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ECOLOGY, BEHAVIOR AND BIONOMICS

Seasonal Fecundity and Body Size in *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae)

CAROLINA REIGADA AND WESLEY A.C. GODOY

Depto. Parasitologia, IB, UNESP, 18618-000 Botucatu, SP

Neotropical Entomology 34(2):163-168 (2005)

Fecundidade Sazonal e Tamanho do Corpo em *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae)

RESUMO - Neste estudo a variação sazonal da fecundidade, tamanhos de asa e tíbia, foi investigada em populações naturais de *Chrysomya megacephala* (Fabricius) a fim de determinar variações nas características bionômicas da espécie em função da sazonalidade. Uma trajetória temporal relativamente constante foi encontrada para fecundidade, tamanhos de asa e tíbia durante doze meses. Correlações positivas e significativas entre tamanho da asa e temperatura, tamanho da tíbia e temperatura e tamanhos da asa e tíbia foram observadas. As implicações desses resultados para a dinâmica populacional de *C. megacephala* foram discutidas.

PALAVRAS-CHAVE: Mosca-varejeira, dinâmica populacional, Muscomorpha, sazonalidade, bionomia

ABSTRACT - In this study the seasonal variation of fecundity, wing and tibia size was investigated in natural populations of *Chrysomya megacephala* (Fabricius) aiming at determining the variations in life history of the species as a function of seasonality. A relative constant temporal trajectory was found for fecundity, wing and tibia size over twelve months. Strong positive correlations between wing size and temperature, tibia size and temperature and between wing and tibia sizes were observed. The implications of the results for population dynamics of *C. megacephala* were discussed.

KEY WORDS: Blowfly, population dynamics, Muscomorpha, seasonality, bionomics

Chrysomya megacephala (Fabricius) is a blowfly widely distributed over Australásia, Paleartic and Oriental regions, and from South African and Afrotropical Island (Zumpt 1965, Baumgartner & Grennberg 1984, Smith 1986), which was found in South America about 1975, together with two other species, C. putoria (Wiedemann) and C. albiceps (Wiedemann). These species rapidly dispersed throughout the Continent, with C. megacephla reaching the United States (Greenberg 1988, Wells 1991). The Chrysomya invasion has apparently caused the displacement of Cochliomyia macellaria Fabricius a native species to the Americas (Guimarães et al. 1979, Prado & Guimarães 1982, Greenberg & Szyska 1984). Biological invasions frequently produce complex interactions at the ecological and genetic level (Pimentel 1993, Brown 1993). Among the main biological factors, dynamic behavior is an important component for the assessment of relevant demographic aspects concerning biological invasions (Hengeveld 1989). However, dynamic behavior usually depends on factors associated to demography, such as growth rate and carrying capacity (Hengeveld 1989, Lande 1993, Uchmanski 1999). The values of demographic parameters associated with population growth may exhibit high variation among different species and populations (Gotelli 1995). The causes of variation are usually diverse and depend on the environment and/or biological attributes of each organism (Brewer 1994).

Among the biological parameters directly associated to growth rate in blowflies, fecundity plays an important role in population persistence since it determines the population growth potential (Von Zuben et al. 1993, Reis et al. 1996, Godov et al. 1996). Recently, studies focusing on dynamic behavior of blowflies analysed by mathematical models have revealed that the stability of population equilibrium depends essentially on survival and fecundity (Godoy et al. 1996, Reis et al. 1996, Teixeira et al. 1998). Using bifurcation theory to perform a parametric sensitivity analysis, Godoy et al. (1996) observed that the variation of fecundity and survival produces qualitative changes in the population dynamics of C. macellaria, C. megacephala and C. putoria. The three species exhibit change from stable equilibrium to a two-point limit cycle (Godoy et al. 1996). However, the increase of fecundity values in C. megacephala promotes successive changes in dynamics behavior, starting with twopoint limit cycle, going through four-point limit cycle and then reaching chaos (Godoy et al. 1996). The values used in these simulations are apparently real in natural populations (Ullyett 1950), nevertheless nothing is known about the seasonal variations in fecundity of *C. megacephala* natural populations.

