

## LIFE TABLE OF THE AUSTRALIAN SHEEP BLOW FLY *LUCILIA CUPRINA* (WIEDEMANN) (DIPTERA: CALLIPHORIDAE)

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### ABSTRACT

The life-history raw data of the Australian sheep blow fly *Lucilia cuprina* (Wiedemann) were collected in the laboratory conditions and analyzed based on the age-stage, two-sex life table to take into consideration both sexes and the variable development rates among individuals. The intrinsic rate of increase ( $r$ ) is  $0.236 \text{ d}^{-1}$ , while the finite rate of population increase ( $\lambda$ ) is  $1.266 \text{ d}^{-1}$ . The net reproductive rate ( $R_0$ ) is 106.1. The mean generation time ( $T$ ) is 19.8 days. The population parameters suggest that *L. cuprina* population is  $r$ -strategist.

### INTRODUCTION

The Australian sheep blow fly *Lucilia cuprina* (Wiedemann) is known to induce primary ovine cutaneous myiasis in many parts of the world (Zumpt, 1965). Scientists are still working on the development of new control strategies against this pest (Londershausen *et al.*, 1996; Levot *et al.*, 1999). For an effective management of pest population, it is necessary to know the population ecology of the target species. The life table of a population gives the most comprehensive description on the growth, survival and fecundity. Therefore, a basic demographic study is fundamental and crucial for an ecological based pest management of *L. cuprina*.

Life table studies of some calliphorid flies have been reported by some authors, e.g., *Lucilia sericata* (Wall, 1993; Hayes *et al.*, 1999), *C. albiceps* (El-Shazley *et al.*, 1995) and *C. megacephala* (Gabre, 1999). The traditional age-specific life table, i.e., the Lewis-Leslie matrix and Lotka-Euler's formula, ignored the male population and the variable developmental rates among individuals. Furthermore, because only the age was taken into consideration, the age-specific life table cannot describe the stage differentiation of insect population. In order to take both sexes and the variable developmental rates into consideration, we studied the life history of *L. cuprina* in the laboratory based on the age-stage, two-sex life table.

### MATERIALS AND METHODS

#### A. Maintenance of the insect colony

The colony of *L. cuprina* was established in the laboratory of the Department of Entomology, Faculty of Science, Cairo University since 1995

using flies collected from El-Arbaeen fish market, Suez Governorate, Egypt. At the beginning of the life table study, a couple of newly emerged virgin male and female was isolated in 1 L beaker covered with a piece of muslin and fastened with a rubber band. A piece of fresh beef meat (10 g) was offered daily for female oviposition. At night, the beef meat was removed and the number of eggs was recorded. Out of 189 eggs laid by the female, 160 larvae hatched successfully. Such larvae were separated into 8 groups and reared till reaching the adult stage. Rearing techniques of *L. cuprina* in laboratory was according to the method described by Abou Zied (2001).

The daily survival rate and fecundity were observed and recorded until the death of all individuals. The temperature ranged from 29 to 32 °C with an average of  $30 \pm 1.5$  °C. The relative humidity ranged from 60 - 70% with an average of  $62 \pm 10\%$ . The experiment was carried out from the beginning of July till the end of August, 2002, where the photoperiod was about L:D = 15:9hr.

### **B. Life table analysis**

The raw data of *L. cuprina* were analyzed according to the theory of age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988) by using the computer program TWOSEX. The TWOSEX program is available at <http://140.120.197.173/Ecology/> and <http://nhsbig.inhs.uiuc.edu/wes/chi.html> (Illinois Natural History Survey, US). The age-stage survival rate, the distribution of mortality rate, the age-stage life expectancy and stable age-stage distribution were calculated. Furthermore, the means and standard errors of the intrinsic rate of increase ( $r$ ), the net reproductive rate ( $R_0$ ), the mean generation time ( $T$ ) and the finite rate of population increase ( $\lambda$ ), were calculated by using the Jackknife method (Sokal and Rohlf, 1981; Meyer *et al.*, 1986).

