

Original article

Life table of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae)

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Abstract

The life history of the oriental latrine fly, *Chrysomya megacephala* (Fabricius), was studied at 26 °C in the laboratory. The raw data were analyzed based on the age–stage, two-sex life table, in order to take both sexes and the variable developmental rate among individuals and between sexes into consideration. The intrinsic rate of increase (r), the finite rate of increase (λ), the net reproduction rate (R_0) and the mean generation time (T) of *C. megacephala* were 0.2182, 1.2438 d⁻¹, 91.7 offspring/individual and 20.7 days, respectively. The life expectancy of a newborn egg is 32 days. The maximum reproductive value of females is on the 19th day, which coincides with the total pre-oviposition period counted from birth. The two-sex life table analysis gives a comprehensive description of the stage differentiation of *C. megacephala*. © 2005 Elsevier SAS. All rights reserved.

Keywords: *Chrysomya megacephala* (Fabricius); Life table; Reproduction

1. Introduction

Blowflies are distributed worldwide and cause medical problems and losses to the animal industry (Zumpt, 1965; Greenberg, 1971, 1973; Kuhlhorn, 1983; Ghandour, 1988). Norris (1965) gave a comprehensive review on the bionomics of blowflies. Among blowflies, the oriental latrine fly *Chrysomya megacephala* (Fabricius) is one of the most common blowflies in Egypt (Gabre 1994) and its range is expanding (Greenberg, 1988; Wells, 1991; Tomberlin et al., 2001). Greenberg (1971, 1973) reported that this species is among the most dangerous dipteran vectors of enteric pathogens. In Malaysia, *C. megacephala* is the dominant vector of helminth parasite eggs (Sulaiman et al., 1988, 1989). On the positive side, *C. megacephala* is an important pollinator of mango in Australia (Anderson et al., 1982), and in Taiwan, farmers increase *C. megacephala* population to increase pollination of mango (Hu et al., 1995). Under laboratory conditions, *C. megacephala* was able to develop on a variety of living

animals including catfish, toads, frogs, lizards, and pigeons (Roy and Dasgupta, 1971). Esser (1990, 1991) and Gabre (1994) studied the factors influencing oviposition, larval growth, mortality, longevity, and reproduction of *C. megacephala*, but no life table was developed.

A life table describes the development, survival, and fecundity of a cohort and provides basic data on population growth parameters. A life table developed from field data may be used to estimate fitness of a population as influenced by various biotic and abiotic factors. Unfortunately, field life tables are often difficult to construct because tracing population survival and reproduction in the open field under variable environmental conditions is exceedingly difficult. On the other hand, life tables constructed using laboratory data collected under controlled conditions and are useful in revealing the maximal growth potential of a population. Traditional life tables, e.g., Lotka (1907, 1922) and Lewis–Leslie matrix (Lewis, 1942; Leslie, 1945), deal only with female populations and ignore the variable developmental rates among individuals. However, most economic species of Lepidoptera, Coleoptera, Orthoptera, and Diptera pests are bisexual having both males and females, and both sexes may cause economical loss or be vectors of disease. Moreover, developmental rates often differ between the sexes and among individuals

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Table 1

The developmental time (days), longevity (days), and fecundity (eggs/female) of *C. megacephala* at 26 °C and 60–70% R.H.

Parameter	Stage	n	Mean	SEM
Developmental time (days)	Egg	100	1	0
	Larva	86	5.4	0.1
	Pupa	85	5.3	0.1
Adult longevity (days)	Male	44	25.3	0.3
	Female	41	25.8	0.4
Adult pre-oviposition period (APOP) of female (days)	Female	41	6.6	0.1
Total pre-oviposition period (TPOP) of female (days)	Female	41	18.9	0.2
Fecundity (F) (eggs/female)	Female	41	223.7	2.4

(Istock, 1981). Wells and Kurahashi (1994) found the variation in the developmental rate in *C. megacephala*, and used the data to construct confidence bands about growth curves for use in forensic entomology. In nature, intra-population variation in developmental time is important for a population to survive the selection of unpredictable harsh environmental conditions (e.g., see Price, 1997 Chapter 14). To consider both sexes and variable development rates among individuals, Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table. The raw data analysis of a two-sex life table is described in detail by Chi (1988), and is used here to calculate the life table parameters for *C. megacephala*.

