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Autor(en): **El-Shazly, Mohammed M. / El-Sherif, Hanaa A. / Omar, Aziza H.**

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# A comparative study on the reproductive strategies of a larviparous and an oviparous fly associated with carrion

MOHAMMED M. EL-SHAZLY, HANAA A. EL-SHERIF & AZIZA H. OMAR

Entomology Department, Faculty of Science, Cairo University, Giza, Egypt.

The basic developmental and reproductive parameters as well as age specific survivorship and fecundity of the oviparous Western banded blow fly, *Chrysomya albiceps* (WIEDEMANN) (Calliphoridae) and the larviparous gray flesh fly *Parasarcophaga argyrostoma* (ROBINEAU-DESVOIDY) (Sarcophagidae) were studied under laboratory controlled conditions. The bionomic strategies of both species were investigated by analyzing life tables at optimum conditions. Analysis of data revealed that both species were "r-strategists". The gross reproductive rate (GRR), net reproductive rate (Ro), mean generation time in days (T), intrinsic rate of natural increase (rm), and the finite rate of population increase ($\lambda$) were 114.87, 79.26, 15.18, 0.29 and 0.75, for *C. albiceps*, respectively. The corresponding values for *P. argyrostoma* were 207.03; 181.09; 32.79 ; 0.16 and 0.85, respectively.

Keywords: *Chrysomya* , *Parasarcophaga,* Development, Bionomic strategy, Population growth

## INTRODUCTION

The Western banded blow fly *Chrysomya albiceps* (WIEDEMANN) and the Gray flesh fly *Parasarcophaga argyrostoma* (ROBINEAU-DESVOIDY) are among the most common calyptrate muscoid flies in Egypt. The medical and veterinary importance of both species, together with other myiasis causing calliphorids and sarcophagids, have been documented by earlier and recent authors (STRICKLAND & ROY, 1942; HERMS, 1947; NOBLE & NOBLE, 1961; KENNEY *et al.,* 1976 and EL-SHERIF, 1986). Detailed information on the reproduction and development of *C. albiceps* were given by SMIT (1931), CUTHBERTSON (1933) OMAR (1974, 1992). On the other hand, the biology and the reproductive cycle of *P. argyrostoma* have been dealt with by ZOHDY & MORSY (1982) and SHOELLER-RACCAUD *et al.* (1992).

Although many blow flies and flesh flies are similar in food habits and occupy almost the same biotopes, comparative studies concerning different ecological aspects between different species of the two families are relatively few (SO & DUDGEON, 1989, 1990 and EESA *et al.,* 1993).

Therefore, the aim of the present paper is to compare the rate of population growth between *C. albiceps* and *P. argyrostoma* by constructing fecundity life tables and analyzing age specific survivorship under specified experimental conditions.

## MATERIAL AND METHODS

The relationships between the intrinsic rate of natural increase (rm) and the natural life tables of artificial populations of *C. albiceps* and *P. argyrostoma* were determined by constructing the appropriate life tables for each species separately (BIRCH, 1948). The exact form of these relations was quoted from MAY (1981):

$$\sum [LxMx.\exp(-rm.X)] \approx 1 \qquad \text{Equation 1}$$

where Lx is the number of females, as a proportion of unity, alive at age interval x (=1 day); Mx is the number of female progeny per female per day.

$$rm = \frac{LnRo}{T} \qquad \text{Equation 2}$$

where Ro is the net reproductive rate, i.e., number of times a population will multiply itself per generation time (T), the latter could be defined also by the straight forward statistical fashion (Equation 3)

$$T = \frac{\sum Lx.Mx.X}{\sum Lx.Mx} \qquad \text{Equation 3}$$

The finite rate of natural increase (λ) and the gross reproductive rate (GRR) were calculated from formulae 4 & 5

$$\lambda = e^{r} \qquad \text{Equation 4}$$

Where r designated rm.

$$GRR = \sum Mx \qquad \text{Equation 5}$$

To calculate the above statistics, it was necessary to calculate several life table properties including survival of eggs, sex ratio, larval and pupal survival and schedules for oviposition or larviposition of the two species under the same experimental conditions. Thus, the development of both species was followed-up by constructing artificial population for each species separately, at 27 °C, 60% R.H. and 14L-10D long day conditions. The effect of cannibalism on larval survivorship and thence the other innate population parameters was completely avoided by supplying the insects with sufficient amounts, of non-fatty meat. Each population consisted of 200 pairs of newly emerged adults, raised in sufficiently large rearing cages (30x30x60 cm). Detailed descriptions of rearing *C. albiceps* and *P. argyrostoma* have been given by OMAR (1974); ZOHDY & MORSY (1982); EL-SHERIF (1986), and OMAR (1992).