## **RESULTS AND DISCUSSION**

### **Survivorship, development and longevity**

The means and standard errors of the development time for each life stage, the total longevity and the fecundity are given in Table 1. Out of 189 eggs, 160 eggs hatched successfully. The mortality rate of egg stage is 15.3%. The detailed survivorship and stage differentiation of the population is listed in Table 2. By using the age-stage, two-sex life table, the development and stage differentiation of *L. cuprina* can be properly illustrated in Fig. 1. The survival rate  $s_{ij}$  is the probability that a newborn will survive to age  $i$  and stage  $j$ . The egg mortality can also be seen in Fig.1 where the survival rate to age  $i$  is 84.7%. The survival rate from egg to adult stage is 46%. There are no significant differences in the developmental times of the egg, larval and pupal stages between both sexes. However, the adult longevity of female (20.56 days) is significantly ( $P < 0.05$ ) longer than that of male (12.76 days) by using  $t$ -test. This also results in a significant difference in the total longevity between female (31.91 days) and male (23.69 days). These results are similar to those reported for other

calliphorid flies. Gabre (1999) stated that the longevity of the adult *C. megacephala* was 26.13 days. El-Shazly *et al.* (1995) reported that the adult stage for male and female *C. albiceps* were 12.06 and 18.07 days, respectively. However, Hayes *et al.* (1999) stated that female *L. sericata* gave a field estimate of 46.2 – 53.3 days for the complete life span. Thomas (1993) stated that the screw worm fly *Cochliomyia hominivorax* showed a life span of 10 days. Fig. 1 and Table 2 show a significant stage overlapping resulted from the variable developmental rate among individuals and between sexes. Since the longevity of male adult is shorter than that of female, there are more females than males after 12 days.

### **Fecundity**

During the life span of female *L. cuprina*, the average number of oviposition was 4.53 batches with a maximum of 9 batches. Similar results were obtained by some authors namely, Froggatt and Froggatt (1916), Mackerras and Freney (1933) and Ratcliffe (1935) in case of *L. sericata* which may live to produce up to 13 egg batches. Browne (2001) reported that *L. cuprina* and some other dipterans display discrete ovarian cycles. Our finding is in coincidence with Browne's report. Since female *L. cuprina* showed a limited tendency to mate more than once, the first mating is the essential one for inseminating the eggs all-over the life span as demonstrated by Smith *et al.* (1988) and Abou Zied (2001). In our study, a maximum of daily fecundity 73.9 eggs had been recorded for a female individual. Because the egg batches were laid at discrete time intervals, 10 peaks of female fecundity ( $f_{ij}$ ) were represented in Fig. 2 where the maximal mean daily fecundity is 50.3 eggs (the first pick of the  $f_{ij}$ ). This figure shows also the age-specific survival rate ( $l_x$ ), the age-specific fecundity ( $m_x$ ) and the age-specific maternity ( $l_x m_x$ ). The age-specific survival rate ( $l_x$ ) gives the probability that a newborn will survive to age  $x$ . It is calculated by including all individuals of both sexes. Similarly, the age-specific fecundity ( $m_x$ ) and the age-specific maternity ( $l_x m_x$ ) were calculated by including all individuals of both sexes. By comparing Table 1 and Fig. 2, the pre-oviposition period ranged from 3 to 23 with a mean and standard error of  $4.14 \pm 0.56$  days. However, this definition ignores the differences in preadult stage among individuals. If we define the total pre-oviposition period (TPOP) as the time interval from the birth of a female individual (from the egg stage) to its first oviposition day, then the total pre-oviposition period of *L. cuprina* ranged from 13 to 35 days. The mean TPOP for *L. cuprina* is  $15.53 \pm 0.63$  days. The TPOP is a more proper description of the "pre-oviposition", because it takes the variation of preadult stage into consideration. The existence of pre-oviposition period can be seen by comparing the Fig. 1 & 2. The female emerged on the 9th day (Fig. 1 and Table 2), while the oviposition started on 13th day in (Fig. 2). Thomas (1993) reported the pre-oviposition period for female *Cochliomyia hominivorax* was 4-5 days. El-Shazley *et al.* (1995) reported a pre-oviposition period 4.25 days for *C. albiceps*. A longer pre-oviposition period of 8-15 days

for female *Calliphora vomitoria* was reported by Kamal (1958). Wall *et al.* (1992) stated that *L. sericata* females required 7 days after emergence (at 20°C) for first egg laying. Gabre (1999) found that *C. megacephala* needed 7 days to lay eggs.

