67e^{-0.00079\,n_t}n_t, \quad (2)$$
$$n_{t+1} = \tfrac{1}{2}13.4e^{-0.00152\,n_t}\,0.69e^{-0.00068\,n_t}n_t. \quad (3)$$

The patterns of competition described by equations (2) and (3) could be analysed by observing the trajectory of the populations in subsequent generations (Figure 1 for 20^0C and Figure 2 for 30^0C). The line of 45^0 intercepted the function at the steady state and the theoretical number of immatures in equilibrium was 1003 at 20 and 721 at 30^0C. The population dynamics of *M. domestica* was described by a monotonic equilibrium (Figures 3 and 4) at both temperatures. For these iterations, no qualitative difference was observed in populations from different temperatures, just a quantitative difference characterized by the different population sizes.

Table 4 - Parameters of regression analysis of fecundity and survival on larval densities at 30^0 C.
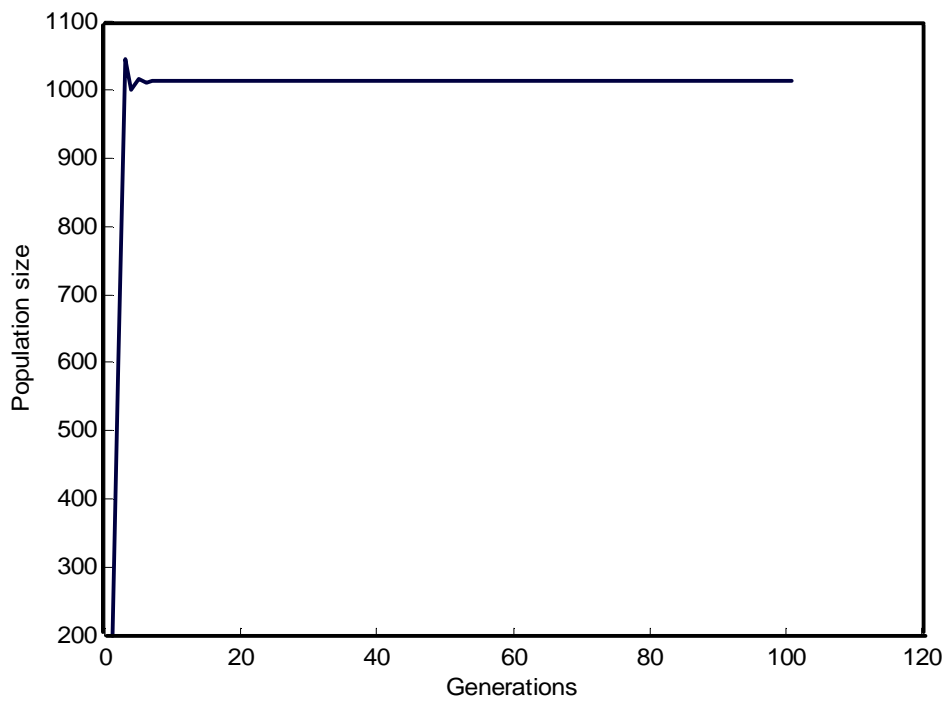
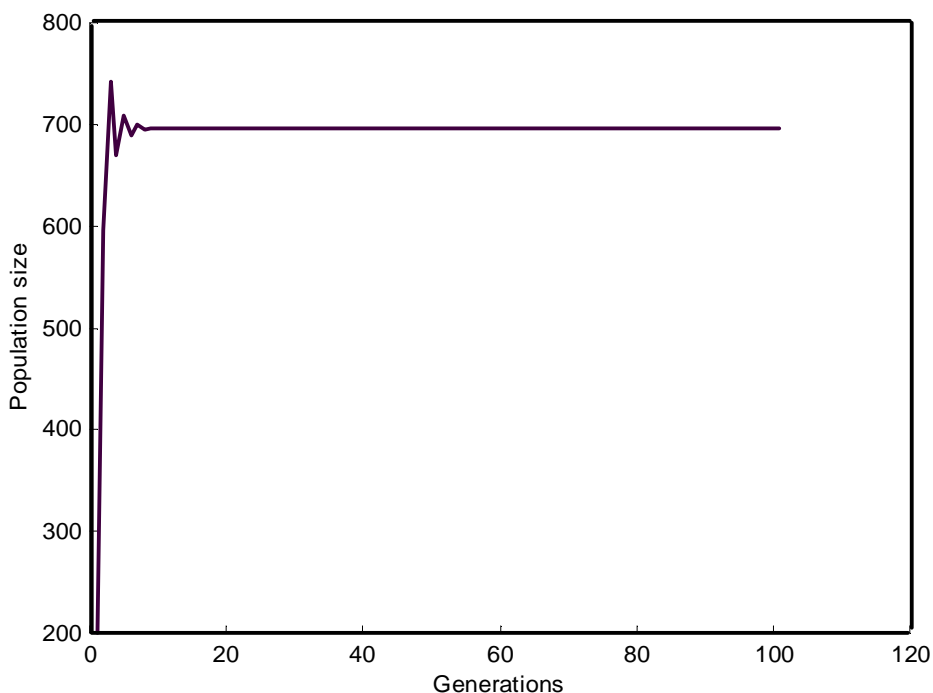|	Results
Maximum F^* value for fecundity	13.4
	0.51
Regression coefficient (f)	1.52×10^{-3}
	$\pm 4.98 \times 10^{-5}$
T value	84.35
r^2	82.0
Anova	937
Maximum S^* value for survival	0.69
	0.055
Regression coefficient (s)	6.8×10^{-4}
	$\pm 1.37 \times 10^{-4}$
T value	4.34
r^2	57
Anova	24.1