## RESULTS AND DISCUSSION

### *Development of immature stages*

Duration of immature stages of *C. albiceps* and *P. argyrostoma* is given in Tab.1 which reflects a highly significant difference between larval and pupal duration of these two species. *C. albiceps* exhausted 5.37 and 5.51 days in larval and pupal stages, respectively. The corresponding values for *P. argyrostoma* were 7.16 and 10.95 days.

Tab.1: Development and survival of immature stages of *P. argyrostoma* as compared to *C. albiceps* .

| Developmental Stage | Stage Duration in Days Mean±SD | | Significance Test | % Survival | | Significance Test |
|---|---|---|---|---|---|---|
| | *Parasarcophaga* | *Chrysomya* | | *Parasarcophaga* | *Chrysomya* | |
| Eggs | - | 1±0 | - | - | 79% | - |
| Larva | 7.16±0.47 | 5.37±0.5 | <0.0001 | 94% | 93% | NS* |
| Pupa | 10.95±0.38 | 5.51±0.5 | <0.0001 | 96% | 95% | NS* |

* Non Significant p>0.05

At constant temperature of 27 °C, OMAR (1974) found that the total larval and pupal stages of *C. albiceps* were 5.5 and 5.2 days respectively. The corresponding figures for *P. argyrostoma* were 7.1 and 13.5 days at 25 °C (ZOHDY & MORSY, 1982). Therefore, it might be concluded that the developmental rate is higher in the blow fly *C. albiceps* than in the gray flesh fly *P. argyrostoma.*

Age specific survivorship curves (Fig. 1) show that survival of *P. argyrostoma* is higher than *C. albiceps*. Indeed, statistical analysis did not reflect any significant difference in the survival of the two species (Tab. 1). The lower survivorship of *C. albiceps* could be attributed to the egg mortality as indicated by the number of hatched larvae within 24 hours from oviposition. Such egg mortality caused a sudden drop in the survivorship of the population (Fig. 1).

### *Reproductive Biology*

*Sexual Maturation:* Tab. 2 indicates that the short preoviposition period (4.25 days) of *C. albiceps* was associated with short female life span (18.07 days), whereas the longer prelarviposition period of *P. argyrostoma* (10.07 days) was associated with longer female life span (30.99 days).