The total fecundity reached 445.69±48.3 eggs/female with a maximum of 1041 eggs/female (Table 1). Similar results were obtained by some authors namely, Zumpt (1965) who found that female *Calliphora vomitoria* could lay 540 – 720 eggs with an average of 180 eggs/batch; *Phaenicia sericata* can lay 2000-3000 eggs in 9-10 batches within 3 weeks; Wall (1993) recorded that female *L. sericata* matured an average of 223 ± 12 oocytes/batch. EL-Shazley *et al.* (1995) stated that *C. albiceps* gives 3 oviposition with a total fecundity of 229.43 ± 30.33 eggs/female. Gabre (1999) found that female *C. megacephala* lays a single batch during the female life span with an average of 224.33± 6.01 eggs/female. These results show that there are significant variations among species.

### **The mortality rates and life expectancy**

Fig. 3 illustrates the distribution of mortality during the whole life span. The first peak of mortality occurs at the egg stage. The second and third major peaks occur at the beginning and end of larval stage. The fourth major peak occurs in the pupal stage (12th day). Out of the 189 eggs, 45 females and 42 males were obtained. The stage-specific mortality rates are 15.3%, 17.5%, 21.2%, 23.8% and 22.2% for egg, larva, pupa, female and male, respectively. Mortality during most time of the adult stage ranged between 0.01 and 0.02% for both sexes showing an even distribution of mortality in adult life span. Hayes *et al.* (1999) recorded a daily mortality rate of 1.88 to 2.16 % per day degree for female *L. sericata*.

Based on the age-stage survival rate, we calculate the life expectancy for each age-stage interval (Fig. 4) for the prediction of the future life of the population. The life expectancy ( $e_{ij}$ ) is the time that an individual of age  $i$  and stage  $j$  is expected to live. From Fig.4 it is obvious that the life expectancy of the female adult is much higher than that of the male adult as reported in Table 1 where the adult longevity of male is much shorter than that of the females. Hayes *et al.* (1999) report that the mean life expectancy of female adults of *L. sericata* collected from two farms were 46 and 53 day-degrees.

### **Life table analysis:**

Population parameters calculated by using the age-stage, two-sex life table are listed in Table 3. The high intrinsic rate of increase ( $r = 0.236 \text{ day}^{-1}$ ) and finite rate of increase ( $I = 1.27 \text{ day}^{-1}$ ) are accompanied by a short mean generation time ( $T = 19.8 \text{ days}$ ) and a high net reproductive rate ( $R_0 = 106.1$ ). These results suggest that if the population reaches the stable age-stage distribution and if there are no mortality factors other than the physiological ones, *L. cuprina* population can multiply 106.1 times with an average of 19.8

days with an exponential rate of 0.236 per day. This finding also shows that *L. cuprina* is *r*-strategist which characterized by a high rate of increase, with a large fecundity and short generation time as postulated by Pianka (1970), Southwood (1981), Haffaker *et al.* (1984) and Ricklefs (1990). The other characteristic of *r*-strategists is the high proportion of young age in the stable age distribution which is clear in case of *L. cuprina* (Fig. 5). The egg alone represents more than 26% of the total population.

In comparison with other species of blow flies, El-Shazly *et al.* (1995) and Gabre (1999) found that the net reproductive rate ( $R_0$ ), the mean generation time in days ( $T$ ), the intrinsic rate of natural increase ( $r$ ) and the finite rate of population increase ( $\lambda$ ) were 97.26, 15.18, 0.29 and 0.75 for *C. albiceps*, and 79.5, 20.7, 0.212 and 1.241 for *C. megacephala*, respectively. Thus *C. albiceps* and *C. megacephala* are also *r*-strategists.

According to Fisher (1930) the life table analysis reveals also the contribution of an individual to the growth of future population. Fig.6 illustrates the age-stage reproductive values of *L. cuprina*. If an individual becomes a female adult, its reproductive value increases dramatically. The female 15th day of age (counted from birth) gives a maximal reproductive value of 153.

From the life table of *L. cuprina* it could be concluded that the repeated oviposition is an innate behavior initiated by the female to overlap or to compensate the mortality rates recorded during its life span. Moreover, such information obtained will be useful for the application of stage-specific control strategies in the future.

