1 **Title: Life Tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae):**

2 **with a Mathematical Invalidation for Applying the Jackknife Technique to the**

3 **Net Reproductive Rate**

4

5 Running title: Life table and jackknife technique

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Abstract

1. Life table data for the melon fly, *Bactrocera cucurbitae* (Coquillett), reared on cucumber (*Cucumis sativus* L.) were collected under laboratory and simulated field conditions.

2. Means and standard errors of life table parameters were estimated for two replicates using the jackknife technique.

3. At 25ºC, the intrinsic rates of increase (r) found for the two replicates were 0.1354 and 0.1002 day^{-1}, and the net reproductive rates (R_0) were 206.3 and 66.0 offspring, respectively.

4. When the cucumbers kept under simulated field conditions were covered with leaves, the r and R_0 for the two replicates were 0.0935 and 0.0909 day^{-1}, 17.5 and 11.4 offspring, respectively. However, when similar cucumbers were left uncovered, the r and R_0 for the two replicates were 0.1043 and 0.0904 day^{-1}, and 27.7 and 10.1 offspring, respectively.

5. Our results revealed that considerable variability between replicates in both laboratory and field conditions is possible; this variability should be taken into consideration in data collection and application of life tables.

6. Mathematical analysis has demonstrated that applying the jackknife technique results in unrealistic pseudo-R_0 and overestimation of its variance.

7. We suggest that the jackknife technique should not be used for the estimation of variability of R_0.

41 **Introduction**

42 The melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), has been one

43 of the most important pests in Taiwan (Huang & Chi, 2011), and in many other

44 regions in Asia (Koyama *et al*., 2004; Dhillon *et al*., 2005) for several decades.

45 Although the agricultural agencies have invested heavily in research, workshops, and

46 control measures related to the fly, it remains a major pest in Taiwan (Huang & Chi,

47 2011).   For sustainable pest management in organic farming, it is crucial to develop a

48 comprehensive understanding of the population ecology of the target pests.   Life

49 table studies should be the first priority in ecologically sound pest management

50 programs because only life tables can provide the most detailed and correct

51 descriptions of the survival, stage differentiation, and reproduction of populations.

52 Age-specific female life tables of *B. cucurbitae* were developed by Vargas *et al*. (1996,

53 1997, 2000) and Yang *et al*. (1994).   However, the theories relating to female

54 age-specific life tables (Lewis, 1942; Leslie, 1945; Birch, 1948) address only female

55 populations and ignore male populations.   Chi & Liu (1985) and Chi (1988)

56 observed that female age-specific life tables cannot correctly describe the growth and

57 stage differentiation of insect and mite populations.   Thus, although numerous

58 female life tables have been published for many insect species, their practical

59 applications are quite limited.   Huang & Chi (2011) reported the first age-stage,

60 two-sex life table for *B. cucurbitae* under laboratory conditions with cucumber slices

61 as the rearing medium.   They demonstrated that an erroneous relationship is obtained

62 if an age-specific female life table is applied to a two-sex population.   Furthermore,

63 they indicated that the study of life tables constructed under field conditions can be

64 helpful by revealing differences between the values of population parameters in the

65 field and in the laboratory.

66   Liquido (1991) demonstrated that fallen fruits on the ground act as a reservoir for

67   melon fly populations.   To construct precise predictions of the dynamics of

68   populations in the field, it is necessary to identify the differences between life tables

69   collected in the laboratory and those actual life tables under field conditions.   On the

70   other hand, due to the tedious and time-consuming work of life table studies, most life

71   table studies are carried out by using single cohort without replication.   To estimate

72   the means and variances of population parameters obtained from a single cohort,

73   jackknife technique is widely used.   Meyer *et al*. (1986) used jackknife and bootstrap

74   techniques in estimating uncertainty in intrinsic rate and concluded that jackknife was

75   more cost-effective based on simulation.   Efron & Tibshirani (1993) discussed the

76   failure of jackknife.   Chi & Yang (2003) pointed out that application of jackknife

77   will result in some degree of discrepancy between the estimated means of population