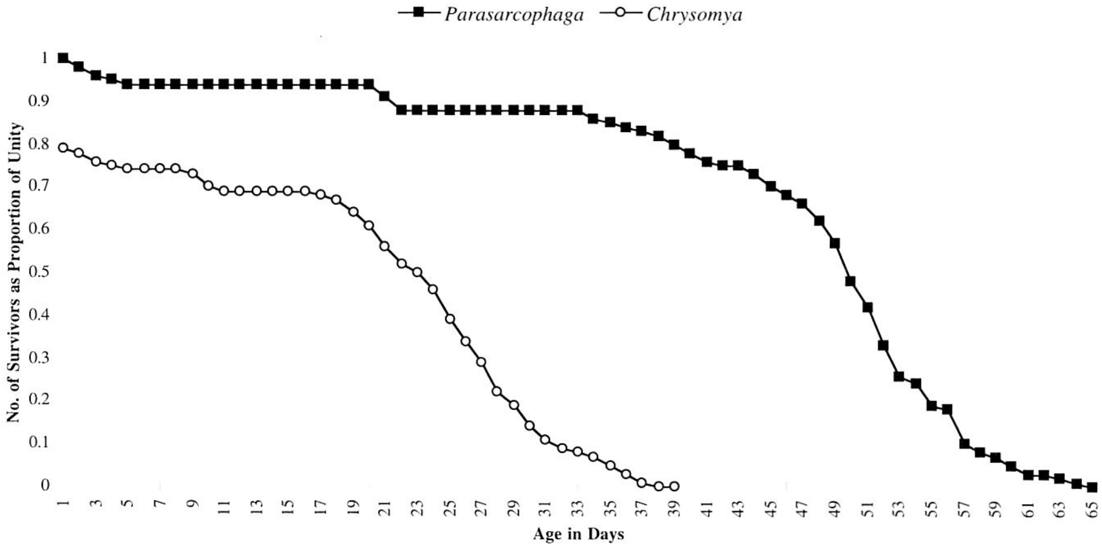

Fig. 1: Age Specific Survivorship of *Parasarcophaga argyrostoma* as compared to *Chrysomya albiceps*.

Tab. 2: Reproductive biology of *P. argyrostoma* as compared to *C. albiceps*

| Parameter Tested | Mean ± SD * | | Significance Test |
|---|---|---|---|
| | *Parasarcophaga* | *Chrysomya* | |
| Preoviposition or prelarviposition period (days) | 10.07±0.36 | 4.25±0.65 | <0.0001 |
| Oviposition or larviposition period (days) | 2.78±0.49 | 1.00±0.00 | <0.0001 |
| Male Longevity (days) | 28.08±5.95 | 12.06±4.10 | <0.0001 |
| Female Longevity (days) | 30.99±7.07 | 18.07±4.60 | <0.0001 |
| Total fecundity larva or egg per female | 461.07±49.1 | 229.43±30.33 | <0.0001 |

* Standard Deviation

A brief survey of recent articles shows a more or less similar figure; thus, FERRAZ & VIENNA-FERRAZ (1992) recorded mean prelarviposition periods of 21.4 and 15.3 days for the sarcophagids, *Peckia chrysostoma* and *Adiscochaeta ingens,* respectively. The mean longevity of the former species was 59.7 days in the presence of protein rich food, the corresponding value of the latter species was 41.3 days. On the other hand, THOMAS (1993) recorded a typical life span of about 10 days and preoviposition period of 4-5 days for the calliphorid *Cochliomyia hominivorax.*

*Fecundity:* Fig. 2 illustrates the reproductive output per female in the two artificial populations irrespective to the number of ovipositing or larvipositing females. Thus a population of *C. albiceps* produce 27.02, 119.60, and 83.08 eggs on the third, forth and fifth day after adult emergence, respectively. The corresponding values for a population of *P. argyrostoma* were 132.32, 219.52, and 61.33 larvae in the tenth, eleventh and twelfth day after adult emergence, respectively. The mean number of progeny per female was 229.43 ± 30.33 eggs and 461.07 ± 49.1 larvae, respectively, for the two species. Such estimation, however, does not reflect any true superiority in the innate capacity of natural increase of *P. argyrostoma* as shown in the life tables (Tab. 3 and 4).

