

1 **Age-Stage, Two-Sex Life Table of the *Menochilus sexmaculatus* (Coccinellidae: Coleoptera)**  
2 **Feeding on Different Aphid Species**

3 **Authors**

4 **Khalid Abbas<sup>1¶</sup>, Muhammad Shah Zaib<sup>1¶</sup>, Muhammad Zakria<sup>1¶</sup>, Umm-e-Hani<sup>1&</sup>**  
5 **, Syed Muhammad Zaka<sup>1¶\*</sup>, Noor-ul-Ain<sup>1&</sup>**

6 **Affiliations**

7 <sup>1</sup>Department of Entomology, Faculty of Agricultural Sciences and Technology, Bahauddin  
8 Zakariya University, Multan Pakistan.

9 **\*Corresponding author address**

10 Email ID: [zaka\\_ento@bzu.edu.pk](mailto:zaka_ento@bzu.edu.pk)

11 <sup>¶</sup> These authors contributed to this work equally.

12 <sup>&</sup> These authors contributed to this work equally.

13 **Abstract**

14 *Ladybird beetle, Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae), is biological  
15 control agent that predate the different aphid species. Both adults and larval stage of *M.*  
16 *sexmaculatus* feed on aphid species. In this experiment Life table and predation data were collected  
17 for *M. sexmaculatus* feed on four different aphid species *Lipaphis erysimi*, *Myzus persicae*, *Aphis*  
18 *nerii* and *Diuraphis noxia*. This experiment was conducted under laboratory conditions at 25±2°C,  
19 60±5% RH and L14: D10 h. Different numbers of aphid were provided as a pray in petri dish. The  
20 pre-adult development duration of *M. sexmaculatus* was maximum when fed on *M. persicae* (12.18  
21 d) and minimum on *D. noxia* (10.64 d). Similarly, male and female duration was maximum on *M.*  
22 *persicae* (26.7 d), minimum on *L. erysimi* (23.67 d) in male and in female maximum on *D. noxia*  
23 (28.00 d), minimum on *A. nerii* (24.33 d). Net reproductive rate ( $R_0$ ) range from 117.9 on *L. erysimi*

24 to 99.55 on *M. persicae* and intrinsic rate of increase ( $r$ ) range was 0.21197 d<sup>-1</sup> on *A. nerii* to  
25 0.021559 d<sup>-1</sup> on *D. noxia*. The finite rate of increase ( $\lambda$ ) range was 1.240592 d<sup>-1</sup> on *D. noxia* to  
26 1.204918 d<sup>-1</sup> on *M. persicae*, the mean of generation (T) range was 24.68 d<sup>-1</sup> on *M. persicae* to  
27 22.476 d<sup>-1</sup> on *A. nerii*, similarly, the gross reproductive rate (GRR) range was 172.2 d<sup>-1</sup> on *D. noxia*  
28 to 115.02 d<sup>-1</sup> on *M. persicae* and Fecundity (F) eggs per female range was 316.8 on *D. noxia* to  
29 199.1 on *M. persicae*. In present Study, age-stage two-sex life table gives complete understanding  
30 of predator biological aspects against different aphid species. This study will help us to improve  
31 mass rearing and use of *M. sexmaculatus* in biological control of aphids.

## 32 **Introduction**

33 Aphids (Hemiptera: Aphididae) are important insect pests of various cultivated plants (1). Suck  
34 cell sap of plants and act as vectors of various virus induced diseases (2). They have abilities to  
35 quickly build their population and their honeydew secretions results into a medium of sooty mold  
36 growth. They can change host metabolism by disturbing their host hormonal balance. Aphids  
37 attack may kill the plant at their early growth stages and reduce yield of crops at later stages (3).  
38 Oleander aphid (*Aphis nerii*), green peach aphid (*Myzus persicae*), Russian wheat  
39 aphid (*Diuraphis noxia*) and mustard aphid (*Lipaphis erysimi*) are among important pests of  
40 cultivated and ornamental plants (4). The *L. erysimi*, most importantly damages *Brassicace* plants  
41 typically mustard, rape, cabbage, cauliflower, broccoli and radish worldwide (5). The *M. persicae*,  
42 is a cosmopolitan pest, feeds on more than 50 plant families (5), including agro-industrial crops  
43 and horticultural crops (6).

44 The *D. noxia*, attacks on cereal crops worldwide with high host range of more than 140 species of  
45 Poaceae plants (7). The *D. noxia*, inject toxin into plants while feeding which causes failure to

46 unrolling and white streaking of plant leaves. Yield loss had been estimated up to 80 to 100%  
47 under heavy attack of *D. noxia*, in wheat crop (8). The *A. nerii*, feeds on plants of Apocynaceae  
48 and Asclepiadaceae families (9) and also had been reported on wheat and Brassica in Pakistan  
49 (10). The *A. nerii*, is an obligate parthenogen, and a sequester of toxic chemicals (cardenolides)  
50 which act as defensive mechanism against its natural enemies (11). Indeed, unjudicious pesticides  
51 use increased ability of pests to survive against pesticides and residues level in crops final produce  
52 ((12) (13) and these factors urge to use alternative methods (e.g. biological control) to reduce aphid  
53 populations which are environmental friendly and risk free for human health.

54 Natural enemies (predators, parasitoids and entomopathogens) used to control aphids population  
55 in biological control (14). Natural enemies are the basic components of insect pest supervision.  
56 Practically 90% of natural pests are controlled by natural enemies (15). Ladybirds are potent  
57 predators of various small herbivorous insects such as aphids (16). The Ladybird beetle,  
58 *Menochilus sexmaculatus* (Fab.), is distributed in Pakistan, India and other south Asian countries  
59 (17). The adults of *M. sexmaculatus* are yellow bright in color and having black zigzag lines. Some  
60 preys are toxic to predators because they feed on toxic plant and ultimately affects food quality for  
61 predators (18). Few studies have been done on biological aspect of *M. sexmaculatus* against  
62 different aphid species. However, there is a need for detail study of survival and reproduction of  
63 *M. sexmaculatus* on aphid species to evaluate suitable prey and alternate prey species. It is  
64 important to know demographic aspects including stage differentiation and predation rate of  
65 predators for mass rearing of predators and true implication into biological control of pests (19).  
66 Therefore, life table was studied to know the development and reproduction of predators against  
67 pests. However, age-stage two-sex life table provides more detail of biological aspects including  
68 stage differentiation than traditional life tables (19). Therefore, present study used age-stage two-

69 sex life table for complete understanding of *M. sexmaculatus* biological aspects against different  
70 aphid species. This study will help us to improve mass rearing and use of *M. sexmaculatus* in  
71 biological control of aphids.

## 72 **Material and Methods**

### 73 **Rearing of Aphids**

74 Four aphid species (*A. nerii*, *M. persicae*, *D. noxia* and *L. erysimi*) were collected from their hosts  
75 from agricultural fields (latitude 30°15'29.9"N, longitude 71°30'54.6"E) of Faculty of Agricultural  
76 Sciences and Technology, Bahauddin Zakariya University, Multan Pakistan and were reared on  
77 their respective host plants. Aphids were reared in plastic cages (51 × 45 cm) along with their  
78 respective hosts under laboratory condition (25 ± 2°C and 70 ± 5% RH with photoperiod of  
79 14L:10D h) (20). This laboratory reared aphids were used for the biological studies of *M.*  
80 *sexmaculatus*.

### 81 **Collection and rearing of *M. sexmaculatus***

82 The larvae of *M. sexmaculatus* were collected from *Calotropis procera* located at head  
83 Muhammad wala fields of Multan (latitude: 30°11'54.97N, longitude: 71°28'7.33E), Punjab,  
84 Pakistan in start of February 2019. Larvae were collected in early morning in plastic jars (25 ×  
85 15.5 cm) with the help of camel hairbrush and transferred to aphid culture in laboratory. The  
86 culture was maintained in an incubator (25±1°C and 60±2% R.H.) with photoperiod 14L:10D h)  
87 (21). The collected larvae were transferred to plastic jars (15 × 11 cm). The mouth of cages was  
88 covered with the muslin cloth and knotted with the elastic band. Different aphid species i.e. *A.*  
89 *nerii*, *M. persicae*, *D. noxia* and *L. erysimi* were supplied as a food to larvae. Emerging adults were

90 reared in plastic boxes ( $14 \times 8 \times 10$  cm) with surfeit different aphid species. Corrugated filter  
91 papers were used as an oviposition substrate of beetles in rearing boxes. Collected eggs from these  
92 adult females were placed in 10-cm petri dishes containing moist filter paper at the bottom to get  
93 larvae. Mature and immature stages of *M. sexmaculatus* were provided with aphids as their food  
94 (22).