2. Materials and methods

The laboratory colony of *C. megacephala* used in this study was initially established in the Department of Entomology, Faculty of Science, Cairo University in 1990 (Gabre, 1994). Adults from the stock colony of *C. megacephala* were kept in cages (38 × 38 × 56 cm) at 26 °C, 14 h photoperiod and 60–70% R.H. The cages were made with a wooden floor, a glass roof, and wire gauze on three of the sides. The fourth side was wooden with a circular hole fitted with a cloth sleeve to facilitate daily feeding, cleaning of the cage, and removal of eggs. Adults were supplied daily with granular sucrose, water, and beef meat (beef hereafter). Water was supplied by dipping a piece of cotton as a wick in a bottle filled with water, and the beef was provided *ad libitum* in a Petri dish. Egg batches were removed daily and transferred to a fresh piece of beef placed in a rearing enamel bowl (35 cm in diameter) covered with muslin secured with a rubber band. At the pre-pupal stage, dry autoclaved sawdust was added to the bowl as a medium for pupation. Pupae were sieved from the sawdust and transferred to adult cages described above for adult emergence. Detailed information on the biology and reproductive cycle of *C. megacephala* is given in Gabre (1994).

2.1. Life table study and data analysis

For the life table study, 100 eggs laid during a 24 h period were collected and put on a piece of fresh beef for hatching. Each day, newly hatched larvae were transferred individually to 10 g beef placed in a 100 ml beaker covered with muslin secured with a rubber band. At the pre-pupal stage, sawdust

was added to the beaker for pupation. The emerged adults were paired and kept in a muslin covered 1 l glass jar, supplied with water, sucrose, and a piece of fresh beef. Sucrose and water were checked daily and renewed as necessary, while the beef was changed daily. Survival and fecundity were recorded for each individual until the death of the adult.

The raw data for 100 individuals were analyzed using the age-stage, two-sex life table approach (Chi and Liu, 1985; Chi, 1988). The standard errors of the life table parameters were estimated by using a Jackknife technique (Sokal and Rohlf, 1995). The computer program used in this analysis (TWOSEX, Chi, 1997) is written in Visual BASIC for the Windows operating system and is available at <http://140.120.197.173/Ecology/prod02.htm> (National Chung Hsing University, Taichung, Taiwan).

3. Results and discussion

Stage developmental time, adult longevity, and fecundity on beef are given in Table 1. In our study, *C. megacephala* females laid only one egg batch averaging 223.7 eggs. All eggs hatched successfully within 1 day, and of these 85 emerged as adults, of which 44 were males and 41 females (a 38% pre-adult survival rate). These results are similar to those of Goodbrod and Goff (1990) who also studied the development of *C. megacephala* on beef liver and found a total pre-adult mortality of 44% at the density of 1 larva/g liver. Another laboratory studies of *C. megacephala* reared on unsalted fresh cod yielded an average of 221 (range 151–228) ripe oocytes per female and produced a 1:1 sex ratio (Esser, 1991).

The age-stage specific survival rate (s_{ij}) of *C. megacephala* (Fig. 1) gives the probability that a newly laid egg will survive to age i and stage j . These curves also show the survivorship and stage differentiation as well as the variable developmental rate. For example, the probability that a newborn egg survives to the adult stage is 0.44 for males and 0.41 for females. All emerged adults survived 20 days and the mean longevity of male and female was 25.3 and 25.8 days, respectively. On salted cod, longevity ranged from 47 to 55 days (Esser, 1991).

The age of first reproduction by females has an important effect on population growth, and many researchers plot the fecundity curve on female age thus defining the pre-

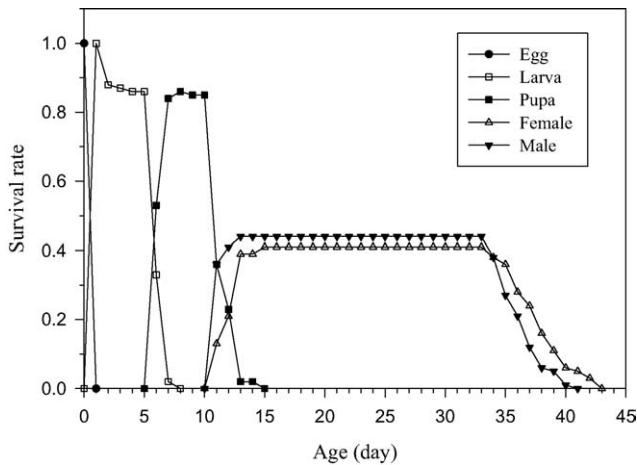


Fig. 1. The age–stage specific survival rate of *Chrysomya megacephala* at 26 °C and 60–70% R.H.

oviposition period as the time between emergence and first oviposition (APOP). Ignoring the length and variation of pre-adult stages, APOP for *C. megacephala* is 6.6 ± 0.1 days (mean \pm SE). Chi (1988) and Chi and Yang (2003) discussed the problem of fecundity curves based only on adult age.