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Table (1): Basic statistics of life history data for *L. cuprina* population

<b>Stage</b>	<b>Sex</b>	<b>No.</b>	<b>Mean</b>	<b>S.E.</b>
Egg	All	160	1	0
Larva	All	127	5.03	0.07
Pupa	All	87	5.4	0.11
Adult	All	87	16.79	0.9
Egg	Female	45	1	0
Larva		45	4.82	0.12
Pupa		45	5.53	0.16
Adult		45	20.56	1.21
Egg	Male	42	1	0
Larva		42	4.67	0.12
Pupa		42	5.26	0.14
Adult		42	12.76	0.105
Egg	N	73	1	0
Larva		40	5.65	0.1
Pupa		---	---	---
Adult		---	---	---
Total longevity	Female	45	31.91	1.29
	Male	42	23.69	1.13
	N	102	7.18	0.55
Fecundity	Female	45	445.69	48.32
		Min.	Max.	Mean $\pm$ S.E.
No of female ovipositions/life:		1	9	4.35 $\pm$ 0.35
Fecundity (eggs/female):		78	1041	445.69 $\pm$ 48.32

N = individuals died before the adult stage.



Table (2): Number of individuals survived to each age-stage group (Matrix N).

Age (day)	Egg	Larva	Pupa	Female	Male
0	189	-	-	-	-
1	-	160	-	-	-
2	-	148	-	-	-
3	-	145	-	-	-
4	-	141	4	-	-
5	-	111	31	-	-
6	-	50	92	-	-
7	-	19	123	-	-
8	-	1	127	-	-
9	-	-	116	5	6
10	-	-	94	15	17
11	-	-	73	23	26
12	-	-	38	39	37
13	-	-	23	39	36
14	-	-	11	43	35
15	-	-	3	45	33
16	-	-	3	44	30
17	-	-	-	44	30
18	-	-	-	43	30
19	-	-	-	42	29
20	-	-	-	42	29
21	-	-	-	41	29
22	-	-	-	40	26
23	-	-	-	39	25
24	-	-	-	35	21
25	-	-	-	33	19
26	-	-	-	31	16
27	-	-	-	28	16
28	-	-	-	28	12
29	-	-	-	26	8
30	-	-	-	26	8
31	-	-	-	19	6
32	-	-	-	18	3
33	-	-	-	18	2
34	-	-	-	17	2
35	-	-	-	16	2
36	-	-	-	15	2
37	-	-	-	12	2
38	-	-	-	11	1
39	-	-	-	11	-
40	-	-	-	9	-
41	-	-	-	6	-
42	-	-	-	5	-
43	-	-	-	5	-
44	-	-	-	4	-
45	-	-	-	4	-
46	-	-	-	3	-
47	-	-	-	3	-
48	-	-	-	2	-
49	-	-	-	1	-
50	-	-	-	0	-

Table (3): Population parameters of *L. cuprina* based on age-stage, two-sex life table.

<b>Population Parameter</b>	<b>Mean <math>\pm</math> SE*</b>
Intrinsic rate of increase ( $r$ )	0.2369 $\pm$ 0.0099
Finite rate of increase ( $\lambda$ )	1.2673 $\pm$ 0.0125
Net reproductive rate ( $R_0$ )	106.1 $\pm$ 17.9
Mean generation time ( $T$ )	19.8 $\pm$ 0.4

\*- The means and standard errors are estimated by using jackknife method (Sokal and Rohlf, 1995 & Meyer *et al.*, 1986).