### 95 **Life table Studies**

96 Fifty healthy eggs of *M. sexmaculatus* were taken from the general population of their respective  
97 hosts and kept separately in single petri dishes (6cm diameter). Egg development period was  
98 recorded after 6-h interval. After egg hatching 1<sup>st</sup> instar larvae of *M. sexmaculatus* were feed on  
99 aphid species and similarly all instar of *M. sexmaculatus* were feed on aphid species. Specified  
100 number of aphids were provided, and data of consumed aphids were recorded on daily basis (23).  
101 After 4<sup>th</sup> instar larvae convert into the pupal stage and then into the adult stage. Duration of All  
102 stages (larvae pupae and adult) were recorded 12-h interval (20, 21, 24). Adult male and female  
103 were paired in plastic jars ( $9 \times 6$  cm) for mating, egg laying and to check the male and female  
104 longevity, reproductive behavior and female oviposition. Similarly, male and female were kept  
105 separately to check the predation rate and observe the fecundity and survival rate of both sexes  
106 were recorded after 24-h until death (24, 25). The software TWOSEX-MS Chart (26) was use to  
107 check the egg to adult development duration, fecundity, adult preoviposition period, oviposition  
108 period, post oviposition period and age two sex life cycle (27, 28). Age-specific survival rates were  
109 find according to (27) life expectancy according to (19) and population growth on different aphid  
110 species.

### 111 **Statistical analysis**

112 Development duration and population parameters were calculated using TWOSEX-MS Chart, to  
113 minimize variation in the results. The bootstrap technique (29) with 100,000 replications was used  
114 to calculate the mean and SE of the population (30). The TIMING-MS Chart program (31) based  
115 on age-stage two sex life table for data of *M. sexmaculatus*. The raw data were used to calculate  
116 the age-stage-specific survival rate ( $s_{xj}$ , where  $x$  = age in days and  $j$  = stage), age-stage specific  
117 fecundity ( $f_{xj}$ ), age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), age-specific net maternity  
118 ( $l_x m_x$ ), age-stage life expectancy ( $e_{xj}$ ), age-stage reproductive value ( $v_{xj}$ ), and life table parameters  
119 (32) ( $R_0$ , net reproductive rate;  $r$ , intrinsic rate of increase;  $\lambda$ , finite rate of increase; and  $T$ , the mean  
120 generation). In the age-stage, two-sex life table, the age-specific survival rate  $l_x$ ,  $m_x$  and  $R_0$  was  
121 calculated as (1 and 2):

$$122 \quad l_x = \sum_{j=1}^k S_{xj} \quad (1)$$

$$123 \quad m_x = \frac{\sum_{j=1}^k S_{xj} f_{xj}}{\sum_{j=1}^k S_{xj}} \quad (2)$$

124 Where  $k$  is the number of stages. The net reproductive rate  $R_0$  is the mean number of offspring laid  
125 by individual during its entire life span. It was calculated by following equation (3):

$$126 \quad R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

127 The intrinsic rate of increase ( $r$ ) was estimated using the iterative bisection method and corrected  
128 with the Euler-Lotka equation (4) with the age indexed from 0 (33):

$$129 \quad \sum_{x=0}^{\infty} e^{-r(x+l)} l_x m_x = 1 \quad (4)$$

130 The finite rate ( $\lambda$ ) was calculated as (5):

131  $\lambda = e^r$  (5)

132 The mean generation time is defined as the length of time that a population needs to increase to  
133  $R_0$ -fold of its population size at the stable age-stage distribution, and is calculated as (6):

134  $T = \ln R_0 / r$  (6)

135 The life expectancy ( $e_{xj}$ ) is the length of time that an individual of age  $x$  and stage  $j$  is expected to  
136 live and it is calculated equation (7) according to as (19).

137  $e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} S'_{iy}$  (7)

138 The comparison between different aphid species were done by using completely randomized  
139 design and means were compared by using LSD test (P=0.05). This analysis was done by using  
140 statistical package SAS (34).

## 141 **Results**

142 When different aphid's species were given to immature stages of beetle, significant (P=0.0032,  
143 F=0.13 and DF=3) different response on survival was recorded (Table 1) i.e. highest survival  
144 (89.1) was recorded when *L. erysimi* was given as a diet. While *A. nerii*, *M. persicae* and *D. noxia*  
145 gave similar result (85, 85 and 84.1, respectively) for immature survival.

146

147

148

149

150 “Table 1” Development period parameters (mean ± SE) of *M. sexmaculatus*

Aphid species	<i>n</i>	<i>Aphis nerii</i>	<i>Myzus persicae</i>	<i>Diuraphis noxia</i>	<i>Lipaphis erysimi</i>	<i>pvalue</i>	<i>f.value</i>	<i>df</i>
Immature survival (%)	20	85.0±6.4b	85±7.3b	84.1±6.7b	89.1±5.0a	0.0032	0.13	3
Adult emergence (%)	20	90.0±6.9b	90±6.9b	95±9a	90±6.9b	0.0054	0.15	3
Developmental rate (d <sup>-1</sup> )	20	00.04c	00.04c	00.04b	00.06a	<0.0001	2.15	3
Male longevity (d)	20	24.30±4.7b	26.7±3.53a	26.33±2.2a	23.67±3.7c	<0.0001	0.19	3
Female longevity (d)	20	24.30±5.9b	25.7±5.5b	28±3.1a	27.33±0.9b	<0.0001	0.16	3
Pre-oviposition period (d)	10	07.0±2.5a	6.33±0.9b	5.33±1.3b	5.67±1.5b	0.0211	0.18	3
Oviposition period (d)	10	15.70±2.3b	18.33±1.9a	14.70±1.3b	10.33±6.9c	<0.0001	0.87	3
Post-oviposition period (d)	10	11.00±3.2a	11.33±3.8a	7.33±1.7c	9.70±4.3b	<0.0001	0.72	3

151 n= number of replication, Mean value; SE, standard error; df, degree of freedom; *F*, value by  
 152 statistical package SAS; *P*, statistical significance level 0.05. Mean followed by different letters in  
 153 the same row are significantly different by statistical package SAS using of difference.

154 The adult emergence was recorded, significant ( $P=0.0054$ ,  $F=0.15$  and  $Df=3$ ) when their immature  
 155 stages fed on different aphid species (Table 1) i.e. maximum adult emergence (95.00 %) was  
 156 recorded when fed on *D. noxia* but when fed on *A. nerii*, *M. persicae* and *L. erysimi* (90, 90 and  
 157 90 %, respectively) the adult emergence recorded was similar.

158 When different species of aphid were offered to immature stages of beetle, significant ( $P<0.0001$ ,  
 159  $F=2.15$  and  $Df=3$ ) difference was recorded in developmental rate (Table 1) i.e. maximum



160 developmental rate was recorded ( $0.057 \text{ d}^{-1}$ ) on *L. erysimi* followed by *D. noxia* ( $0.042 \text{ d}^{-1}$ ). While,  
161 similar result of developmental rate ( $0.038$  and  $0.035 \text{ d}^{-1}$ , respectively) was observed when  
162 immatures were fed on *A. nerii* and *M. persicae*.