Fecundity, survival, developmental rate, weight and body size are generally density-dependent characters influenced by environmental factors in insect populations (Reis *et al.* 1994, Ribeiro *et al.* 1995, James & Partridge 1998). Thus, it is possible that the population density of blowflies is strongly associated with seasonality, since competitive ability has been considered different among species and populations (Partridge *et al.* 1994, James & Partrigde 1998, Reis *et al.* 1999).

In the present study we analysed the seasonal variation of fecundity, wing and tibia sizes in natural populations of *C. megacephala* as an attempt to understand the population dynamics of the species.

Material and Methods

Specimens of C. megacephala were collected monthly from April (2000) to March (2001) in the vicinities of campus of Universidade Estadual Paulista, Botucatu, São Paulo, Brazil. A total of 826 blowfly females was collected over the period investigated. Table 1 shows the number of blowfly monthly collected, which were maintained under laboratory conditions in cages (30 cm x 30 cm x 30 cm) covered with nylon at $25 \pm 1^{\circ}$ C and were fed water and sugar ad libitum. Adult females were fed fresh liver to permit complete development of the gonotrophic cycle (Linhares 1988). The fresh liver given to C. megacephala does not cause any influence on the fecundity, wing or tibia size in natural populations since these life history values are determined over larval stage, as a function of the larval density (Ullvett. 1950. Von Zuben et al. 1993. Reis et al. 1994). Females were dissected and the number of eggs was recorded. Body size was estimated by measuring right wing and tibia length of the flies. Seasonal fecundity and wing and tibia sizes were compared by one-way ANOVA. Pearson's coefficient was used to analyse the correlation between life-history parameters. Mean monthly temperatures for Botucatu area were obtained from Meteorological Station of State of São Paulo University at Botucatu. SP, Brazil.

Table 1. Number of *C. megacephala* females dissected by month.

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Month	N
April	85
May	93
June	93
July	21
August	19
September	34
October	86
November	80
December	99
January	99
February	63
March	54

Results and Discussion

C. megacephala exhibited a relatively stable temporal trajectory for fecundity, tibia and wing over twelve months with two decreases in July/2000 and February/2001 (Figs. 1-3). There was a weak but non-significant negative correlation between fecundity and temperature (r = -0.09, P > 0.05). Figs. 4 and 5 respectively show a strong negative

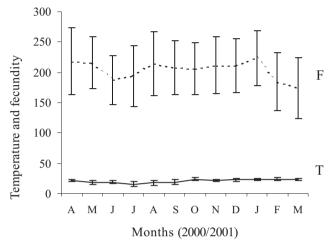
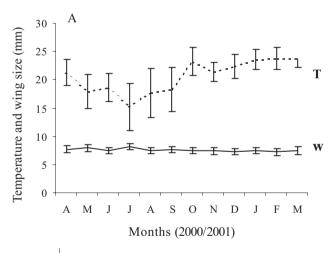


Figure 1. Seasonal variation of fecundity (dashed line) and temperature (solid line)



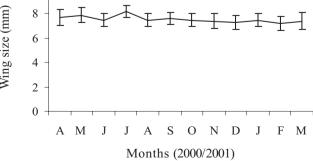
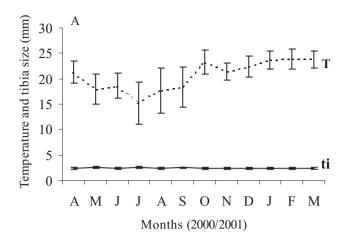


Figure 2. A. Seasonal variation of wing size (solid line) and temperature (dash line) and B. Stable trajectory of wing size.