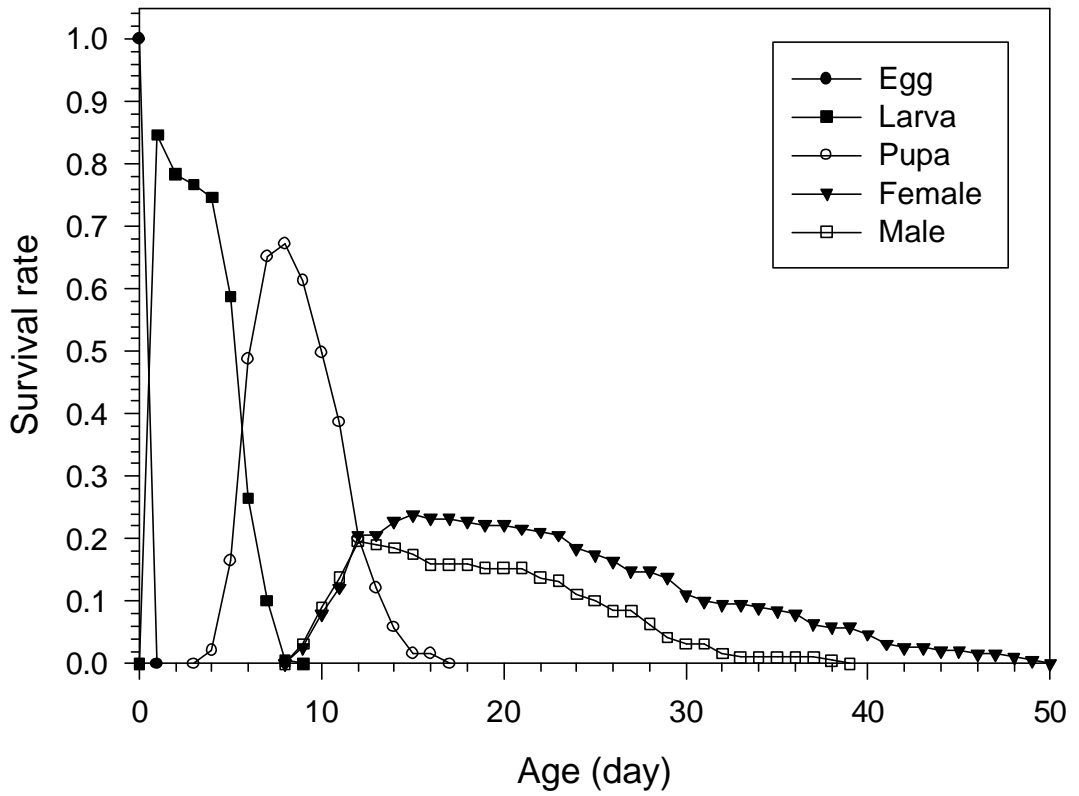


Figure 1. The age-stage survival rate ( $s_{ij}$ ) of *L. cuprina*.

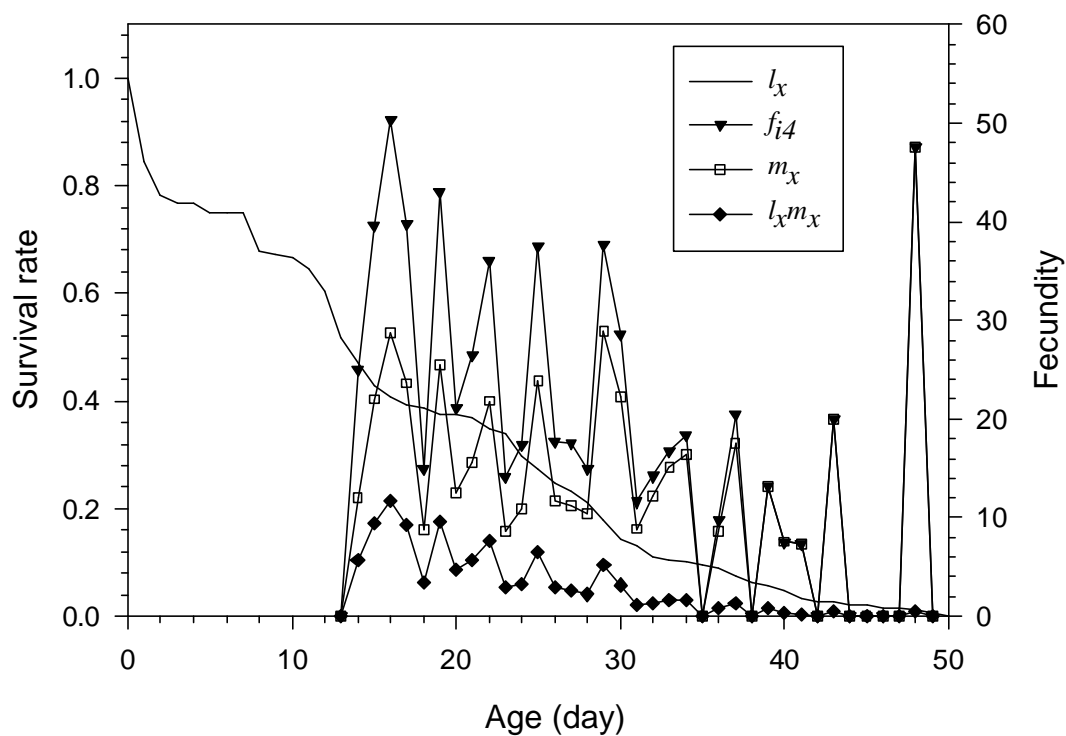


Figure 2. The age-specific survival rate ( $l_x$ ), the age-stage fecundity of female ( $f_{i4}$ ), the age-specific fecundity of the cohort ( $m_x$ ) and the age-specific maternity ( $l_x m_x$ ) of *L. cuprina*.