163 The significant difference in adult longevity of both males and females was observed when  
164 different aphid species were provided as a diet (Table 1). The significantly ( $P < 0.0001$ ,  $F = 0.19$  and  
165  $Df = 3$ ) maximum male longevity was observed on *M. persicae* and *D. noxia* ( $26.7$  and  $26.33 \text{ d}$ ,  
166 respectively), followed by *A. nerii* ( $24.33 \text{ d}$ ). While minimum male longevity was observed when  
167 *L. erysimi* was given as a diet ( $23.67 \text{ d}$ ). In case of female, significant response was recorded  
168 ( $P < 0.0001$ ,  $F = 0.19$  and  $Df = 3$ ), maximum longevity was recorded on *D. noxia* ( $28.00 \text{ d}$ ) followed  
169 by *L. erysimi*, *M. persicae* and *A. nerii* ( $27.33$ ,  $25.7$  and  $24.33 \text{ d}$ , respectively).

170 When beetle was provided different aphid species as a diet, significant ( $P = 0.0211$ ,  $F = 0.18$  and  
171  $Df = 3$ ) difference in the pre-oviposition period was recorded (Table 1) i.e. maximum pre-  
172 oviposition period of beetle was recorded when fed on *A. nerii* ( $7.00 \text{ d}$ ). While, when *M. persicae*,  
173 *L. erysimi* and *D. noxia* ( $6.33$ ,  $5.67$  and  $5.33 \text{ d}$ , respectively) were provided as a diet to beetle  
174 showed same result.

175 The oviposition period of beetle, significant ( $P < 0.0001$ ,  $F = 0.87$  and  $Df = 3$ ) difference was recorded  
176 when they fed on different aphid species (Table 1), i.e. highest oviposition period was recorded  
177 ( $18.33 \text{ d}$ ) when fed on *M. persicae*. The oviposition period of beetle was recorded ( $15.70$  and  $14.70$   
178  $\text{d}$ , respectively) similar when they fed on *A. nerii* and *D. noxia*, respectively, and followed by *L.*  
179 *erysimi* ( $10.33 \text{ d}$ ).

180 The post-oviposition period of beetle, significant ( $P < 0.0001$ ,  $F = 0.72$  and  $Df = 3$ ) difference was  
181 observed when they were provided four different aphid species (Table 1) i.e. maximum post-

182 oviposition was recorded (11.33 and 11.00 d, respectively) on *M. persicae* and *A. nerii* and  
 183 followed by *L. erysimi* (9.7 d). While minimum post-oviposition period was observed (7.33 d) on  
 184 *D. noxia*.

185 When different aphid species were provided to *M. sexmaculatus* the significant (P=0.0146, F=5.15  
 186 and Df=3) difference in incubation period was recorded (Table 2) i.e. maximum incubation period  
 187 was noted on *M. persicae* (2.53 d), followed by *A. nerii*, *L. erysimi* and *D. noxia* (2.23, 2.10 and  
 188 2.04 d, respectively).

189 “Table 2” Immature developmental time (mean ± SE) of *M. sexmaculatus*

Predator Stage	n	<i>Aphis nerii</i>	<i>Myzus persicae</i>	<i>Diuraphis noxia</i>	<i>Lipaphis erysimi</i>	pvalue	f.value	Df
Eggs	50	2.23±0.085b	2.53±0.085a	2.043±0.088b	2.10±0.122b	0.0146	5.15	3
L1	20	2.25±0.120a	2.050±0.18a	1.00±2.190c	1.45±0.180b	<.0001	19.32	3
L2	20	1.10±0.10ab	1.00±000b	1.10±1.070ab	1.30±0.130a	0.0638	2.56	3
L3	20	1.00±0.000a	1.05±0.050a	1.45±1.120a	1.20±0.090a	0.321	1.19	3
L4	20	2.10±0.1004b	2.30±0.180b	2.40±2.470ab	2.80±0.150a	0.012	3.98	3
Pupa	20	3.05±0.180ab	3.25±0.16a	2.65±3.480b	3.30±0.280a	0.331	1.15	3

190 L1-L4 represent the larval instar of *M. sexmaculatus*, n= replications. Mean value; SE, standard  
 191 error; df, degree of freedom; F, value by statistical package SAS; P, statistical significance level  
 192 0.05. Mean followed by different letters in the same row are significantly different by statistical  
 193 package SAS using of difference.

194 Different species of aphid were given to different larval stages of *M. sexmaculatus*, the significant  
 195 difference in developmental time was recorded (Table 2). The significantly (P<0.0001, F=19.32

196 and Df=3) highest first instar (L1) developmental time was recorded on *A. nerii* and *M. persicae*  
 197 (2.25 and 2.05 d, respectively), followed by *L. erysimi* (1.45 d). While shortest developmental time  
 198 was recorded on *D. noxia* (1.00 d). The maximum significant (P=0.0638, F=2.56 and Df=3)  
 199 developmental time of second instar (L2) was recorded on *L. erysimi* (1.30 d) followed by *A. nerii*  
 200 and *D. noxia* (1.10 and 1.10 d, respectively). Whereas minimum developmental time was recorded  
 201 on *M. persicae* (1.00 d). The developmental time of third instar (L3) observed was non-significant  
 202 (P=0.321, F=1.19 and Df=3) on all four aphid species. The highest significant (P=0.012, F=3.98  
 203 and Df=3) developmental time of fourth instar (L4) was noted on *L. erysimi* (2.80 d) followed by  
 204 *D. noxia* (2.40 d). The lowest developmental time was recorded on *M. persicae* and *A. nerii* (2.30  
 205 and 2.10 d, respectively).

206 The developmental time of pupae on all four aphid species was recorded non-significant (P=0.331,  
 207 F=1.15 and Df=3) (Table 2).

208 When different species of aphid were provided the significant difference in intrinsic rate of  
 209 increase (r) was recorded (Table 3) i.e. maximum intrinsic rate of increase (0.21197 d<sup>-1</sup>) when fed  
 210 on *A. nerii* and followed by *L. erysimi* and *M. persicae* (0.198695 and 0.186412 d<sup>-1</sup>, respectively).

211 While minimum intrinsic rate of increase (r) was recorded (0.021559 d<sup>-1</sup>) when fed on *D. noxia*.

212 “Table 3” Life table parameters mean of *M. sexmaculatus*

Aphid species	<i>Aphis nerii</i>	<i>Myzus persicae</i>	<i>Diuraphis noxia</i>	<i>Lipaphis erysimi</i>
r (d <sup>-1</sup> )	0.21197	0.186412	0.021559	0.198695
λ (d <sup>-1</sup> )	1.236111	1.204918	1.240592	1.21981

R <sub>o</sub> (Offspring individual <sup>-1</sup> )	117.25	99.55	158.4	117.9
T (d)	22.476	24.68	23.494	24.006
GRR	131.92	115.02	172.2	125.67
F	260.56	199.1	316.8	235.8

213  $r$ = intrinsic rate of increase,  $\lambda$ = finite rate of increase,  $R_{o=}$  net reproductive rate  $T$ = the mean of  
 214 generation,  $GRR$ = the gross reproductive rate and  $F$ = Fecundity (eggs per female).

215 The significant difference in finite rate of increase ( $\lambda$ ) was recorded when different aphid species  
 216 were given to *M. sexmaculatus* (Table 3) i.e. maximum finite rate of increase ( $\lambda$ ) was reported  
 217 (1.240592 d<sup>-1</sup>) when fed on *D. noxia* followed by (1.236111 and 1.21981 d<sup>-1</sup>, respectively) when  
 218 fed on *A. nerii* and *L. erysimi*, respectively. Minimum finite rate of increase was recorded when  
 219 fed on *M. persicae* (1.204918 d<sup>-1</sup>).

220 When different aphid species were given to *M. sexmaculatus* the significant difference in net  
 221 reproductive rate ( $R_o$ ) was recorded (Table 3) i.e. maximum net reproductive rate ( $R_o$ ) was  
 222 recorded (158.4 d<sup>-1</sup>) when fed on *D. noxia* followed by *L. erysimi* and *A. nerii* (117.9 and 117.25  
 223 d<sup>-1</sup>, respectively), whereas minimum net reproductive rate ( $R_o$ ) recorded when fed on *M. persicae*  
 224 (99.55 d<sup>-1</sup>).