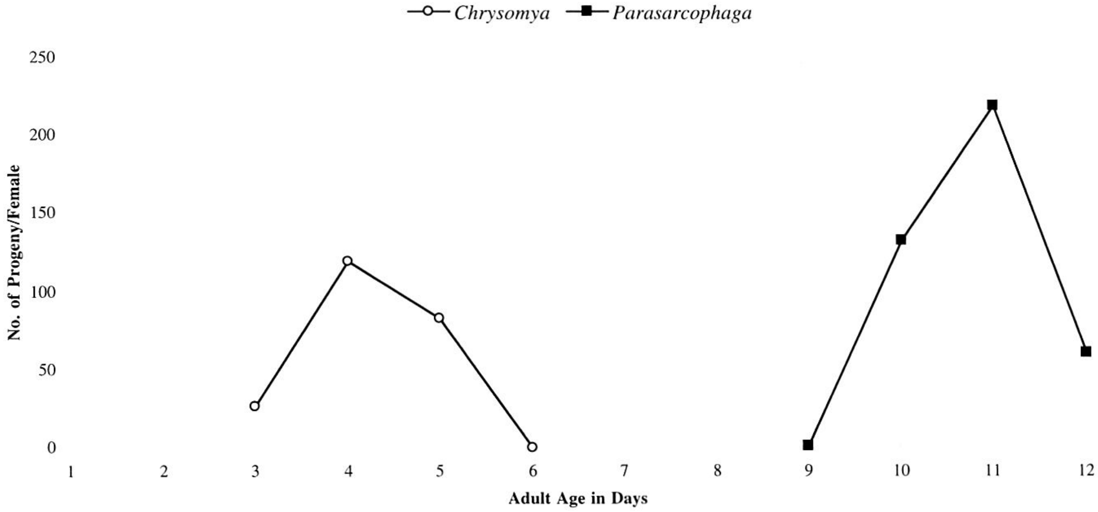

Fig. 2: Age Specific Fecundity of *Parasarcophaga argyrostoma* as compared to *Chrysomya albiceps.*

Tab. 3 : Life table analysis of *P. argyrostoma*

| X | Lx | Mx | LxMx | Equation | |
|---|---|---|---|---|---|
| **1** | 1.00 | 0.000 | 0.000 | 0.000 | **Ro = 181.09** |
| **2** | 0.98 | 0.000 | 0.000 | 0.000 | **T = 32.79** |
| **3** | 0.96 | 0.000 | 0.000 | 0.000 | **rm = 0.16** |
| **4** | 0.95 | 0.000 | 0.000 | 0.000 | **$\lambda$ = 0.85** |
| **5** | 0.94 | 0.000 | 0.000 | 0.000 | **GRR = 207.03** |
| **6** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **7** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **8** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **9** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **10** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **11** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **12** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **13** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **14** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **15** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **16** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **17** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **18** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **19** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **20** | 0.94 | 0.000 | 0.000 | 0.000 | |
| **21** | 0.91 | 0.000 | 0.000 | 0.000 | |
| **22** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **23** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **24** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **25** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **26** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **27** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **28** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **29** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **30** | 0.88 | 0.000 | 0.000 | 0.000 | |
| **31** | 0.88 | 0.450 | 0.395 | 0.003 | |
| **32** | 0.88 | 66.158 | 57.999 | 0.363 | |
| **33** | 0.88 | 109.758 | 96.221 | 0.514 | |
| **34** | 0.86 | 30.667 | 26.476 | 0.121 | |
| **35** | 0.85 | 0.000 | 0.000 | 0.000 | |
| **36** | 0.84 | 0.000 | 0.000 | 0.000 | |
| **37** | 0.83 | 0.000 | 0.000 | 0.000 | |
| **38** | 0.82 | 0.000 | 0.000 | 0.000 | |
| **39** | 0.80 | 0.000 | 0.000 | 0.000 | |
| **40** | 0.78 | 0.000 | 0.000 | 0.000 | |
| **41** | 0.76 | 0.000 | 0.000 | 0.000 | |
| **42** | 0.75 | 0.000 | 0.000 | 0.000 | |
| **43** | 0.75 | 0.000 | 0.000 | 0.000 | |
| **44** | 0.73 | 0.000 | 0.000 | 0.000 | |
| **45** | 0.70 | 0.000 | 0.000 | 0.000 | |
| **46** | 0.68 | 0.000 | 0.000 | 0.000 | |
| **47** | 0.66 | 0.000 | 0.000 | 0.000 | |
| **48** | 0.62 | 0.000 | 0.000 | 0.000 | |
| **49** | 0.57 | 0.000 | 0.000 | 0.000 | |
| **50** | 0.48 | 0.000 | 0.000 | 0.000 | |
| **51** | 0.42 | 0.000 | 0.000 | 0.000 | |
| **52** | 0.33 | 0.000 | 0.000 | 0.000 | |
| **53** | 0.26 | 0.000 | 0.000 | 0.000 | |
| **54** | 0.24 | 0.000 | 0.000 | 0.000 | |
| **55** | 0.19 | 0.000 | 0.000 | 0.000 | |
| **56** | 0.13 | 0.000 | 0.000 | 0.000 | |
| **57** | 0.10 | 0.000 | 0.000 | 0.000 | |
| **58** | 0.08 | 0.000 | 0.000 | 0.000 | |
| **59** | 0.07 | 0.000 | 0.000 | 0.000 | |
| **60** | 0.05 | 0.000 | 0.000 | 0.000 | |
| **61** | 0.03 | 0.000 | 0.000 | 0.000 | |
| **62** | 0.03 | 0.000 | 0.000 | 0.000 | |
| **63** | 0.02 | 0.000 | 0.000 | 0.000 | |
| **64** | 0.01 | 0.000 | 0.000 | 0.000 | |
| **65** | 0.00 | 0.000 | 0.000 | 0.000 | |