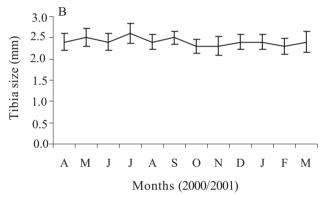


Figure 3. A. Seasonal variation of tibia size (solid line) and temperature (dash line) and B. Stable trajectory of tibia size.

correlation observed between wing size and temperature (r = -0.76, P < 0.05) and tibia size and temperature (r = -0.77, P < 0.05). A moderate positive correlation (r = 0.30, P < 0.05) between wing size and fecundity (Fig. 6), and tibia size and fecundity (r = 0.30, P < 0.05) was also detected (Fig. 7). Analysis of the correlation between wing and tibia sizes showed a strong positive correlation (r = 0.66, P < 0.05) between the two variables (Fig. 8).

The weak oscillations found for fecundity, wing and tibia size indicate that the three characters are kept relatively constant over the year, suggesting a weak impact of the seasonality. The negative correlation between body size (wing and tibia) and temperature was expected since over warm months the abundance of flies is larger than in cold months, resulting frequently in strong competition for food (Von Zuben *et al.* 1993, Reis *et al.* 1994). Considering the usual strong correlation of body size to fecundity found in most Diptera (So & Dudgeon 1989a,b; Armbruster & Hutchinson 1998; Bochdanovits & De Jong 2003), the results here obtained are surprising, but perhaps stems from rather restricted variation in body size in this tropical local.

Seasonal fluctuations in the physical environment may affect the resource base on which the organisms feed (Hannon & Ruth 1997). The temporal oscillations in blowflies have been studied frequently to analyze the

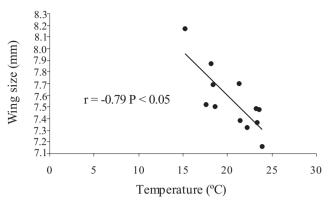


Figure 4. Correlation analysis between wing size and temperature.

association between seasonality and abundance of adults (Linhares 1981, Mendes & Linhares 1993, Wall *et al.* 2001). The results of these studies have revealed that *Chrysomya* species have been colonizing new areas in Americas with noticeable success. As a consequence, the structure of the Brazilian blowfly fauna has been modified.

Among all environmental factors, temperature has been considered essential since it can directly influence the population dynamics of insects, such as the population growth of *Musca domestica* (Linnaeus), particularly in equatorial and tropical zones, where there are high densities of this species (Levine & Levine 1991). Although some studies have been designed to investigate population behavior in response to temperature, they have focused specifically on geographic variation, genetic divergence and natural selection (Huey *et al.* 1991, Partridge *et al.* 1994, Santos *et al.* 1997), differing from the present investigation, which focused on the census of life history characters.

The effects of temperature on the development and survival of insects have been extensively investigated (Roy et al. 1991, Bhattacharya & Banerjee 2001, Thind & Dunn 2002). The rates of physiological processes are strongly influenced by body temperature (Hochachka & Somero 1984, Prosser 1986) and this thermal sensitivity can profoundly affect

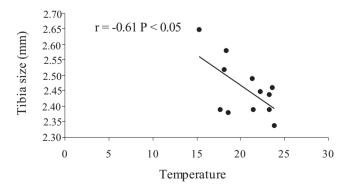


Figure 5. Correlation analysis between tibia size and temperature.

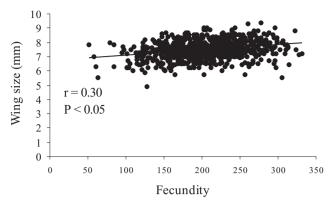


Figure 6. Correlation analysis between wing size and fecundity.

the behaviour, ecology and evolution of ectotherms (Heinrich 1981, Huey 1982).