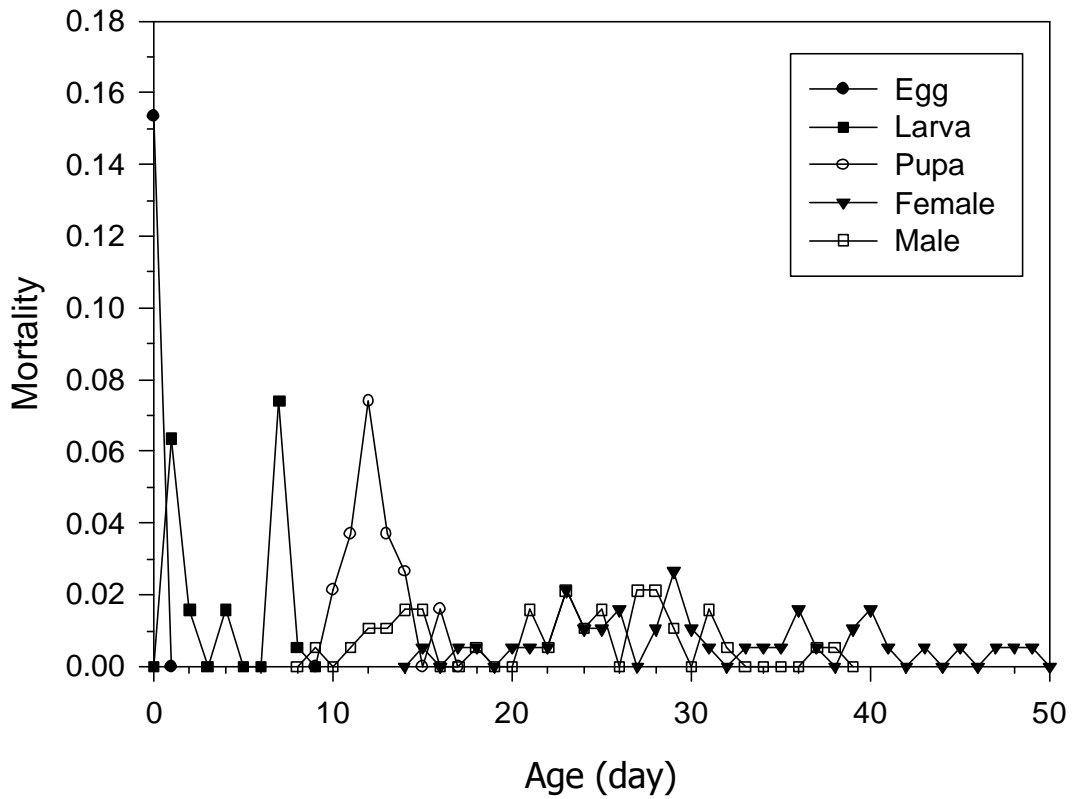


Figure 3. The age-stage specific mortality of *L. cuprina*.