78   parameters and their theoretical definition.   When we use the jackknife method to

79   estimate the mean value of the net reproductive rate, we often obtain some pseudo-R_0

80   value of zero.   An mathematical explanation is needed to justify or falsify the use of

81   jackknife technique.   In this study, eggs of melon flies were artificially introduced

82   into whole cucumbers (*Cucumis sativus* L.), then kept at 25ºC and under field with

83   replications.   Life tables were constructed and the population parameters were

84   measured for replicates.   Furthermore, we derived a mathematical proof to

85   demonstrate the problem of the jackknife method for the estimation of the mean and

86   standard error of the net reproductive rate.

87

88   **Materials and methods**

89   *Life Table Study*

90   Melon flies were collected in a field used to grow vegetables and subsequently

91   reared on cucumber (*Cucumis sativus* L.).   The colony was maintained in the

92   laboratory of the Department of Entomology, National Chung Hsing University

93   (Taichung, Taiwan) for two generations before the beginning of the life table study.

94   For the life table study, eggs laid within 24 h were collected using piled cucumber

95   slices following the method of Huang & Chi (2011).   For implanting eggs into the

96   cucumber, a pyramid-shaped hole with a rectangular base (1.5 cm each side, 1.5 cm

97   height) was cut with an arrowhead-shaped knife.   Twenty eggs were placed in the

98   hole with a fine writing brush.   Before the pyramid-shaped cucumber piece was

99   replaced, its tip was removed to leave a space for the eggs.   To study the cohort life

100   tables at 25°C, five cucumbers with eggs were kept in a plastic jar (26 cm height, 23

101   cm diameter) with loamy soil.   The mouth of the jar was covered with fine mesh net

102   and kept at a constant temperature of 25ºC in a growth chamber under a photoperiod

103   of 12:12 (L:D) h.   To study the life table under field conditions, five cucumbers with

104   eggs were placed in a jar, kept in a shaded area and covered with dried mango leaves.

105   Another five cucumbers with eggs were placed in a jar and kept under direct sunlight

106   in the field with no leaf cover.   The field study was conducted from 5 June to 9

107   September 2006.   The average field temperature was 28.1ºC.   Two replicates were

108   used for each treatment.   The numbers of emerged adults were observed, and pairs of

109   adults were formed.   The eggs laid daily by the melon flies were collected on sliced

110   cucumber as described in Huang & Chi (2011).

111

112   *Demographic Analysis*

113   The life history data were analyzed according to the age-stage, two-sex life table

114   theory (Chi & Liu, 1985) and the method described by Chi (1988).   The means and

115   standard errors of the life table parameters were estimated with the jackknife method

116   (Sokal & Rohlf, 1995). The population parameters estimated were the intrinsic rate

117   of increase (r), the finite rate of increase (λ), the gross reproductive rate (GRR), the

118   net reproductive rate (R_0) and the mean generation time (T). In this paper, the

119   intrinsic rate of increase is estimated with the iterative bisection method from the

120   Euler-Lotka formula

121
$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{1}$$

122   with age indexed from 0 (Goodman, 1982). The mean generation time is defined as

123   the length of time that a population needs to increase to R_0-fold of its size (i.e., $e^{rT} =$

124   R_0 or $\lambda^T = R_0$) at the stable age-stage distribution and is calculated as $T = (\ln R_0)/r$.

125   The age-stage life expectancy (e_{xj}) is calculated according to Chi & Su (2006). To

126   facilitate the tedious process of raw data analysis, a computer program

127   TWOSEX-MSChart for the age-stage, two-sex life table analysis (Chi, 2010) in

128   Visual BASIC (version 6, service pack 6) for the Windows system is available at

129   http://140.120.197.173/ Ecology/ (Chung Hsing University) and at

130   http://nhsbig.inhs.uiuc.edu.tw/www/chi.html (Illinois Natural History Survey). We

131   used a Tukey-Kramer procedure (Dunnett, 1980) to compare the difference among

132   treatments following the description of Sokal & Rohlf (1995).