225 The significant difference in mean of generation ( $T$ ) was recorded when different aphid species  
 226 were provided to *M. sexmaculatus* (Table 3) i.e. maximum mean of generation ( $T$ ) was reported  
 227 (24.68 d<sup>-1</sup>) when fed on *M. persicae* followed by (24.006, 23.494 d<sup>-1</sup>, respectively) *L. erysimi*, *D.*  
 228 *noxia* respectively. While minimum mean of generation ( $T$ ) was recorded (22.476 d<sup>-1</sup>) when fed  
 229 on *A. nerii*.

230 The significant difference in gross reproductive rate ( $GRR$ ) of *M. sexmaculatus* was observed when  
231 different aphid species were provided (Table 3) i.e. maximum gross reproductive rate ( $GRR$ ) was  
232 recorded ( $172.2\text{ d}^{-1}$ ) when fed on *D. noxia* followed by ( $131.92$  and  $125.67\text{ d}^{-1}$ , respectively) *A.*  
233 *nerii* and *L. erysimi*, respectively. While minimum gross reproductive rate ( $GRR$ ) was reported  
234 ( $115.02\text{ d}^{-1}$ ) when fed on *M. persicae*.

235 When different aphid species were given to *M. sexmaculatus* the significant difference was  
236 observed in fecundity ( $F$ ) i.e. maximum fecundity ( $F$ ) was recorded ( $316.8$ ) when fed on *D. noxia*  
237 followed by ( $260.56$  and  $235.8$ , respectively) *A. nerii* and *L. erysimi* respectively. While minimum  
238 fecundity ( $F$ ) was recorded ( $199.1$ ) when *M. persicae* was given (Table. 3).

239 Age-stage-specific survival rate ( $s_{xj}$ ) curves (Fig 1) show that stage survival curves are overlapping  
240 with each other due to difference in developmental duration. *M. sexmaculatus* when feed on *M.*  
241 *persicae* show maximum survival to adult stage than *D. noxia*, *L. erysimi* and *A. nerii*. Whereas  
242 adult survival of *M. sexmaculatus* was similar in *M. persicae* and *D. noxia*.

243 “Fig 1” Age-stage-specific survival rate ( $s_{xj}$ ) of *M. sexmaculatus* fed on four aphid species.

244 *M. sexmaculatus* evinced similar but maximum survival rate both on *M. persicae* and *D. noxia*  
245 according to age specific survival rate (Fig 2). The age-stage-specific female fecundity ( $f_{x7}$ ) and  
246 age-specific fecundity ( $m_x$ ) shows that beetle maximum oviposition was  $29.4$  eggs at age of  $23$   
247 days (fig. 2) and  $15.5$  eggs, respectively (Fig 2). The values of ( $f_{x7}$ ) and ( $m_x$ ) of beetle were  
248 minimum on turnip aphids. The age-specific net maternity ( $l_x m_x$ ) shows that highest age-specific  
249 net maternity ( $l_x m_x$ ) was recorded on *D. noxia* followed by *L. erysimi* and *A. nerii*. Whereas  
250 minimum was recorded on *M. persicae*.

251 “Fig 2” Age-specific survival rate ( $l_x$ ), age-stage-specific fecundity ( $f_{xj}$ ), age-specific fecundity  
252 ( $m_x$ ), and age-specific maternity ( $l_x m_x$ ) of *M. sexmaculatus* fed on three aphid species.

253 Age-stage-specific reproductive rates ( $v_{xj}$ ) shows (Fig 3) that it is highest in case of *D. noxia* (110)  
254 at the age of 22 days. The highest reproductive values *A. nerii* *L. erysimi* and *M. persicae* are 98  
255 at 21days, 96 at 22 days, and 73 at 20 days, respectively.

256 “Fig 3” Age-stage-specific reproductive rate ( $v_{xj}$ ) of *M. sexmaculatus* fed on four aphid species.

257 Life expectancy curves ( $e_{xj}$ ) of females are similar in case of *D. noxia* and *L. erysimi* however are  
258 larger than *M. persicae* and *A. nerii*. Life expectancy curves presented (Fig 4) the survival of  
259 individual age  $x$  and stage  $j$ . Freshly hatched eggs of *M. sexmaculatus* estimated to live for 35, 35,  
260 34.5 and 32.5 days on *M. persicae*, *L. erysimi*, *D. noxia* and *A. nerii*, respectively. Usually female  
261 life expectancy greater than male life expectancy but in case of *A. nerii* and *L. erysimi* male life  
262 expectancy was greater than female life expectancy. Female and male life expectancies were  
263 reported 30 and 28 days after age of 12.5 and 10 days on *D. noxia*, respectively, while greater than  
264 *M. persicae* (29 and 26 days after age of 11 and 11.5 days, respectively).

265 “Fig 4” Age-stage-specific life expectancy ( $e_{xj}$ ) of *M. sexmaculatus* fed on four aphid species.

## 266 **Discussion**

267 *M. sexmaculatus* is good predator of aphids and an important biological control agent. The present  
268 study was carried out to understand the effect of different aphid species on the development,  
269 fecundity and survival rate of *M. sexmaculatus*. The results of present study showed that quality  
270 and availability of prey affect the development of *M. sexmaculatus*. These results closely related  
271 with work of (35) who reported that the quality and nature of the prey affect the development,

272 fecundity and survival rate of predator. Low quality and insufficient quantity of prey reduce the  
273 development of predator, whereas good quality and enough quantity of prey increase the  
274 development of predator (36).

275 Results showed that on comparison between *L. erysimi* and *M. persicae*, the maximum male  
276 longevity was recorded on *L. erysimi* while minimum was recorded on *M. persicae*. These results  
277 correlate with the study (24, 37) where *C. septempunctata* males exhibited maximum longevity on  
278 *L. erysimi* as compared to *M. persicae*. While in case of female, maximum longevity was recorded  
279 on *M. persicae* as compared to *L. erysimi*, this contradict with the result of *C. septempunctata*  
280 female population which showed maximum longevity on *L. erysimi* then *M. persicae*. This might  
281 be due to different species of beetles.

282 The results of present study revealed that statistically maximum male and female longevity was  
283 recorded on *D. noxia* while minimum longevity was recorded on *L. erysimi*. These results contrary  
284 with the study conducted on *C. septempunctata* that the adult longevity was maximum on *L.*  
285 *erysimi* than other aphid species (24, 38). In current study, highest fecundity was recorded on *D.*  
286 *noxia*. These results contrary with the study carried out on *C. septempunctata* where the maximum  
287 fecundity was reported on *M. persicae* (24, 39). There is a relation among predator longevity and  
288 fecundity. The predator has long longevity it does not mean that they have maximum fecundity.  
289 Because quality of host affects the longevity and fecundity of predator (39, 40).

290 The results of current study revealed that maximum age stage specific survival rate ( $s_{xj}$ ) was  
291 recorded on *M. persicae*. These results resembled with the study conducted on *C. septempunctata*  
292 that the maximum survival rate was recorded on *M. persicae* (19, 24, 41, 42). In this study  
293 maximum developmental rate was observed on *L. erysimi*. These findings closely resembled with

294 the study performed on *C. septempunctata*. Which also showed maximum developmental rate was  
295 on *L. erysimi* as compared to other aphid species. The reason was that the quality and quantity of  
296 prey affect the developmental rate of both immature and adult stages (43).

297 The biological parameters of predator are heavily affected by several factors like type of prey. The  
298 findings of current study revealed that the maximum  $R_0$  and  $\lambda$  was recorded on *D. noxia*. The  
299 maximum  $r$  was recorded on *A. nerii*. The highest  $T$  was noted on *M. persicae*. These results  
300 contrary with the study conducted on *C. septempunctata* that the maximum  $R_0$ ,  $\lambda$  and  $r$  was  
301 recorded on *M. persicae*, whereas maximum  $T$  was recorded on *L. erysimi* (24, 44, 45). The results  
302 of present study revealed that the maximum TPOP was recorded on *A. nerii*. These results  
303 contradict with the study performed on *C. septempunctata* that the maximum TPOP of *C.*  
304 *septempunctata* was recorded on *L. erysimi* (21, 24). In laboratory conditions TPOP of *M.*  
305 *sexmaculatus* was recorded minimum by Zhao et al. (25). The reason was that the difference in  
306 biotic and abiotic factors are responsible for changes in the findings (44).