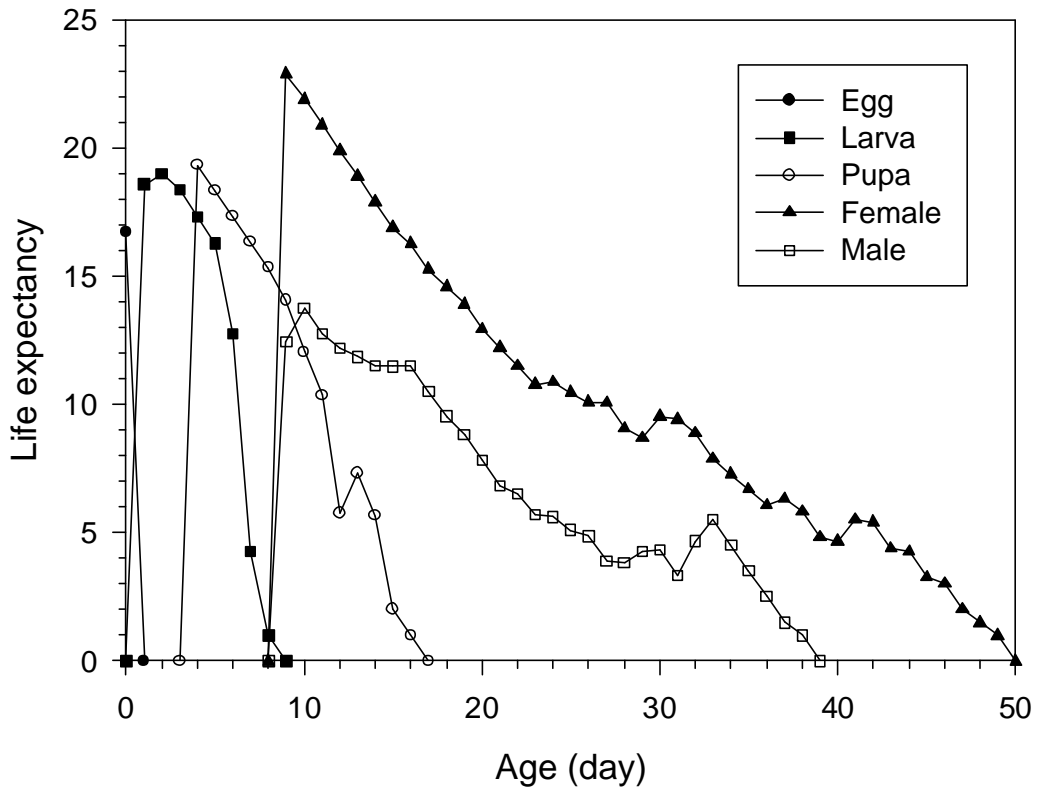


Figure 4. The age-stage specific life expectancy ( $e_{ij}$ ) of *L. cuprina*.

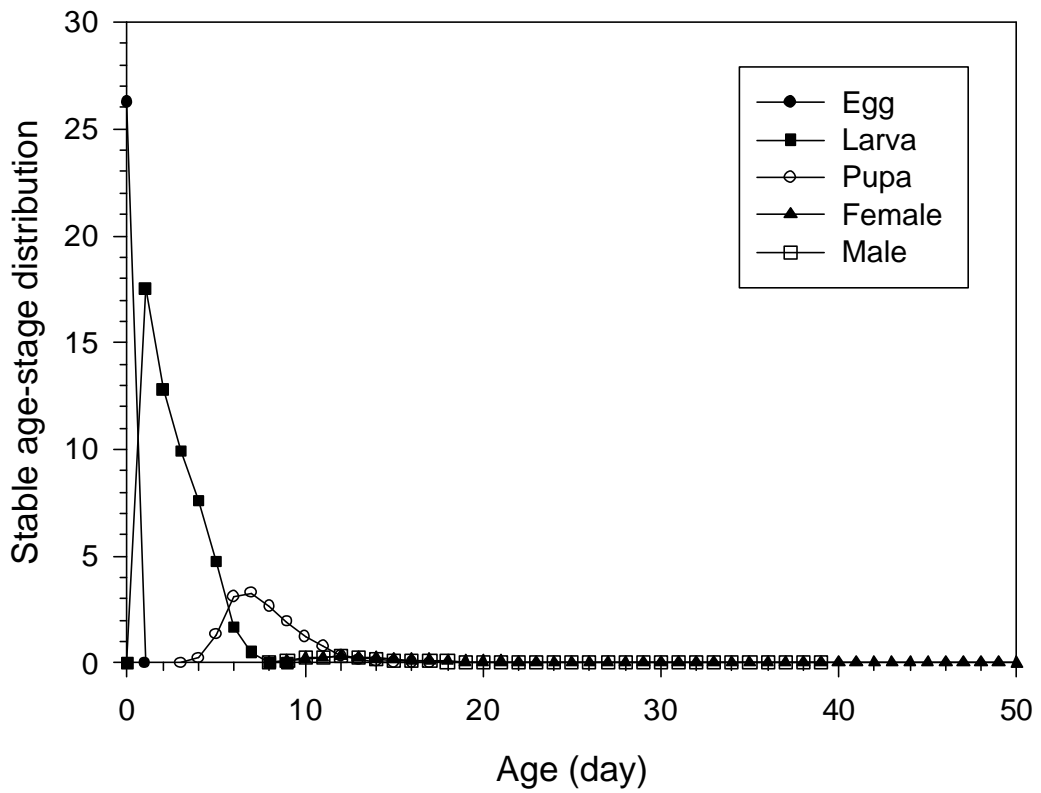


Figure 5. The stable age-stage distribution of *L. cuprina*.