133

134   **Results**

135   *Life Table of* B. cucurbitae

136   The developmental times for each stage are listed in Table 1. At 25 ºC, the

137   duration of the preadult stage in whole cucumber was 17.8 and 18.5 d (two replicates).

138   This value was much greater than the corresponding value for growth in cucumber

139   kept under field conditions with or without leaf coverage. The adult

140   pre-ovipositional periods (APOP) in the different treatments ranged from 7.0 to 9.1 d.

141   There were no significant differences among these values.   The total

142   pre-ovipositional period (TPOP) at 25°C was, however, significantly longer than those

143   found in the field.   The adult longevities of both male and female adults at 25°C are

144   also longer than those observed under field conditions.   The total fecundity varied

145   significantly among treatments (Table 2).   Significantly higher fecundities (859 and

146   660 eggs/female) were observed in females reared at 25ºC than in females emerged

147   under field conditions.   The high coefficients of variation (CV) of mean fecundities

148   showed the high reproductive variability among individuals.

149   The detailed age-stage survival rates (s_{xj}) of *B. cucurbitae* for the different

150   treatments are plotted in Fig. 1.   The parameter s_{xj} is the probability that a newborn

151   will survive to age x and stage j.   The survival rate curves of *B. cucurbitae* cohorts

152   vary significantly between replicates for populations reared in whole cucumbers.   In

153   general, the survival rate in the laboratory is higher than in the other treatments.   At

154   25°C, cohorts in the laboratory survived longer than those in the field.   This

155   difference is also evident from the longer developmental time of the preadult stage

156   and from the adult longevities (Table 1).

157   The daily mean number of offspring produced by individual *B. cucurbitae* of

158   age x and stage j per day is shown with the age-stage fecundity (f_{xj}) in Fig. 2.

159   Because only adult females produce offspring, there is only a single curve f_{x2} (i.e., the

160   adult female is the second life history stage).   The age-specific survival rate (l_x) and

161   the age-specific fecundity (m_x) are also plotted in Fig. 2.   The l_x curve describes the

162   change in the survival rate of the cohort with age.   Significant variability can be

163   observed between the two replicates.   In one replicate at 25ºC, more than 40% *B.*

164   *cucurbitae* survived to the adult stage, but the corresponding value in another

165   replicate was much smaller, approximately 20%.   However, at 25°C, the survival

166   rates in the laboratory are higher than those in the field (Fig. 2).

167

168   *Population Parameters*

169   The means and standard errors of population parameters of *B. cucurbitae* in the

170   different treatments investigated are listed in Table 2.   For the eggs artificially

171   placed in cucumber and kept at 25ºC, the intrinsic rates of increase (*r*) found for the

172   two replicates were 0.1354 and 0.1002 day^{-1}, the net reproductive rates (R_0) were

173   206.3 and 66.0 offspring, and the mean generation times (*T*) were 39.5 and 42.6 days,

174   respectively.   For the cucumbers kept in the field and covered with leaves, the

175   population parameters (*r*, R_0 and *T*) were 0.0935 and 0.0909 day^{-1}, 17.5 and 11.4

176   offspring, and 34.0 and 35.0 days, respectively.   However, for the cucumbers kept

177   in the field without leaves, the population parameters (*r*, R_0 and *T*) were 0.1043 and

178   0.0904 day^{-1}, 27.7 and 10.1 offspring, and 32.8 and 27.2 days, respectively.   The

179   maximum intrinsic rate of increase (0.1354 d^{-1}) was obtained at 25ºC in the

180   laboratory.   All parameters have very high values of CV.

181   The age-stage specific life expectancy (e_{xj}) (Fig. 3) is the lifespan remaining for

182   an individual of age *x* and stage *j*.   The contribution of an individual of age *x* and

183   stage *j* to the future population is described by the age-stage reproductive value (v_{xj})

184   (Fig. 4).   The reproductive value of a newborn (v_{01}) is exactly equal to the finite rate

185   of increase.