307 In previous studies problems were associated with the traditional life table i.e. consider female  
308 population, neglect male population and stage differentiation between individuals and sexes. In  
309 present study age stage two sex life table was used to assess the difference between age specific  
310 survival rate and age specific fecundity which also consider the male survival curve and stage  
311 differentiation between individuals. The difficulties and errors associated with the female age  
312 specific life table briefly addressed by (19, 46).

313 The results of present study showed that oviposition period was maximum when they fed on *M.*  
314 *persicae*. These results contradict with the study conducted on *C. septempunctata* that the  
315 maximum oviposition period was recorded on *L. erysimi* (24, 47). The results of present study



316 revealed that the maximum fecundity curve (29.4 eggs) was reported on 23<sup>rd</sup> day, daily and lifelong  
317 fecundity were recorded on *D. noxia* (23.70 and 110 eggs, respectively). These results contradict  
318 with the study conducted on *C. septempunctata* that the maximum fecundity curve was reported  
319 (36.111 eggs) on 43<sup>rd</sup> day, daily and lifelong fecundity (39 and 470 eggs, respectively) were  
320 reported on *M. persicae* (24, 47, 48). The reason was that the nutritional value and quality of prey  
321 species affect the predator fecundity (49, 50). The life expectancy is that an adult is supposed to  
322 live at age  $x$  and stage  $j$ . The results of this study expressed that the life expectancy was reduced  
323 with the age of an adult. These results resembled with the study conducted on *C. septempunctata*  
324 that the adult's life expectancy reduced with the age. Without giving any stress adult's life  
325 expectancy gradually reduced with the age under laboratory conditions (24, 51, 52). The life  
326 expectancies of same age individuals can be changed, by the difference in life stages of individuals  
327 (19).

328 The current study was designed to evaluate the population growth in association with the number  
329 of individuals instead of  $r$ . That provides evidence about the growth potential of a population at an  
330 even age distribution (53). It was intended that *M. sexmaculatus* reached a stable age stage after  
331 23 days when reared on *D. noxia*. The maximum population was observed on *D. noxia* as compared  
332 to other species. It is reflected that *D. noxia* is most suitable host for mass rearing of *M.*  
333 *sexmaculatus* under laboratory conditions.

### 334 **Conclusion**

335 It was concluded that the prey specificity and availability affect the life table parameters of *M.*  
336 *sexmaculatus*. The appropriate host for mass rearing of *M. sexmaculatus* is *D. noxia* under  
337 laboratory conditions. Moreover, both male and female includes in age-stage two-sex life table.

338 Because age-stage two-sex life table gives brief information about the efficacy and use of *M.*  
339 *sexmaculatus* population in biological control. Future studies should consist on field application  
340 and evaluation of *M. sexmaculatus* for the management of aphid.

## 341 **Acknowledgment**

342 The authors would like to thank Mr. Yasir Hameed, Muhammad Sarmad and Muhammad Farrukh  
343 Hamid for their help during the work. Moreover, we grateful to Department of Entomology,  
344 Faculty of Agricultural Sciences & Technology, Bahauddin Zakariya University Multan for  
345 providing support and facilities to perform the Research.

## 346 **References**

- 347 1. Dong M, Zhang D. The relationship between aphids and their natural enemies and the ecological  
348 management. *Acta Phytophylacica Sinica*. 2011;38(4):327-32.
- 349 2. Saljoqi A, van Emden HF, Yu-rong H. Antixenosis to the peach-potato aphid, *Myzus persicae*  
350 (Sulzer) in potato cultivars. *Asian Journal of Plant Sciences*. 2003;2(12):932-5.
- 351 3. Kennedy G, Abou-Ghadir M. Bionomics of the turnip aphid on two turnip cultivars. *Journal of*  
352 *Economic Entomology*. 1979;72(5):754-7.
- 353 4. Elliott N, French B, Burd J, Kindler S, Reed D. Parasitism, adult emergence, sex ratio, and size of  
354 *Aphidius colemani* (Hymenoptera: Aphidiidae) on several aphid species. *The Great Lakes Entomologist*.  
355 2017;27(3):2.
- 356 5. Yue B, Liu T-X. Host selection, development, survival, and reproduction of turnip aphid  
357 (Homoptera: Aphididae) on green and red cabbage varieties. *Journal of Economic Entomology*.  
358 2000;93(4):1308-14.

- 359 6. Silva AX, Jander G, Samaniego H, Ramsey JS, Figueroa CC. Insecticide resistance mechanisms in  
360 the green peach aphid *Myzus persicae* (Hemiptera: Aphididae) I: a transcriptomic survey. PLoS ONE.  
361 2012;7(6):e36366.
- 362 7. Yazdani M, Baker G, DeGraaf H, Henry K, Hill K, Kimber B, et al. First detection of Russian  
363 wheat aphid *Diuraphis noxia* Kurdjumov (Hemiptera: Aphididae) in Australia: a major threat to cereal  
364 production. Austral Entomology. 2018;57(4):410-7.
- 365 8. Hughes R, Maywald G. Forecasting the favourableness of the Australian environment for the  
366 Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian  
367 wheat yields. Bulletin of Entomological Research. 1990;80(2):165-75.
- 368 9. Colvin SM, Yeargan KV. Predator fauna associated with oleander aphids on four milkweed species  
369 and the effect of those host plants on the development and fecundity of *Cycloneda munda* and *Harmonia*  
370 *axyridis*. Journal of the Kansas Entomological Society. 2014;87(3):280-99.
- 371 10. Mushtaq S, Rana SA, Khan HA, Ashfaq M. Diversity and abundance of family aphididae from  
372 selected crops of Faisalabad, Pakistan. Pak J Agri Sci. 2013;50(1):103-9.
- 373 11. Malcolm SB. Chemical defence in chewing and sucking insect herbivores: plant-derived  
374 cardenolides in the monarch butterfly and oleander aphid. Chemoecology. 1990;1(1):12-21.
- 375 12. Foster SP, Harrington R, Dewar AM, Denholm I, Devonshire AL. Temporal and spatial dynamics  
376 of insecticide resistance in *Myzus persicae* (Hemiptera: Aphididae). Pest management science.  
377 2002;58(9):895-907.
- 378 13. Bakırcı GT, Acay DBY, Bakırcı F, Ötleş S. Pesticide residues in fruits and vegetables from the  
379 Aegean region, Turkey. Food chemistry. 2014;160:379-92.
- 380 14. Gilkeson L, Kelin M. Natural enemies of insect pests coop. Ext Cornell Univ Ithea NY. 2001;63.
- 381 15. Ulrichs C, Mewis I, Schnitzler W. Efficacy of neem and diatomaceous earth against cowpea aphids  
382 and their deleterious effect on predating Coccinelidae. Journal of Applied Entomology.  
383 2001;125(9-10):571-5.