**List of Abbreviations**

| | |
|---|---|
| **x** | Age in days |
| **Lx** | Proportion of females alive at age |
| **Mx** | Number of female progeny/female |
| **Ro** | Net reproductive rate |
| **T** | Mean generation time |
| **rm** | Intrinsic rate of natural increase |
| **l** | Finite rate of natural increase |
| **GRR** | Gross reproductive rate |

FERRAZ & VIENNA-FERRAZ (1992) recorded mean numbers of 183.8 and 78.5 viable larvae per female flesh fly *Peckia chrysostoma* and *Adiscochaeta ingens*, respectively. On the other hand, analysis of reproductive age distribution of the blow fly *C. bezziana* estimated a mean life time fecundity of 146 female progeny (SPRADBERY & VOGT, 1993). Working with the blow fly, *Lucilia sericata*, WALL (1993) found that females of this species matured an average of 223 oocytes per batch when given access to protein ad libitum in the laboratory. The impact of fecundity on the rate of population growth of any species can be judged only through an exact analysis of life table properties.

*Life Table Analysis*

Previous workers studied the biology of *C. albiceps* and *P. argyrostoma* under various extrinsic factors (OMAR, 1974; ADHAM & HASSAN, 1979; ADHAM *et al.,* 1980 a,b; ZOHDY & MORSY, 1982, and SCHOELLER-RACCAUD *et al.,* 1992).

In the present investigation both species were raised under similar specified experimental conditions where food and space were unlimited to allow the population of each species to express its innate biotic potential. Thus data presented in Tab. 3+4 indicate that the net reproductive rate of *P. argyrostoma* is higher than that of *C. albiceps* (Ro = 181.09 & 79.26, respectively). Because the mean generation times (T) varied tremendously between both species (T= 32.79 & 15.18, respectively), it is not statistically useful to compare them using Ro which is the net replacement rate per generation.

The growth rate of the populations could be compared by estimation of the intrinsic rate of natural increase (rm) for the two species. It seemed that the rate is much greater in the blow fly than the flesh fly (rm = 0.29 & 0.16, respectively). PRICE (1984) pointed out that rm is a more useful statistics for comparing growth rates of populations of different species than Ro.

The finite rate of natural increase of a population (l) is the discrete analog of its instantaneous rate of natural increase ($\lambda = e^r$) The comparison between life tables of *P. argyrostoma* and *C. albiceps* indicates that under the same environmental conditions the return time of a population of the former species is smaller than the latter (TR =$1/\lambda$, SOUTHWOOD, 1981).

The data discussed above assume that, when there are no mortality factors other than physiological ones, a population of *P. argyrostoma* can multiply 181.09 times (Ro) in an average of 32.79 days (T) with 0.16 daily rate of increase (rm); while *C. albiceps* will multiply 79.26 times in an average of 15.18 days with 0.29 daily rate of increase.

The reproductive strategy of the larviparous fly, *P. argyrostoma* is based on the egg protection, and consequently the elimination of an important factor limiting its population growth; viz egg mortality. This is evident from the age specific survivorship curve Fig. 1. Thus, the high value of GRR and Ro was arrived at by higher survivorship (Ro =$\sum$ Lx.Mx). On the other hand, the reproductive strategy of the oviparous fly, *C. albiceps* is based on the compensation of egg mortality by a high innate reproductive capacity (rm). This was achieved by the short generation time as (rm) is more sensitive to (T) than (Ro) in Equation 2.