186

Discussion

188   *Life Table of* B. cucurbitae

189   The shorter preadult stage in the treatment under field conditions with leaf

190   coverage might be due to the higher temperature and the higher humidity.   These

191   conditions can promote the decay of cucumber and thereby generate conditions

192   favorable for flies.   Vayssières *et al*. (2008) reported that the total preadult

193   development time of *B. cucurbitae* on cucumber at 25 and 30ºC was 17.2 and 13.2

194   days, respectively.   Huang & Chi (2011) reported that the total preadult development

195   time of *B. cucurbitae* was 15.1 days at 25ºC.   These studies show that the preadult

196   development time of *B. cucurbitae* decreases as the temperature increases.   Under

197   field conditions, melon flies in different fallen fruits may experience different

198   micro-environments and may result in higher variations in developmental rate,

199   survival and reproduction.

200   Because the variable developmental rate among individuals is incorporated in

201   the age-stage, two-sex life table, the overlap between stages can be observed in Fig. 1.

202   If the survival curves were constructed based on the means of each stage or adult age

203   (e.g., Marcic, 2003, 2005; Legaspi, 2004; Legaspi & Legaspi, 2005; Lin & Ren, 2005;

204   Liu, 2005; Kivan & Kilic, 2006; Kontodimas & Stathas, 2005; Tsoukanas *et al*.,

205   2006), the stage overlap would not have been observed and would have resulted in

206   errors in the survival curves as well as the fecundity curves.   Liu (2005) noticed the

207   overlap of the stages of *Delphastus catalinae* (Coleoptera: Coccinellidae).

208   Nevertheless, he ignored the variable developmental rate and constructed

209   age-specific fecundity schedules based on adult age.   Yu *et al*. (2005) and Chi & Su

210   (2006) gave detailed explanations and a mathematical proof to address the errors in

211   life tables based on adult age.

212   In Vargas *et al*. (1997), the fecundity of *B. cucurbitae* at 24ºC was 578.6 eggs.

213   In Huang & Chi (2011), the mean fecundity of melon flies reared on cucumber at

214   25ºC was 341 eggs.   Jiang *et al*. (2006) reported that the mean fecundity of melon

215   flies reared on cucumber at 30ºC was 895.65 eggs.   In this study, the mean

216   fecundity of *B. cucurbitae* reared on whole cucumber at 25ºC was higher than the

217   fecundity given in Huang & Chi (2011).   If the survival rate and fecundity are

218   constructed based solely on the adult age, the differences in preadult development are

219   ignored, and it is assumed that all adults emerge on the same day.   These artificial

220   manipulations and assumptions will not only falsely diminish the real variability

221   among individuals, but also consequently result in errors in the survival and

222   fecundity curves (Chi, 1988; Yu *et al*., 2005; Chi & Su, 2006; Huang & Chi, 2011).

223

224   *Population Parameters*

225   Due to the problems associated with the female age-specific life table (Huang &

226   Chi, 2011), we used the age-stage, two-sex life table to calculate the population

227   parameters of *B. cucurbitae*.   The intrinsic rate of increase (*r*) ranged from 0.0904

228   to 0.1354 days^{-1}.   The treatments did not differ significantly based on the estimated

229   means and standard errors obtained by using the jackknife technique and

230   Tukey-Kramer procedure.   The net reproductive rate (R_0) of melon flies reared in

231   the laboratory at 25ºC was higher than the corresponding rate under field conditions.

232   The relationship between the net reproductive rate R_0 and the mean female

233   fecundity *F* was given by Chi (1988) for the two-sex life table as

234
$$R_0 = F \cdot \left(\frac{N_f}{N} \right) \qquad (2)$$

235   where *N* is the total number of eggs used for the life table study at the beginning and

236   N_f is the number of female adults emerged.   Yu *et al*. (2005) gave the relationship

237   among the gross reproductive rate (*GRR*), the net reproductive rate (R_0) and the

238   preadult survivorship (l_a) as

239
$$GRR > l_a \cdot GRR > R_0 \qquad (3)$$

240   All of our results for *B. cucurbitae* at different treatments are consistent with the

241   relationships given by equations 2 and 3.   If a life table is constructed based on