Fig. 2 illustrates the age-specific survival rate (l_x), female age-stage specific fecundity ($f_{x,t}$), the age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) in *C. megacephala*. The age-specific survival rate (l_x) is the probability that a new egg will survive to age x and is calculated by pooling all individuals of both sex. The curve of l_x is a simplified version of the curves in Fig. 1. The m_x curve is plotted on the age since birth.

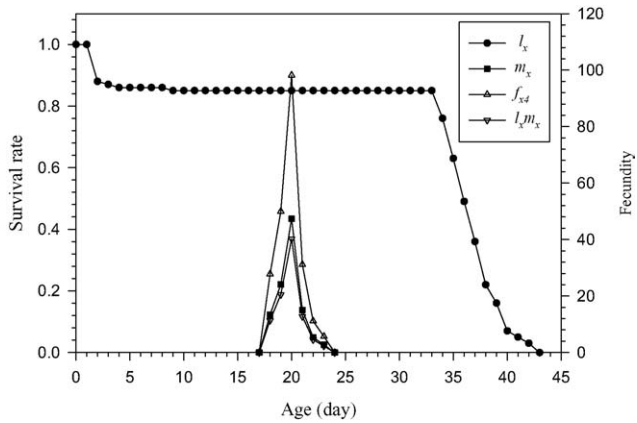


Fig. 2. The age-specific survival rate (l_x), the age–stage specific fecundity ($f_{x,t}$) of the female stage, the age-specific fecundity (m_x) and the age-specific maternity ($l_x m_x$) of *Chrysomya megacephala* at 26 °C and 60–70% R.H.

Table 2
The population parameters of *C. megacephala* at 26 °C and 60–70% R.H.

Population parameter	Calculated by using all individuals	Estimated by using Jackknife method	
		Mean \pm SE	CV \times 100
The intrinsic rate of increase r (d^{-1})	0.2182	0.2185 ± 0.0062	2.83
The finite rate of increase λ (d^{-1})	1.2438	1.2442 ± 0.0077	0.62
The net reproduction rate R_0 (offspring/individual)	91.7	91.7 ± 11.1	12.1
The mean generation time T (d)	20.7	20.7 ± 0.2	0.97

The intrinsic rate of natural increase (r), the finite rate of natural increase (λ), the net reproduction rate (R_0) and the mean generation time (T) of *C. megacephala* were $0.2182 d^{-1}$, $1.2438 d^{-1}$, 91.7 offspring/individual, and 20.7 days, respectively (Table 2). In the two-sex life table, the relationship between the mean fecundity of female (F) and the net reproduction rate (R_0) is given as $F = (N/N_f) R_0$ (Chi, 1988), where N is the number of eggs used at the beginning of the life table study, and N_f is the number of females emerging from the N eggs. In this paper, $N = 100$, $N_f = 41$, $F = 223.7$, $R_0 = 91.7$. The variability of population parameters estimated using the Jackknife method (Sokal and Rohlf, 1995; Meyer et al., 1986) are given in Table 2, and show that the coefficient of variation is relatively large only for R_0 (i.e., 12.1%). The intrinsic rate of increase (r) is a more useful statistic for comparing the population growth potential of different species than is R_0 (Price, 1997). According to Southwood (1981) and Huffaker et al. (1984), r -strategists are characterized by a high r , a large fecundity (large R_0) and short generation time (T). El-Shazly et al. (1995) studied the blowflies *Chrysomya albiceps* and *Parasarcophaga argyrostoma*, and found that r and the finite rate increase (λ) of *C. albiceps* were 0.29 and 0.75, respectively, and those for *P. argyrostoma* were 0.16 and 0.85. They concluded that both species are r -strategists. However, because λ equals e^r and because $r > 0$, $\lambda > 1$ suggesting calculation errors by El-Shazly et al. (1995). Recomputing λ for *C. albiceps* and *P. argyrostoma* yields values for λ of 1.34 and 1.17 respectively. In *C. megacephala*, $r = 0.2182$ and $\lambda = 1.2438$ suggesting that it is also an r -strategist.

The life expectancy (e_{ij}) of each age-stage group of *C. megacephala* is plotted in Fig. 3. The e_{ij} estimate the time individuals of age i and stage j are expected to live. For example, the life expectancy of a new egg is 32 days with the life expectancy decreasing with age. The reproductive value (v_{ij}) is the expectation of future offspring of individuals of age i and stage j (Fig. 4) (Fisher, 1930; Pianka, 1994). The reproductive value for a new egg (v_{01}) is the finite rate of increase (λ), while peak reproductive value occurred at age 19 days. This implies that, compared to other ages, female individuals of age 19 make the highest contribution to the population. If the pre-oviposition period is counted as time from birth to first reproduction in females (the total pre-oviposition period, TPOP), the mean TPOP for all *C. megacephala* females is 18.9 ± 0.2 days (mean \pm SE) – a value close to the age of peak reproductive value (Fig. 4).