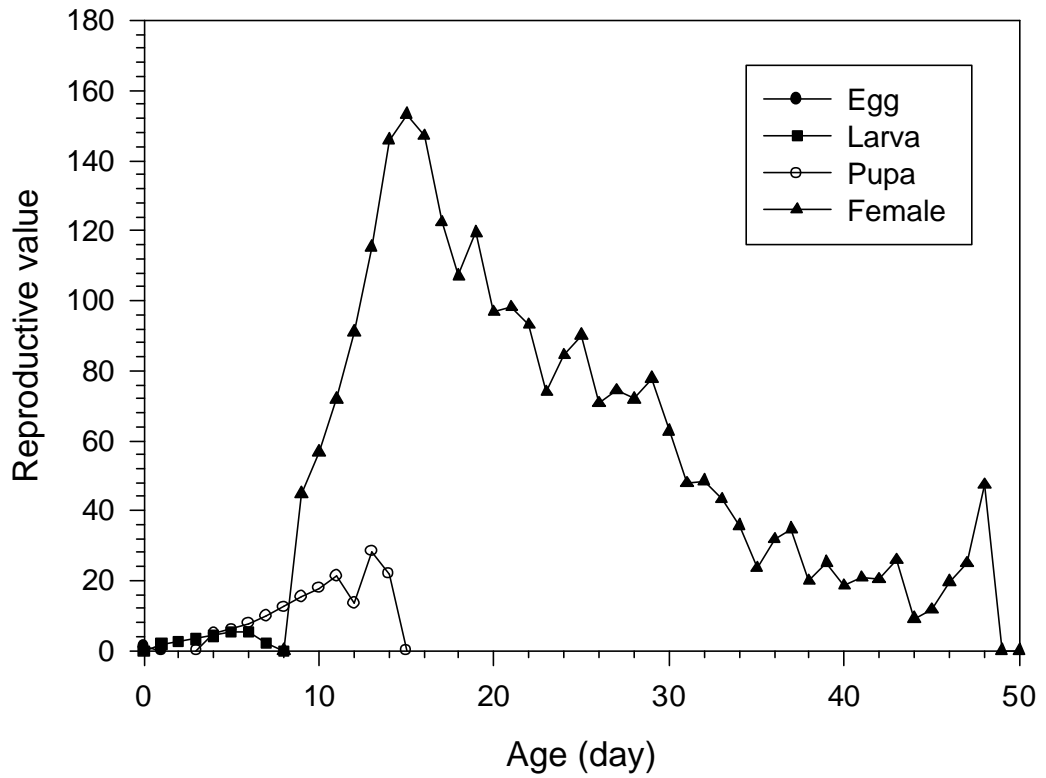


Figure 6. The age-stage reproductive value ( $v_{xj}$ ) of *L. cuprina*.



الجدول الحياتى لذبابة الأغنام الأسترالية *لوسيليا كوبرينا* (فيدمان) (ثنائية الأجنحة - كاليفوردي)

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تمت دراسة الجدول الحياتى لذبابة الأغنام الأسترالية *لوسيليا كوبرينا* (فيدمان) وتبين من التحليل الإحصائى لدراسة عمر وطور كلا الجنسين، إضافة إلى معدلات النمو المختلفة خلال الجيل الواحد، أن:

مؤشر معدل الزيادة اللانهائية للعشيرة ( $\lambda$ ) = ١.٢٦٦ وبينما سجل صافى معدل التكاثر ( $R_0$ ) = ١.٠٦، وبلغ متوسط نمو عمر الجيل الواحد ( $T$ ) = ١٩.٨ يوما.  
وبناء على النتائج المتحصل عليها يمكننا القول بأن عشيرة ذبابة *لوسيليا كوبرينا* لها القدرة على النمو سريعا، حيث تتميز باستراتيجية ( $r$ ) (وضع كمية كبيرة من البيض خلال فترة عمر وجيزة).