$P < 0.001$
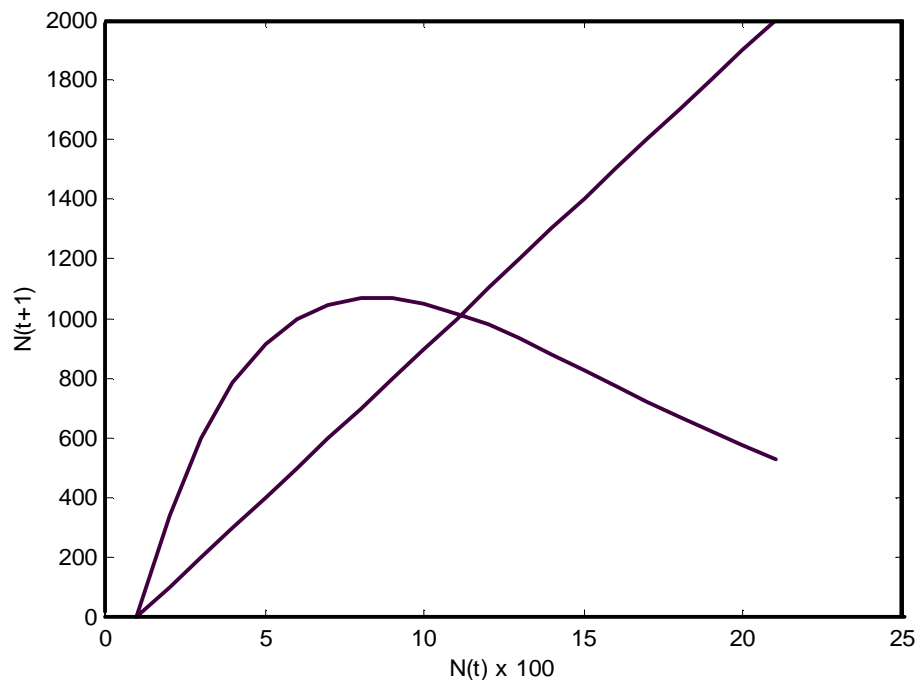
Figure 1 - Recurrence of the number of immatures at 20^0 C.
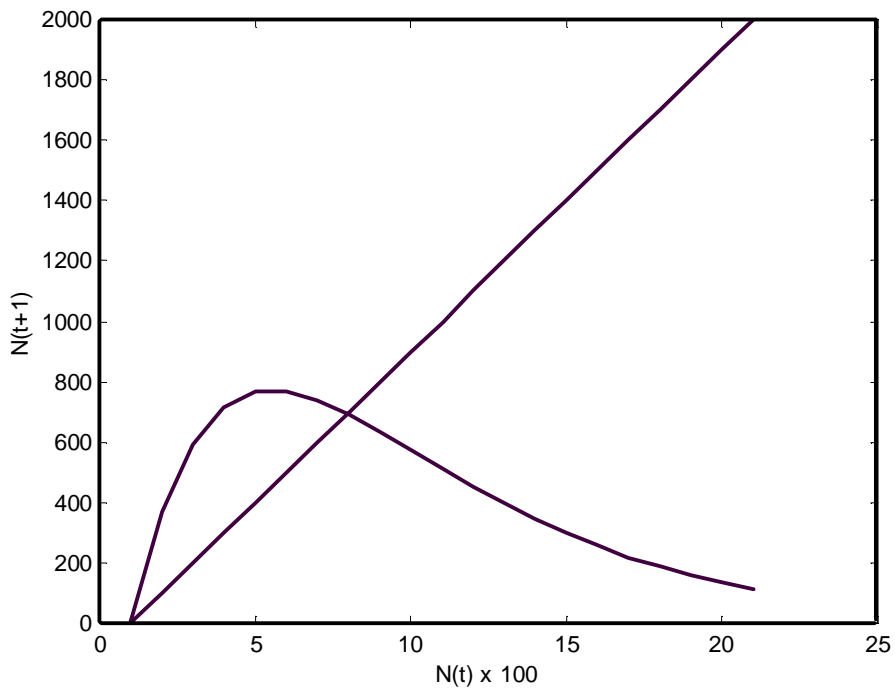
Figure 2 - Recurrence of the number of immatures at 30^0 C.

Figure 3 - Evolution of the population across generations at 20^0 C.