242   adult age and ignores the preadult mortality, an erroneous relationship between the

243   mean fecundity and the net reproductive rate will be obtained.   Yu *et al*. (2005) and

244   Chi & Su (2006) discussed this problem in detail.

245   The shorter preoviposition period will cause a higher intrinsic rate of increase if

246   fecundity remains the same (Lewontin, 1965).   In the study of Huang & Chi (2011),

247   the TPOP of *B. cucurbitae* reared on cucumber at 25ºC was 23.1 d.   In our study, the

248   TPOP, i.e., the duration from egg to first oviposition, of melon flies reared in the

249   laboratory at 25ºC was longer than that under field conditions.   This result might be

250   explained by the higher field temperature (28ºC) and humidity.   At 25ºC, the

251   age-stage life expectancy gradually decreases with age because no other adverse

252   effects occur in the laboratory.   Under field conditions, however, the life

253   expectancies were lower and varied significantly due to the variable abiotic factors.

254   The life expectancy is calculated using the age-stage specific survival rate (s_{xj})

255   without assuming that the population reaches the stable age-stage distribution (Chi &

256   Su, 2006).   Thus, it can be used to predict the survival of a population under those

257   conditions.   For example, at 25ºC both newly emerged female and male adults can

258   be expected to remain alive, on average, more than two months.   The life

259   expectancy based on the age-stage, two-sex life table reveals the difference among

260   individuals of the same age but of different stages or different sexes.   Chi (1988),

261   Chi & Yang (2003) and Chi & Su (2006) discussed in detail the differences between

262   the traditional female age-specific life table and the age-stage, two-sex life table and

263   identified possible errors in the survival and fecundity curves based on the adult age.

264   Fisher (1930) defined the reproductive value as the contribution of an individual

265   to the future population.   The reproductive value significantly increases at the time

266   of emergence of the adult females.   For example, when a female adult emerges at

267   age 15 d at 25ºC (Fig. 1), the reproductive value increases from a value of less than

268   10 for a nymph to 36 for a female (Fig. 4).   The contribution of males to the future

269   population is not defined by Fisher (1930), and there is no curve for males.

270   The research reported here demonstrates that only life table study can

271   completely depict the development, stage differentiation, and reproduction of *B.*

272   *cucurbitae* and the variability of these processes in whole cucumber.   Moreover, it

273   revealed significant differences between life tables collected in the laboratory and the

274   field.   Thus, computer simulations of the growth of field populations should

275   incorporate considerations of these differences.   Chi (1990) noted that a simulation

276   based on the age-stage, two-sex life table can be used to time pest management by

277   taking the stage-specific susceptibility to pesticide applications into consideration.

278   Chi & Getz (1988) constructed a mass-rearing model based on the age-stage, two-sex

279   life table.   For an ecology-oriented integrated pest management of *B. cucurbitae*,

280   life tables collected under different conditions should play important roles in the

281   future.   However, because a variety of wild cucurbits serve as a host for the melon

282   fly and form a reservoir for this fly (Uchida *et al*., 1990), it might be necessary to

283   understand the life table of the fly on the major wild cucurbits.

284

285   *Using the Jackknife Method to Estimate of the Net Reproductive Rate*

286   Our results showed high values of CV in female mean fecundity and population

287   parameters.   The high CV in mean fecundity is calculated by using basic descriptive

288   statistical method and they reflect the differences among female individuals.   The

289   high CVs of population parameters are, however, estimated by using the jackknife

290   technique.   The jackknife technique is a resampling method which is usually used

291   when replication is impossible or difficult.   Because life table studies are time- and

292   labor-consuming, replication is in general impractical in most cases.   The jackknife

293   method is thus used to estimate the means and standard errors of population

294   parameters (Chi & Getz, 1988; Maia *et al*., 2000; Huang & Chi, 2011).   In the

295   jackknife method, we first use data on all individuals (n) to calculate the intrinsic rate

296   of increase of the whole cohort (r_{all}).   We then calculate the intrinsic rate r_i by

297   omitting individual i.   The pseudo-value $r_{i\text{-}pseudo}$ is then calculated as:

$$r_{i-pseudo} = n \cdot r_{all} - (n-1)r_i \qquad (4)$$

299   where n is the total number of individuals used at the beginning of the life table study.