The responses to temperature seem to vary among species and taxonomic groups. Outbreaks of many defoliator species are apparently synchronised over wide geographical areas (Royama 1984, Shepherd et al. 1988). Explanations of synchrony include among other factors, the theory of climate release (Wellington et al. 1950, Greenbank 1956). C. megacephala is currently one of the most abundant blowfly species in Brazil. We believe that the present results explain at least in part the success of the species after the occurrence of the biological invasion, since it maintains a very stable fecundity in spite of seasonal changes. Von Zuben et al. (1996) investigated the survivorship curve and entropy and observed that the shape of the survivorship curves for males and females of C. megacephala are close to a rectangular distribution. characterising a tendency of occurrence of the majority of deaths at later ages. These results indicate that C. megacephala is probably a species, which exhibits low mortality rates over the fertility period, guaranteeing its offspring to next generation. In conclusion, the success of C. megacephala both as invader and coloniser is probably strongly associated to fecundity and survivorship strategy.

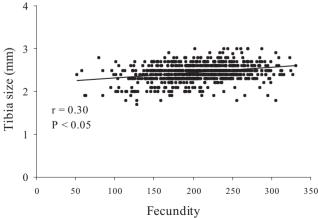


Figure 7. Correlation analysis between tibia size and fecundity.

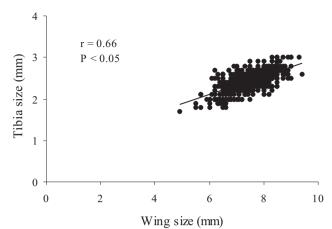


Figure 8. Correlation analysis between wing and tibia size.

Acknowledgements

CR was supported by scholarship from FAPESP (00/07992-9). WACG was partially supported by a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico.

Literature Cited

Armbruster, P. & R.A. Hutchinson. 2002. Pupal mass and wing length as indicators of fecundity in *Aedes albopictus* and *Aedes geniculatus* (Diptera: Culicidae). J. Med. Entomol. 39: 699-704.

Baumgartner, D.L. & B. Greenberg. 1984. The genus *Chrysomya* (Diptera: Calliphoridae). J. Med. Entomol. 21: 105-113.

Bhattacharya, B. & T.C. Banerjee. 2001. Factors affecting egg-laying behaviour and fecundity of *Callosobruchus chinensis* (L.) (Coleoptera: Bruchidae) infesting stored pulses. Orien. Ins. 35: 373-386.

Bochdanovits, Z. & G. De Jong. 2003. Temperature dependent larval resource allocation shaping adult body size in *Drosophila melanogaster*. J. Evol. Biol. 16: 1159–1167.

Brewer, R. 1994. The science of ecology. Saunders College Publishing, 2nd ed., Ft Woth, USA, 773p.

Brown, M.W. 1993. Population dynamics of invading pests: Factors governing success, p.203-218, In K.C. Kim & B.A. Mc Pheron (eds.), Evolution of insect pests: Patterns of variation. John Wiley & Sons, New York, 493p.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick I. The role of climate. Can. J. Zool. 34: 453-476.