- 384 16. Solangi BK, Hullio MH, Baloch N. Biological parameters and prey consumption by zigzag beetle  
385 *Menochilus sexmaculatus* Fab. against *Rhopalosiphum maidis* Fitch, *Aphis gossypii* Glov. and *Therioaphis*  
386 *trifolii* Monell. *Sarhad J Agric.* 2007;23(4).
- 387 17. Agarwala BK, Yasuda H. Overlapping oviposition and chemical defense of eggs in two co-  
388 occurring species of ladybird predators of aphids. *Journal of Ethology.* 2001;19(1):47-53.
- 389 18. Harvey JA, Van Dam NM, Gols R. Interactions over four trophic levels: foodplant quality affects  
390 development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid. *Journal of*  
391 *Animal Ecology.* 2003;72(3):520-31.
- 392 19. Chi H, Su H-Y. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead)(Hymenoptera:  
393 Braconidae) and its host *Myzus persicae* (Sulzer)(Homoptera: Aphididae) with mathematical proof of the  
394 relationship between female fecundity and the net reproductive rate. *Environmental Entomology.*  
395 2006;35(1):10-21.
- 396 20. Ning S, Zhang W, Sun Y, Feng J. Development of insect life tables: comparison of two  
397 demographic methods of *Delia antiqua* (Diptera: Anthomyiidae) on different hosts. *Scientific reports.*  
398 2017;7(1):4821.
- 399 21. Ali A, Rizvi PQ. Age and stage specific life table of *Coccinella septempunctata* (Coleoptera:  
400 Coccinellidae) at varying temperature. *World Journal of Agricultural Sciencies.* 2010;6(3):268-73.
- 401 22. Arif MJ, Gogi MD, Abid AM, Muhammad I, Shahid MR, Sabir H, et al. Predatory potential of  
402 some native coccinellid predators against *Phenacoccus solenopsis*, Tinsely (Pseudococcidae: Hemiptera).  
403 *Pakistan Entomologist.* 2011;33(2):97-103.
- 404 23. Zhang Y, Wang Z, Su M, Zhao H, Ma X, Xue M. Selective studies on *Delia antique* (Meigen) to 4  
405 host plants. *China Vegetables.* 2012(4):83-6.
- 406 24. Farooq M, Shakeel M, Iftikhar A, Shahid MR, Zhu X. Age-stage, two-sex life tables of the lady  
407 beetle (Coleoptera: Coccinellidae) feeding on different aphid species. *Journal of Economic Entomology.*  
408 2018;111(2):575-85.

- 409 25. Zhao J, Li S, Gao X-W, Zhang F, Wang S. Comparison of life tables of *Cheilomenes sexmaculata*  
410 (Coleoptera: Coccinellidae) under laboratory and greenhouse conditions. *Journal of Economic Entomology*.  
411 2015;108(4):1700-7.
- 412 26. Chi H. TWSEX-MSChart: a computer program for the age-stage, two-sex life table analysis  
413 <http://140.120.197.173/Ecology/Download>. Two-sex MSChart zip. 2016.
- 414 27. Chi H, Liu H. Two new methods for the study of insect population ecology. *Bull Inst Zool Acad*  
415 *Sin*. 1985;24(2):225-40.
- 416 28. Chi H. Life-table analysis incorporating both sexes and variable development rates among  
417 individuals. *Environmental Entomology*. 1988;17(1):26-34.
- 418 29. Chen Q, Li N, Wang X, Ma L, Huang J-B, Huang G-H. Age-stage, two-sex life table of *Parapoynx*  
419 *crisonalis* (Lepidoptera: Pyralidae) at different temperatures. *PLoS ONE*. 2017;12(3):e0173380.
- 420 30. Efron B, Tibshirani RJ. *An introduction to the bootstrap*: CRC press; 1994.
- 421 31. Chi H. TIMING-MSChart: a computer program for the population projection based on age-stage,  
422 two-sex life table. National Chung Hsing University, Taichung, Taiwan. 2015.
- 423 32. Huang YB, Chi H. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett)(Diptera:  
424 Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect  
425 populations. *Insect Science*. 2012;19(2):263-73.
- 426 33. Goodman D. Optimal life histories, optimal notation, and the value of reproductive value. *The*  
427 *American Naturalist*. 1982;119(6):803-23.
- 428 34. Institute s. SAS 9.1 for Windows. SAS Institute Cary, NC; 2002.
- 429 35. Moghaddam MG, Golizadeh A, Hassanpour M, Rafiee-Dastjerdi H, Razmjou J. Demographic traits  
430 of *Hippodamia variegata* (Goeze)(Coleoptera: Coccinellidae) fed on *Sitobion avenae* Fabricius (Hemiptera:  
431 Aphididae). *J Crop Prot*. 2016;5:431-45.
- 432 36. Snyder WE, Joseph SB, Preziosi R, Moore AJ. Nutritional benefits of cannibalism for the lady  
433 beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environmental*  
434 *Entomology*. 2000;29(6):1173-9.

- 435 37. Sarwar M, Saqib SM. Rearing of predatory seven spotted ladybird beetle *Coccinella*  
436 *septempunctata* L.(Coleoptera: Coccinellidae) on natural and artificial diets under laboratory conditions.  
437 *Pakistan Journal of Zoology*. 2010;42(1).
- 438 38. Mahyoub JA, Mangoud AA, AL-Ghamdi KM. Method For Mass Production the Seven Spotted  
439 Lady Beetle, *Coccinella Septempunctata* (Coleoptera: Coccinellidae) and Suitable Manipulation of Egg  
440 Picking Technique Jazem A. Mahyoub<sup>1</sup>, Ashraf AH Mangoud<sup>2</sup>, Khaled. M. AL-Ghamdi<sup>1</sup> and Hamed A.  
441 Al-Ghramh<sup>3</sup>. 2013.
- 442 39. Solano Y, Delgado N, Morales J, Vásquez C. Biological studies and life table of *Cycloneda*  
443 *sanguinea* (L.)(Coleoptera: Coccinellidae) on *Aphis craccivora* Koch (Hemiptera: Aphididae).  
444 *Entomotropica*. 2016;31(34):267-75.
- 445 40. Dixon AFG, Dixon AE. Insect predator-prey dynamics: ladybird beetles and biological control:  
446 Cambridge University Press; 2000.
- 447 41. Yu J-Z, Chi H, Chen B-H. Life table and predation of *Lemnia biplagiata* (Coleoptera:  
448 Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross  
449 reproduction rate, net reproduction rate, and preadult survivorship. *Annals of the Entomological Society of*  
450 *America*. 2005;98(4):475-82.
- 451 42. Amir-Maafi M, Chi H. Demography of *Habrobracon hebetor* (Hymenoptera: Braconidae) on two  
452 pyralid hosts (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America*. 2006;99(1):84-  
453 90.
- 454 43. Ali A, Rizvi PQ. Development and predatory performance of *Coccinella septempunctata*  
455 L.(Coleoptera: Coccinellidae) on different aphid species. *J Biol Sci*. 2007;7(8):1478-83.
- 456 44. Kontodimas DC, Stathas GJ. Phenology, fecundity and life table parameters of the predator  
457 *Hippodamia variegata* reared on *Dysaphis crataegi*. *Biocontrol*. 2005;50(2):223-33.
- 458 45. Davoodi Dehkordi S, Sahragard A, Hajizadeh J. The effect of prey density on life table parameters  
459 of *Hippodamia variegata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Hemiptera: Aphididae) under  
460 laboratory conditions. *ISRN Entomology*. 2013;2013.

- 461 46. Huang YB, Chi H. Life tables of *B actrocera cucurbitae* (Diptera: Tephritidae): with an  
462 invalidation of the jackknife technique. *Journal of Applied Entomology*. 2013;137(5):327-39.
- 463 47. Sattar M, Hamed M, Nadeem S. Biology of *Coccinella septempunctata* Linn.(Coleoptera:  
464 Coccinellidae) and its predatory potential on cotton aphids, *Aphis gossypii* Glover (Hemiptera: Aphididae).  
465 *Pakistan Journal of Zoology*. 2008;40(4).
- 466 48. Kontodimas DC, Milonas PG, Stathas GJ, Papanikolaou NE, Skourti A, Matsinos YG. Life table  
467 parameters of the aphid predators *Coccinella septempunctata*, *Ceratomegilla undecimnotata* and *Propylea*  
468 *quatuordecimpunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*. 2008;105(3):427.
- 469 49. Kajita Y, Evans EW. Ovarian dynamics and oosorption in two species of predatory lady beetles  
470 (Coleoptera: Coccinellidae). *Physiological Entomology*. 2009;34(2):185-94.
- 471 50. Hodek I, Honěk A. *Ecology of coccinellidae*: Springer Science & Business Media; 2013.
- 472 51. Bailey R, Chang N-T, Lai P-Y. Two-sex life table and predation rate of *Cybocephalus flavocapitis*  
473 *Smith* (Coleoptera: Cybocephalidae) reared on *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae), in  
474 Taiwan. *Journal of Asia-Pacific Entomology*. 2011;14(4):433-9.
- 475 52. Atlihan R, Chi H. Temperature-dependent development and demography of *Scymnus subvillosus*  
476 (Coleoptera: Coccinellidae) reared on *Hyalopterus pruni* (Homoptera: Aphididae). *Journal of Economic*  
477 *Entomology*. 2008;101(2):325-33.
- 478 53. Ebrahimi M, Sahragard A, Talaei-Hassanloui R, Kavousi A, Chi H. The life table and parasitism  
479 rate of *Diadegma insulare* (Hymenoptera: Ichneumonidae) reared on larvae of *Plutella xylostella*  
480 (Lepidoptera: Plutellidae), with special reference to the variable sex ratio of the offspring and comparison  
481 of jackknife and bootstrap techniques. *Annals of the Entomological Society of America*. 2013;106(3):279-  
482 87.
- 483
- 484

bioRxiv preprint doi: <https://doi.org/10.1101/2020.01.15.907576>; this version posted January 15, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