300   The mean value of all $r_{i\text{-}pseudo}$ is the estimated mean value of the intrinsic rate of

301   increase of the cohort:

$$r = \frac{\sum_{i=1}^{n} r_{i-pseudo}}{n} \qquad (5)$$

303   Similarly, if we use the jackknife method to calculate the mean value of the net

304   reproductive rate, we first use data on all individuals in the cohort to calculate $R_{0,all}$:

$$R_{0,all} = \sum_{x=0}^{\infty} l_x m_x . \qquad (6)$$

306   If the total number of eggs laid by all surviving individuals at age x is F_x, the total

307   eggs laid by the whole cohort from birth to death is F_{total} and can be calculated as

308   $\sum_{x=0}^{\infty} F_x$.   Then, the $R_{0,all}$ can also be calculated as

$$R_{0,all} = \sum_{x=0}^{\infty} l_x m_x = \sum_{x=0}^{\infty} \frac{n_x}{n} \cdot \frac{F_x}{n_x} = \sum_{x=0}^{\infty} \frac{F_x}{n} = \frac{1}{n}\sum_{x=0}^{\infty} F_x = \frac{F_{total}}{n} \qquad (7)$$

310   where n_x is the number of surviving individuals at age x.   Equation 7 shows that the

311   net reproductive rate is F_{total} divided by the total number of individuals n used at the

312   beginning of the life table study.   If the omitted individual i is type N (those dying at

313   immature stages) or M (male), we define the total eggs laid by n-1 individuals at age

314   x as $F_{x,i}$.   It is clear that $F_{x,i} = F_x$ for all ages, because types N and M do not lay eggs.

315   The net reproductive rate with individual i omitted, i.e., $R_{0,i}$, can be calculated as

316
$$R_{0,i} = \sum_{x=0}^{\infty} \frac{n_{x,i}}{n-1} \cdot \frac{F_{x,i}}{n_{x,i}} = \sum_{x=0}^{\infty} \frac{F_{x,i}}{n-1} = \sum_{x=0}^{\infty} \frac{F_x}{n-1} = \frac{1}{n-1} \sum_{x=0}^{\infty} F_x \qquad (8)$$

317   where $n_{x,i}$ is the number of surviving individuals at age x if individual i is omitted.

318   The pseudo-value for the omission of individual i is calculated analogously to

319   Equation 4:

320
$$R_{0,i-pseudo} = n \cdot R_{0,all} - (n-1) \cdot R_{0,i} \qquad (9)$$

321   Replacing $R_{0,i}$ according to the proofs of Equation 7 and 8, we find

322
$$R_{0,i-pseudo} = n\left(\frac{1}{n}\sum_{x=0}^{\infty} F_x\right) - (n-1)\left(\frac{1}{n-1}\sum_{x=0}^{\infty} F_x\right) \qquad (10)$$

323   Consequently, we obtain

324
$$R_{0,i-pseudo} = \sum_{x=0}^{\infty} F_x - \sum_{x=0}^{\infty} F_x = 0 \qquad (11)$$

325   Thus, we prove that if the omitted individual i is type N or M, the pseudo-value

326    $R_{0,i-pseudo}$ will always be zero.

327   If the omitted individual i is a female and can produce $b_{x,i}$ eggs at age x, the total

328   number of eggs laid by this female during its life span can be calculated as

329
$$B_i = \sum_{x=0}^{\infty} b_{x,i} \qquad (12)$$

330   If individual i is omitted, then the total eggs produced by the remaining individuals in

331   cohort at age x is $F_{x,t}$.   It is clear that

332
$$F_{x,i} = F_x - b_{x,i} \quad \text{or} \quad F_x = F_{x,i} + b_{x,i} \qquad (13)$$