- **Greenberg, B. 1988.** *Chrysomya megacephala* (F.) (Diptera: Calliphoridae) collected in North America and notes on *Chrysomya* species present in the New World. J. Med. Entomol. 25:199-200.
- Greenberg, B. & M.L. Szyska. 1984. Immature stages and biology of fifteen species of Peruvian Calliphorid (Diptera). Ann. Entomol. Soc. Am. 77: 88-517.
- Godoy, W.A.C., C.J. Von Zuben, S.F. Reis & F.J. Von Zuben. 1996. Dynamics of experimental populations of native and introduced blowflies (Diptera: Calliphoridae): Mathematical modelling and the transition from asymptotic equilibrium to bounded oscillations. Mem. Inst. Oswaldo Cruz 97: 641-648.
- **Gotelli, N.J. 1995.** A primer of ecology. Sinauer Associates Inc, Sunderland, 206p.
- Guimarães, J.H., A.P. Prado & M. Buralli. 1979. Dispersal and distribution of three newly introduced species of *Chrysomya* Robineau-Desvoidy in Brasil (Diptera, Calliphoridae). Revta. Bras. Ent. 23: 245-255.
- Hannon, B. & M. Ruth. 1997. Modelling dynamic biological systems. Springer, New York, 399p.
- **Hanselman, D. & B. Littlefield. 1997.** Matlab, the language of technical computing. Prentice Hall, N. J, 429p.
- **Heinrich**, **B. 1981.** Ecological and evolutionary perspectives, p.236-302. In B. Heinrich (ed.), Insect thermoregulation. John Wiley & Sons, New York, 329p.
- **Hengeveld, R. 1989.** Dynamics of biological invasions, Chapman & Hall, London, 160p.
- Hochachka, P.W. & G.N. Somero. 1984. Biochemical adaptation, Princeton University Press. Princeton, NJ, 537p.
- Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles p. 25-91. In C. Gans & F.H. Pough (eds.), Biology of the Reptilia. Academic Press, Cambridge, UK, 199p.
- **Huey, R.B., L. Partridge & K. Fowler. 1991.** Thermal sensitivity of *Drosophila melanogaster* responds rapidly to laboratory natural selection. Evolution 45: 751-756.
- **James, A.C. & L. Partridge. 1998.** Geographic variation in competitive ability in *Drosophila melanogaster*. Am. Natur. 151: 530-537.
- **Lande, R. 1993.** Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Natur. 142: 911-927.
- Levine, O.S. & M.M. Levine. 1991. Houseflies (Musca

- domestica) as mechanical vectors of Shigellosis. Inf. Imm. 31: 445-452.
- **Linhares, A.X. 1981.** Synanthropy of Calliphoridae and Sarcophagidae (Diptera) in the city of Campinas, São Paulo, Brazil. Revta. Bras. Ent. 25: 189-215.
- **Linhares**, **A.X. 1988.** The gonotrophic cycle of *Chrysomya megacephala* (Diptera: Calliphoridae) in the laboratory. Revta. Bras. Ent. 32: 383-392.
- **Mendes, J. & A.X. Linhares. 1993.** Atratividade por iscas e estágios de desenvolvimento ovariano em várias espécies sinantrópicas de Calliphoridae (Díptera). Revta. Bras. Ent. 37: 157-164.
- Pimentel, D. 1993. Habitat factors in new pest invasions p. 165-181. In K.C. Kim & B.A. McPheron (eds.) Evolution of insect pests: Patterns of variation. John Wiley & Sons, New York, 493p.
- Partridge, L., B. Barrie, K. Fowler & V. French. 1994. Evolution and development of body and cell size in *Drosophila melanogaster* in response to temperature. Evolution 48: 1269-1276.
- Prado, A.P. & J.H. Guimarães. 1982. Estado atual da dispersão e distribuição do gênero *Chrysomya* Robineau-Desvoidy na região neotropical (Diptera, Calliphoridae). Revta. Bras. Ent. 26: 225-231.
- **Prosser, C.L. 1986.** Adaptational Biology: Molecules to organisms. John Wiley & Sons, New York, 766p.
- Reis, S.F., C.J. Von Zuben & W.A.C. Godoy. 1999. Larval aggregation and competition for food in experimental populations of *Chrysomya putoria* (Wied.) and *Cochliomyia macellaria* (F.) (Dipt. Calliphoridae). J. Appl. Entomol. 123: 485–489.
- Reis, S.F., G. Stangenhaus, W.A.C. Godoy, C.J. Von Zuben & O.B. Ribeiro. 1994. Variação em caracteres bionômicos em função da densidade larval em *Chrysomya megacephala* e *Chrysomya putoria* (Diptera, Calliphoridae). Revta. Bras. Ent. 38: 33-46.
- **Reis, S.F., M.A. Teixeira, F.J. Von Zuben, W.A.C. Godoy** & C.J. Von Zuben. 1996. Theoretical dynamics in experimental populations of introduced and native blowflies (Diptera: Calliphoridae). J. Med. Entomol. 33: 537-544.
- **Ribeiro, S.C., A.M. Souza & C. Lomônaco. 1995.** Influência de fatores ambientais na determinação do tamanho de *Musca domestica* L. (Diptera: Muscidae). Rev. Bras. Biol. 55: 633-637.
- Roy, R., A.B. das & T. Farkas. 1991. Role of environmental thermal fluctuation in seasonal-variation of fatty-acid