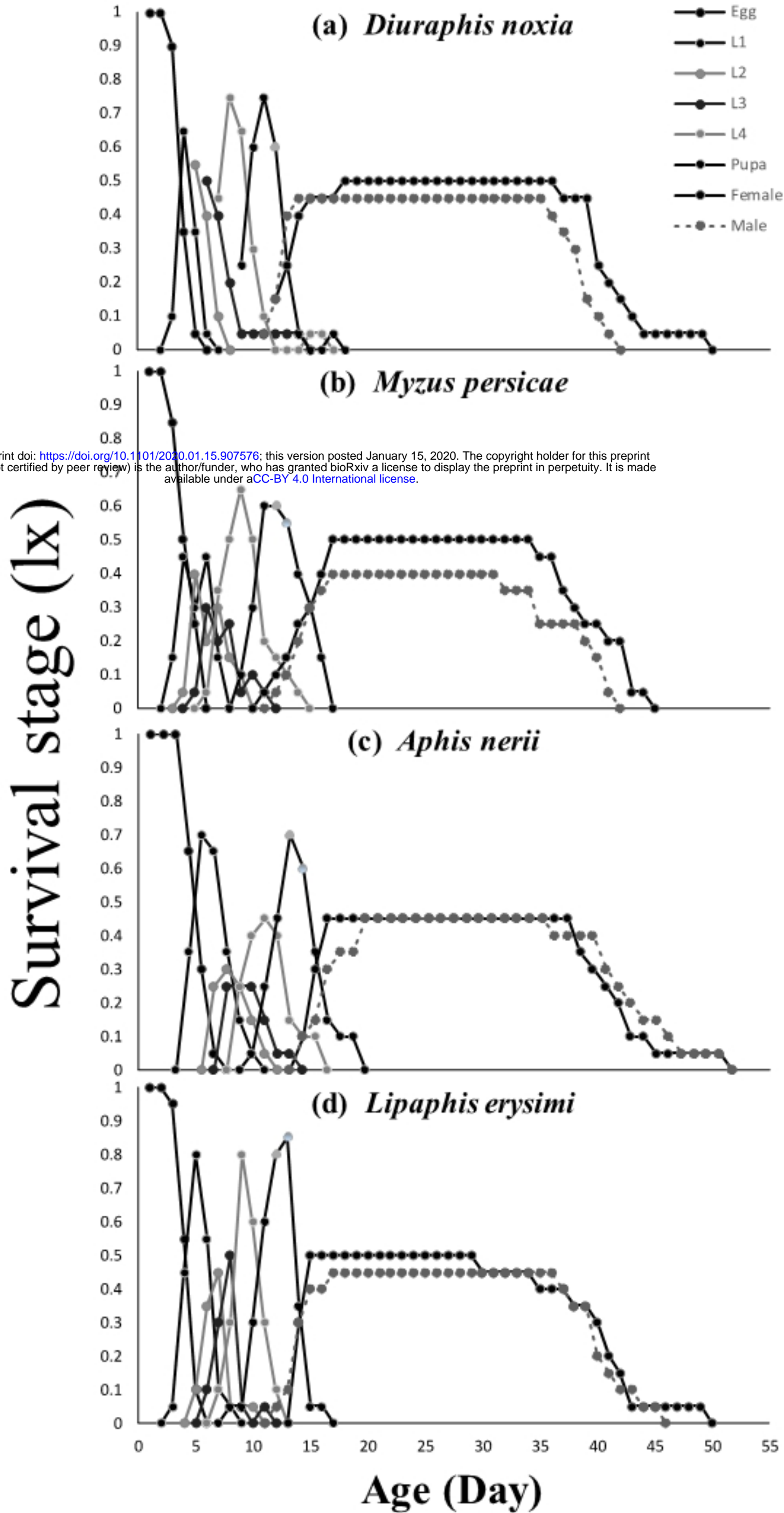


Figure 1



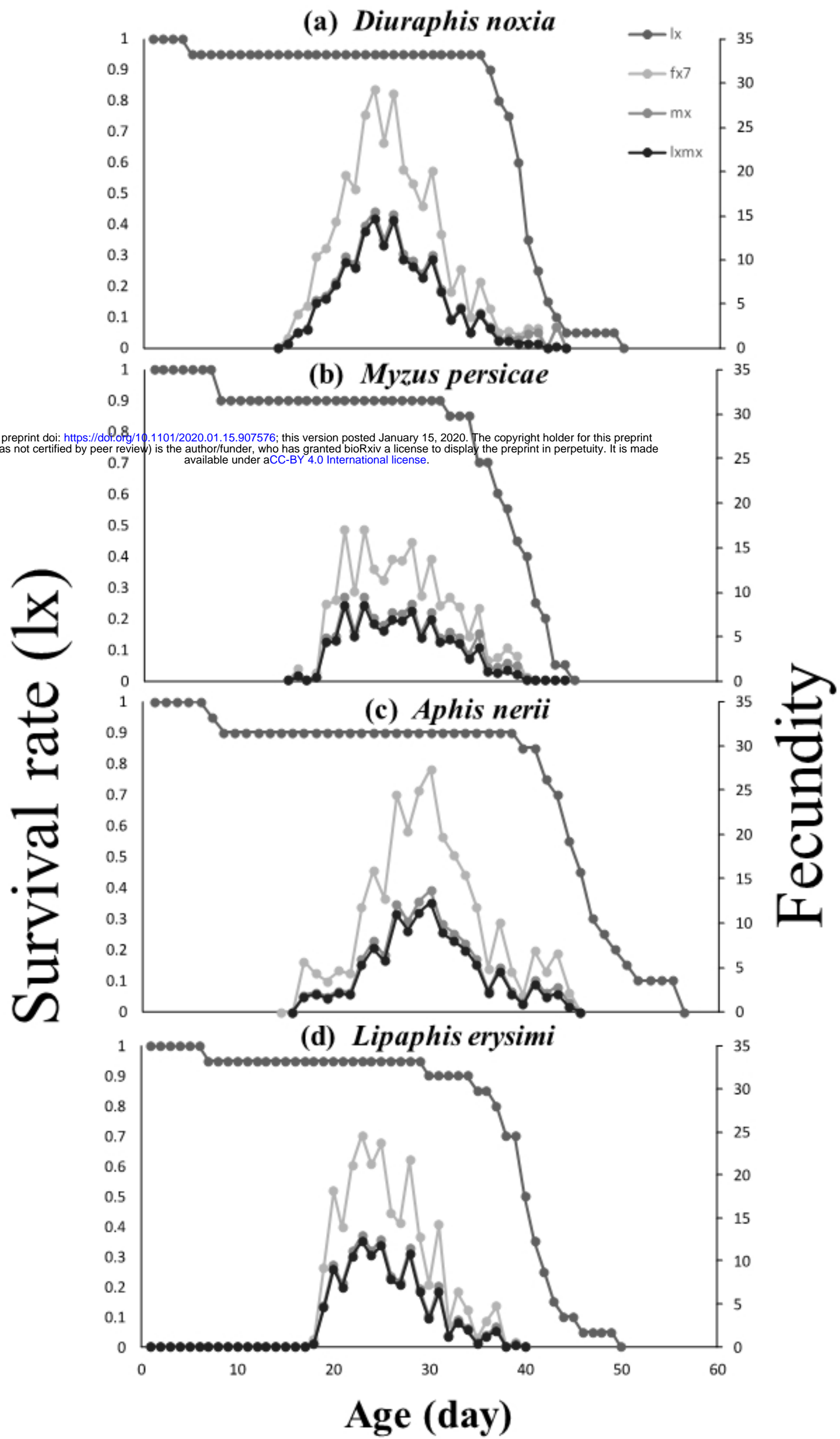


Figure 2

Reproductive Value ( $V_{xj}$ )