Figure 4 - Evolution of the population across generations at 30^0 C.

DISCUSSION

Fecundity and survival decreased as a function of larval densities at both temperatures investigated. Similar results have been observed in blowfly populations (Von Zuben et al., 1993; Godoy et al., 1993; Reis et al., 1996; Godoy et al., 1997, 2001; Silva et al., 2003). Competition for food has been investigated in insect populations and Nicholson (1954) divided competition into the scramble and contest modes. The concept of the two forms of competition is probably much more associated with their ecological outcomes than the underlying behaviour involved. Gains of competitors in contests are all or nothing, whereas in scrambles, all individuals achieve some gains, if sometimes less than enough to survive and/or reproduce (Parker, 2000). The pattern of competition exhibited by both blowflies and *M. domestica* was scramble since there was a homogenous distribution of resources among the individuals that competed for food (Von Zuben et al., 1993; Godoy et al., 1993; Silva et al., 2003). In this sense, standard deviations seemed to exhibit an apparently small magnitude in response to the kind of food distribution.

The temperatures investigated in this study produced no qualitative change in terms of dynamic behaviour, i. e. the population dynamics of *M. domestica* was characterized by a stable equilibrium at both temperatures. However, the steady state was influenced by the results obtained at different temperatures. The difference between the eigenvalues obtained at the two temperatures was probably the cause of the difference between the distinct steady states.

Stability of equilibrium has been investigated in insect populations (Dennis et al., 1995; Costantino et al., 1995, 1997, 1998; Cushing et al., 1998) and perhaps the most important question arising in this context is what governs the transitions from stable to unstable equilibrium. The effects produced by the manipulation of parameter values are well known in theoretical population models (May and Oster, 1976; Edelstein-Keshet, 1998) and evidence for such changes comes from theoretical and empirical studies (Cavalieri and Koçak, 1995; Costantino et al., 1995, 1997; Dennis et al., 1995, 1997). Experiments designed to test predictive models have shown that shifts in dynamic behavior

can occur from monotonic stable equilibrium to stable cycles, to aperiodic cycles in response to changes in adult mortality (Costantino et al., 1995, 1997; Dennis et al., 1995, 1997; Godoy et. al., 2001).

The absence of change of dynamic behavior observed in *M. domestica* suggested that the species tended to keep a monotonic stable dynamics. Prout's model has also been used to understand the dynamics of three invader blowfly species, *C. megacephala, C. putoria and C. albiceps*, and two native species, *C. macellaria and Lucilia eximia* (Godoy et al., 1993; Von Zuben et al., 1993; Godoy et al., 1996; Reis et al., 1996; Godoy et al., 1997; Teixeira et al., 1998; Silva et al., 1999; Godoy et al., 2001; Silva et al., 2003). *Lucilia eximia* and *C. macellaria* are blowfly species which exhibit the same behavior, showing stable equilibrium (Godoy et al., 1997; Silva et al., 2003). On the other hand, all *Chrysomya* species have shown a two-point limit cycle (Godoy et al., 2001). We strongly believed that these results occured as a function of the demographic parameters, survival and fecundity, which were of small magnitude in *M. domestica, L. eximia* and *C. macellaria* if compared to other fly species, such as *C. megacephala, C. putoria* and *C. albiceps* (Reis et al., 1996; Godoy et al., 1997, 2001). Effectively, *M. domestica* has a smaller body size than blowflies and this factor is certainly associated with its fecundity (Reis et al., 1994).

It was interesting to observe that, even though *M. domestica* was a cosmopolitan species highly successful in terms of colonization, its body size was small and its fecundity low if compared to most blowflies. Could be possible that the success of species such as *M. domestica* and *L. eximia* may be attributed to the low magnitude of their demographic parameters. This profile may involve fewer requirements in terms of carrying capacity than in species which show limit cycles such as *Chrysomya* species, or any more complex behavior. Based on these results, we believed that the success of *M. domestica* was probably associated with both its life history and its population dynamics. The stable equilibrium seems to provide suitable conditions for the success of some fly species. Studies of this nature are important, mainly on species of sanitary importance, since they may describe population trends important for invader and cosmopolite species within a context of dispersal, invasion and colonization of new areas.

RESUMO

Neste estudo a dinâmica populacional de *M. domestica* foi avaliada em duas temperaturas, 20^0 e 30^0 C. A dinâmica foi modelada utilizando um modelo de crescimento populacional dependente da densidade. As temperaturas investigadas no estudo não produziram mudança qualitativa em termos de comportamento dinâmico, ou seja, a dinâmica populacional de *M. domestica* foi caracterizada por um equilíbrio estável em ambas as temperaturas. Entretanto, o ponto de equilíbrio foi influenciado pelos resultados obtidos nas diferentes temperaturas. A diferença entre os autovalores obtidos nas duas temperaturas foi a provável causa da diferença entre os pontos de equilíbrio. As implicações destes resultados para a dinâmica populacional de *M. domestica* são discutidas.

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