- composition of total lipid in fat-body of the cockroach, *Periplaneta americana* (Linn). J. Therm. Biol. 16: 211-215.
- **Royama, T. 1984.** Population dynamics of the spruce budworm, *Choristoneura fumiferana*. Ecol. Mon. 54: 429-462.
- Santos, M., D.J. Borash, A. Joshi, N. Bounlutay & L.D. Mueller. 1997. Density-dependent natural selection in *Drosophila*: Evolution of growth rate and body size. Evolution 51: 420-432.
- Sheperd, R.F., D.D. Benett, J.W. Dale, S. Tunnock, R.E. Dolph & R.W. Thier. 1988. Evidence of synchronised cycles in outbreak patterns of douglas-fir tussock moth, *Orgyia pseudotsugata*. Mem. Entomol. Soc. Can. 146: 107-121.
- **Smith, K.G.V. 1986.** A manual of forensic entomology. University Printing House, Oxford, 205p.
- **So, P.M. & D. Dudgeon. 1989a.** Variation in the life history parameters of *Hemipyrellia ligurriens* (Diptera: Calliphoridae) in response to larval competition for food. Ecol. Entomol. 14: 109-166.
- **So, P.M. & D. Dudgeon. 1989b.** Life history responses of larviparous *Boettcherisca formosensis* (Diptera: Sarcophagidae) to larval competition for food, including comparisons with oviparous *Hemipyrellia ligurriens* (Calliphoridae). Ecol. Entomol. 14: 349-356.
- Teixeira, M.A., F.J. Von Zuben, W.A.C. Godoy, C.J. Von Zuben & S.F. Reis. 1998. Delay density dependence at the immature stage in insects and the dynamic behavior of nonlinear difference equations. Ciênc. Cult. 50: 268-272.
- **Thind, B.B. & J.A. Dunn. 2002.** A laboratory evaluation of a regulated airflow through wheat at four combinations of temperature and humidity on the

- productivity of three species of stored product mites. Exp. Appl. Acarol. 27: 89-102.
- **Uchmanski, J. 1999.** What promotes persistence of a single population: An individual bases model. Ecol. Mod.115: 227-241.
- **Ullyett, G.C. 1950.** Competition for food and allied phenomena in sheep-blowfly populations. Phil. Trans. Roy. Soc. Lond. 234B: 79-174.
- Wall, R., J.J. Howard & J. Bindu. 2001. The seasonal abundance of blowflies infesting drying fish in southwest India. J. App. Ecol. 38: 339-348.
- Wellington, W.G., J.J. Fettes, K.B. Turner & M. Belya. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. J. Res. Section D. Zoology 28: 308-331.
- Wells, J.D. 1991. *Chrysomya megacephala* (Diptera: Calliphoridae) has reached the continental United States: Review of its biology, pest status and spread around the world. J. Med. Entomol. 28: 471-473.
- **Zuben, C.J. Von, S.F. Reis, J.B.R. Val, W.A.C. Godoy & O.B. Ribeiro. 1993.** Dynamics of a mathematical model of *Chrysomya megacephala* (Diptera: Calliphoridae). J. Med. Entomol. 30: 443-448.
- **Zuben, C.J. Von, W.A.C. Godoy, E.L.A. Monteiro-Filho. 1996.** Curva de sobrevivência e estimativa de entropia em *Chrysomya megacephala* (Diptera, Calliphoridae). Revta. Bras. Ent. 40: 221-224.
- **Zumpt, F. 1965.** Myiasis in man and animals in the Old World. Butterworths, London, 267p.

Received 05/IV/04. Accepted 14/XII/04.