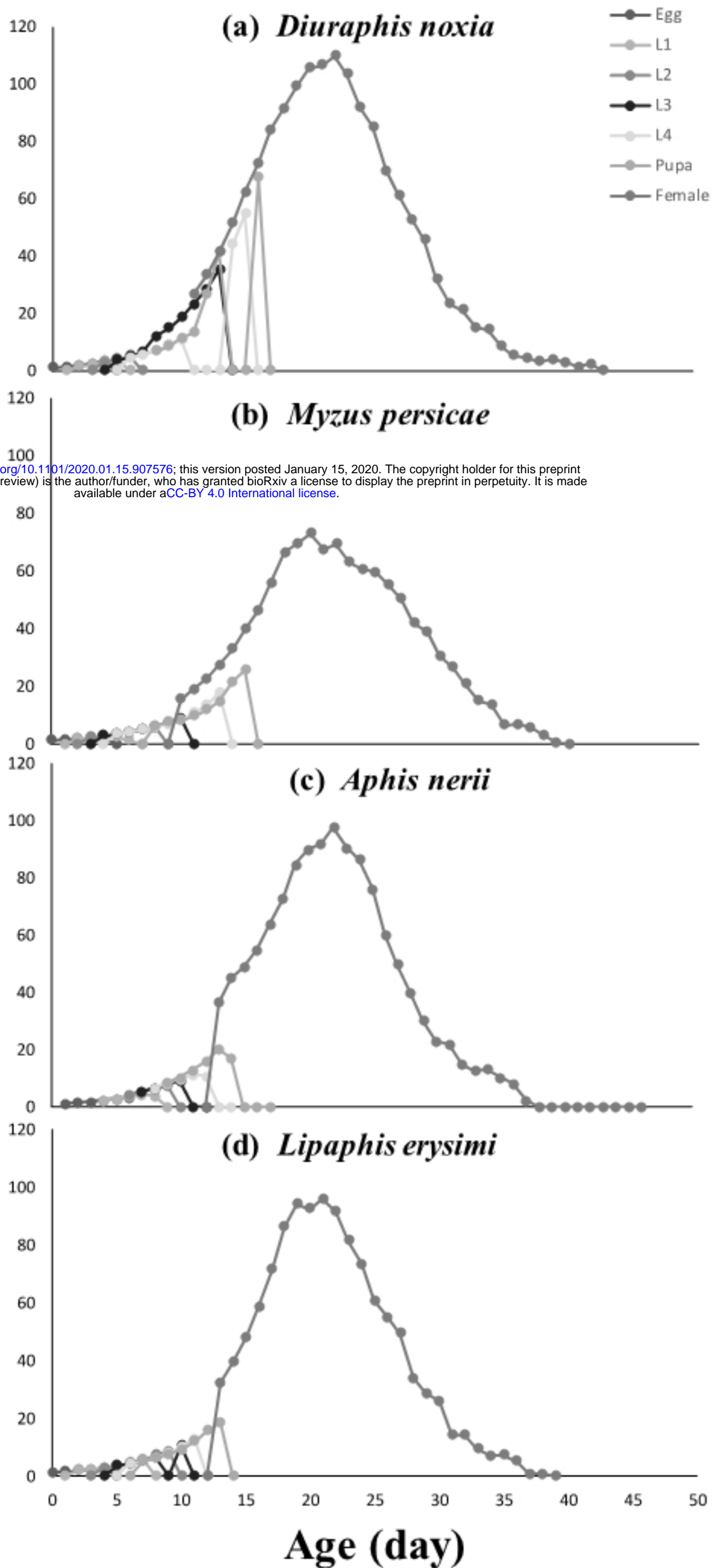


Figure 3

Life Expectancy (exj)

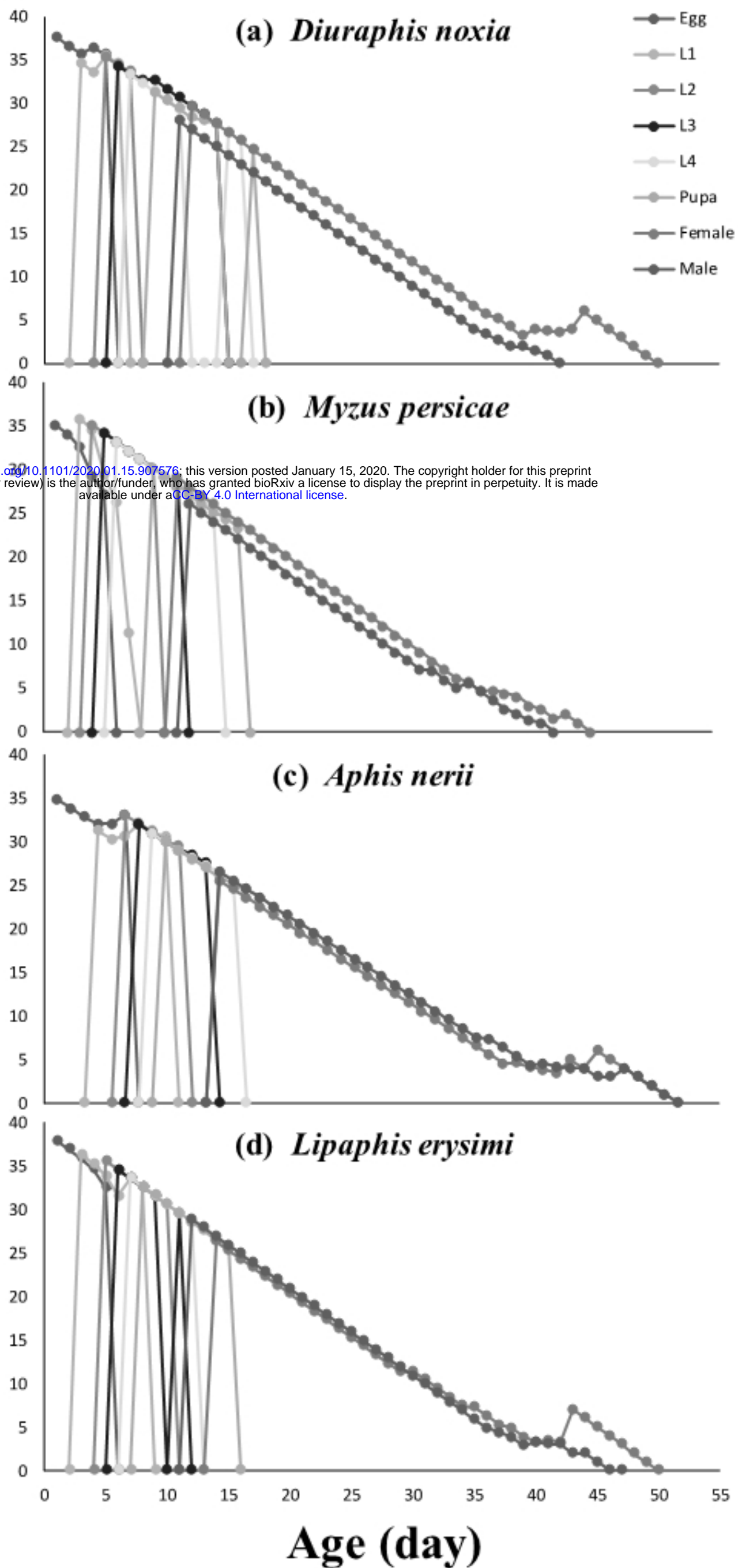


Figure 4