333   According to Equation 8, we have

334
$$R_{0,i} = \frac{1}{n-1}\sum_{x=0}^{\infty}F_{x,i} = \frac{1}{n-1}\sum_{x=0}^{\infty}\left(F_x - b_{x,i}\right) \tag{14}$$

335 The pseudo-value for the omission of individual i is

336
$$R_{0,i-pseudo} = n \cdot R_{0,all} - (n-1)\cdot R_{0,i} \tag{15}$$

337 Replacing $R_{0,i}$ of Equation 15 with its value in Equation 14, we can simplify

338 Equation 15 to 16.

339
$$R_{0,i-pseudo} = n \cdot \left(\frac{1}{n}\sum_{x=0}^{\infty}F_x\right) - (n-1)\left[\frac{1}{n-1}\sum_{x=0}^{\infty}\left(F_x - b_{x,i}\right)\right]$$

340
$$R_{0,i-pseudo} = \sum_{x=0}^{\infty}F_x - \sum_{x=0}^{\infty}F_x + \sum_{x=0}^{\infty}b_{x,i} = \sum_{x=0}^{\infty}b_{x,i} = B_i \tag{16}$$

341 It is clear that if the omitted individual i is a female, the pseudo-value of the net

342 reproductive rate is exactly the total fecundity of individual i itself,

343
$$R_{0,i-pseudo} = \sum_{x=0}^{\infty}b_{x,i} = B_i \tag{17}$$

344 This analysis shows that if the jackknife method is used, the pseudo-value of the net

345 reproductive rate obtained by omitting individual i is exactly the total number of eggs

346 laid by individual i.   It is exactly the fecundity of individual i.   The mean of all

347 pseudo-values is the total number of eggs laid by all individuals divided by n:

348
$$\hat{R}_0 = \frac{\sum_{i=1}^{n}R_{0,i-pseudo}}{n} = \frac{\sum_{i=1}^{n}B_i}{n} \tag{18}$$

349 By definition, it is clear that $\sum_{i=1}^{n}B_i = \sum_{x=0}^{\infty}F_x$.

350 The mean of all $R_{0,i-pseudo}$ is then

351
$$\hat{R}_0 = \frac{\sum_{i=1}^{n}B_i}{n} = \frac{\sum_{i=0}^{\infty}F}{n} = R_{0,all}. \tag{19}$$

352   The above proof can be concluded by making the following four observations: 1)

353   the mean value of the net reproductive rate estimated with the jackknife method is

354   exactly the same as the $R_{0,all}$ without the use of the jackknife method; 2) the net

355   reproductive rate equals the total eggs of the cohort divided by n, i.e., the total

356   number of newborns used for the life table study; 3) if the omitted individual is one

357   of the males or one of those that died at an immature stage, the pseudo-value is zero;

358   and 4) if the omitted individual is female, the pseudo-value is the fecundity of that

359   omitted female.

360   In Fig. 5, the frequency distributions of pseudo-R_0 values of three treatments

361   showed the zeros obtained by using the jackknife technique.   It is clear that the

362   omission of a single individual of type N or M will generate a pseudo-R_0 of zero.

363   The higher the preadult mortality or proportion of male, the higher the zero

364   pseudo-R_0 bar.   Because there is generally preadult mortality, the bar of zero

365   pseudo-R_0 will be an important factor determining the frequency distribution of all

366   life table data.   This is also the reason why statistical software shows the pseudo-R_0

367   failed the normality test and instead suggests Mann-Whitney Rank Sum test or others.

368   The omission of a single individual of type N or M caused the pseudo-R_0 of the

369   resampled population to zero.   If we carry out a true replication of life table study as

370   we did in this study, however, we will generally not get a population with zero net

371   reproductive rate, i.e., all individuals are either type N or M.   This shows the

372   jackknife technique will generate biologically unrealistic pseudo-R_0, which results in

373   an overestimation of variances and standard errors of the net reproductive rates.

374   The overestimation of variances and standard errors consequently make significant

375   differences between treatments undetectable by using statistical tests.