The ability to predict stage differentiation of a pest population is important in many applied areas of research. For

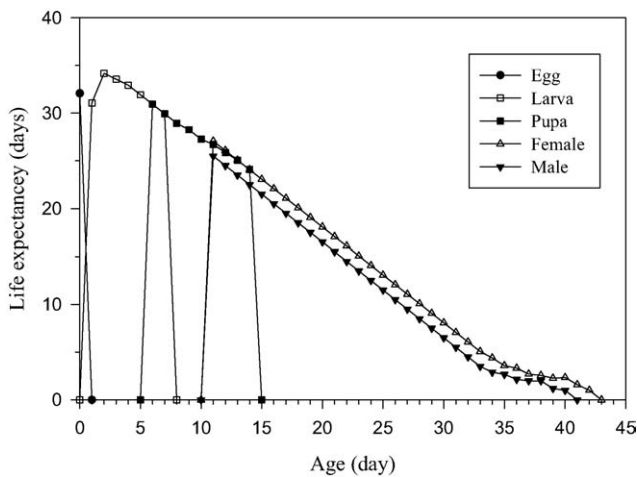


Fig. 3. The life expectancy of each age-stage group of *Chrysomya megacephala* at 26 °C and 60–70% R.H.

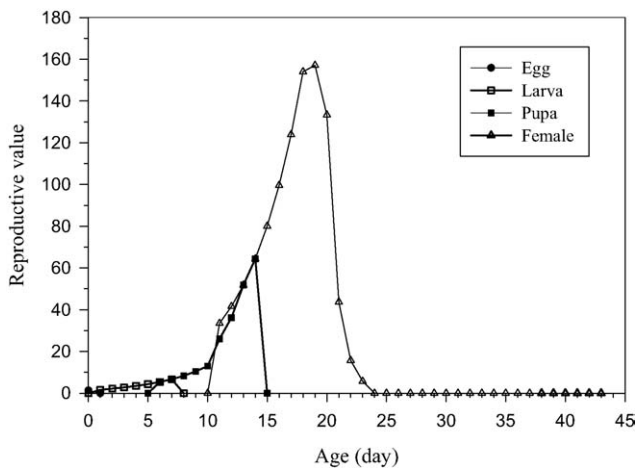


Fig. 4. The reproductive value of each age-stage group of *Chrysomya megacephala* at 26 °C and 60–70% R.H.

example, in forensic entomology Nishida (1984) studied the growth rate of *C. megacephala* at different temperatures and found the data could be used to estimate the postmortem intervals with considerable accuracy. The two-sex life table gives a comprehensive overview on the changes in stage structure in *C. megacephala*, and this information can be useful in determining the postmortem intervals, especially if the stage structure of the fly population on the corpse is recorded in a death investigation. Also susceptibility to insecticide varies among developmental stages in many economic species, and hence information on stage structure may be crucial in pest and vector management. Chi (1990) used the two-sex life table to simulate timing of pest control based on the change of age-stage structure during the growth of a population. The inclusion of predator and prey age structure is important in understanding predator–prey relationship in biological control (e.g., Hassell, 1978). Chi and Yang (2003) studied the predation rate of *Propylaea japonica* Thunberg based on the age-stage, two-sex life table, and showed how changes in predation rate with age and stage could be incorporated in a life table study.

Life table studies may be very time-consuming, and as Norris's (1965) cautioned blowfly studies under laboratory conditions may be of dubious value in evaluating their potential in the field because many biotic and abiotic factors influence their survival, developmental rates, and fecundity. However, while this is in part true, life history studies made under laboratory conditions allow researchers to collect the data needed for life table analysis to estimate their biotic potential under specific conditions, and these data can be used as basis for simulation models for field use that include other factors (Gutierrez, 1996).

Hence, for a thorough understanding of the population dynamics of *C. megacephala*, data suitable for life table analysis must be collected on major diets under both laboratory and field conditions. For example, nutrients and food preference play important roles on the developmental rate and fecundity of organisms. *C. megacephala* preferentially oviposited on fish spiked with recently laid eggs (Esser, 1990), and D'Almeida et al. (1996) found that meat is a less suitable diet than fish for *C. megacephala*.

Because of *C. megacephala*'s medical and veterinary importance and its expanding geographic distribution, the ecology of *C. megacephala* deserves more attention than it has received so far.

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