It may be evident from the biology and behaviour of certain insect species that they are r-strategists; however, the numerical values of different population parameters are prerequisite for the decision of the binomic strategy of any species. Thus, according to SOUTHWOOD (1981) and HUFFAKER (1984), r-strategists are character-

Tab. 4: Life table of *C. albiceps*

| X | Lx | Mx | LxMx | Equation | |
|---|---|---|---|---|---|
| **1** | 0.79 | 0.000 | 0.000 | 0.000 | **Ro = 79.26** |
| **2** | 0.78 | 0.000 | 0.000 | 0.000 | **T= 15.18** |
| **3** | 0.76 | 0.000 | 0.000 | 0.000 | **rm = 0.29** |
| **4** | 0.75 | 0.000 | 0.000 | 0.000 | **$\lambda$ = 0.75** |
| **5** | 0.74 | 0.000 | 0.000 | 0.000 | **GRR = 114.87** |
| **6** | 0.74 | 0.000 | 0.000 | 0.000 | |
| **7** | 0.74 | 0.000 | 0.000 | 0.000 | |
| **8** | 0.74 | 0.000 | 0.000 | 0.000 | |
| **9** | 0.74 | 0.000 | 0.000 | 0.000 | |
| **10** | 0.73 | 0.000 | 0.000 | 0.000 | |
| **11** | 0.70 | 0.000 | 0.000 | 0.000 | |
| **12** | 0.69 | 0.000 | 0.000 | 0.000 | |
| **13** | 0.69 | 0.000 | 0.000 | 0.000 | |
| **14** | 0.69 | 13.508 | 9.321 | 0.165 | |
| **15** | 0.69 | 59.817 | 41.274 | 0.549 | |
| **16** | 0.69 | 41.542 | 28.664 | 0.286 | |
| **17** | 0.69 | 0.000 | 0.000 | 0.000 | |
| **18** | 0.68 | 0.000 | 0.000 | 0.000 | |
| **19** | 0.67 | 0.000 | 0.000 | 0.000 | |
| **20** | 0.64 | 0.000 | 0.000 | 0.000 | |
| **21** | 0.61 | 0.000 | 0.000 | 0.000 | |
| **22** | 0.56 | 0.000 | 0.000 | 0.000 | |
| **23** | 0.52 | 0.000 | 0.000 | 0.000 | |
| **24** | 0.50 | 0.000 | 0.000 | 0.000 | |
| **25** | 0.46 | 0.000 | 0.000 | 0.000 | |
| **26** | 0.39 | 0.000 | 0.000 | 0.000 | |
| **27** | 0.34 | 0.000 | 0.000 | 0.000 | |
| **28** | 0.29 | 0.000 | 0.000 | 0.000 | |
| **29** | 0.22 | 0.000 | 0.000 | 0.000 | |
| **30** | 0.19 | 0.000 | 0.000 | 0.000 | |
| **31** | 0.14 | 0.000 | 0.000 | 0.000 | |
| **32** | 0.11 | 0.000 | 0.000 | 0.000 | |
| **33** | 0.09 | 0.000 | 0.000 | 0.000 | |
| **34** | 0.08 | 0.000 | 0.000 | 0.000 | |
| **35** | 0.07 | 0.000 | 0.000 | 0.000 | |
| **36** | 0.05 | 0.000 | 0.000 | 0.000 | |
| **37** | 0.03 | 0.000 | 0.000 | 0.000 | |
| **38** | 0.01 | 0.000 | 0.000 | 0.000 | |
| **39** | 0.00 | 0.000 | 0.000 | 0.000 | |
| **40** | 0.00 | 0.000 | 0.000 | 0.000 | |

List of Abbreviations

| | |
|---|---|
| **x** | Age in days |
| **Lx** | Proportion of females alive at age x |
| **Mx** | Number of female progeny/female |
| **Ro** | Net reproductive rate |
| **T** | Mean generation time |
| **rm** | Intrinsic rate of natural increase |
| **$\lambda$** | Finite rate of natural increase |
| **GRR** | Gross reproductive rate |

ized by a high rm arrived at by a large fecundity (large Ro) and short generation time (T). Therefore, FORSYTH & ROBERTSON (1975) considered that the sarcophagid *Blaseoxipha fletcheri* was K-strategist because of the low fecundity of this species (11 larvae per female compared with 50-170 in other sarcophagids). The previous data on the distribution and biology of *P. argyrostoma* and *C. albiceps* (OMAR, 1979, and MOHAMMED & ABDEL-RAHMAN, 1982), together with data presented in the present work, place the two species towards the r-end of the spectrum inspite of the differences in their reproductive biology, age specific survivorship, fecundity, and population growth rates.

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