376   Variance analysis is important for revealing the variability of experimental

377   results.   The question of the suitability of the jackknife method for the estimation of

378 the mean and standard errors of the net reproductive rate is not the only difficulty

379 associated with life table analysis. The sample size must be sufficiently large to

380 prevent inaccurate estimation of the standard errors. Because there are many

381 problems associated with female life tables and analyses based on adult age (Chi &

382 Liu, 1985; Chi, 1988; Yu *et al*., 2005; Chi & Su, 2006; Huang & Chi, 2011), the

383 application of the jackknife method to female life tables (Leslie, 1945; Birch, 1948;

384 Maia *et al*., 2000) or in analyses based on female population and adult age (Maia *et*

385 *al*., 2000) will not produce correct estimates.

386 The significant differences between replicates in this study showed, however,

387 that the variability in developmental rate, survival, and reproduction of a life table

388 could not be properly described and estimated with the jackknife method. For this

389 reason and many others, the prediction of population dynamics under field conditions

390 is difficult. In this paper, we limit our discussion to the application of jackknife

391 method to the net reproductive rate. There are other resampling methods, e.g.,

392 bootstrapping, permutation test, cross validation, etc. Similar analysis is required to

393 re-evaluate their application in the estimation of means and variances of population

394 parameters. Despite these difficulties and problems, the life table is the only solid

395 theory which can correctly describe the survival, stage differentiation, and

396 reproduction in detail. The necessity and the difficulties associated with life table

397 study demonstrate that we need to draw the attention of scientists to life table theory

398 and data analysis in insect ecology, integrated pest management, as well as biological

399 control.

400 **Acknowledgments**

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518   proof on relationship among gross reproduction rate, net reproduction rate and

519   preadult survivorship. *Annuals of the Entomological Society of America*, **98**,

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521

522   Table 1.   Means and standard errors of the developmental time, longevity, adult preoviposition period (APOP) and total preoviposition period

523   (TPOP) of *Bactrocera cucurbitae* for different treatments

Parameter	Stage	25ºC		Field conditions			
				Without leaf coverage		With leaf coverage	
		Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Developmental time (days)	Preadult	17.8 ± 0.2 a	18.5 ± 0.2 b	11.4 ± 0.2 c	11.4 ± 0.1 c	11.0 ± 0.0 c	11.2 ± 0.2 c
Adult longevity (days)	Male	74.8 ± 7.1 a	63.2 ± 9.5 a	33.6 ± 13.1 b	34.7 ± 11.8 b	63.9 ± 9.8 a	13.2 ± 8.7 b
	Female	58.9 ± 6.5 a	45.6 ± 12.0 a	55.4 ± 11.6 a	16.3 ± 4.7 b	28.5 ± 8.9 a	22.6 ± 14.5 a
APOP (days)	Female	8.7 ± 0.3 a	8.9 ± 0.6 a	9.1 ± 0.3 a	8.6 ± 0.4 a	9.0 ± 0.6 a	7.0 ± 2.0 a
TPOP (days)	Female	26.7 ± 0.3 a	28.0 ± 0.8 b	20.7 ± 0.3 c	20.0 ± 0.3 c	20.0 ± 0.6 c	18.5 ± 1.5 c

524   Means in the same row followed by the same letter are not significantly different ($P > 0.05$) using the Tukey-Kramer procedure.

525 Table 2. Means, standard errors, and coefficients of variation (CV) (in parentheses) of the population parameters of *Bactrocera cucurbitae* for

526 different treatments

Population parameters	25ºC		Field conditions			
			Without leaf coverage		With leaf coverage	
	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Mean fecundity (F) (eggs/female)	859.5 ± 107.8 a (61.4%)	660.1 ± 179.9 a (86.2%)	345.9 ± 92.5 b (75.6%)	112.1 ± 42.8 b (114.4%)	218.5 ± 115.5 b (149.5%)	227.6 ± 162.3 b (159.5%)
The intrinsic rate of increase r (days^{-1})	0.1354 ± 0.0060 a (44.0%)	0.1002 ± 0.0116 a (116.2%)	0.1043 ± 0.0151 a (145.2%)	0.0904 ± 0.0197 a (217.3%)	0.0935 ± 0.0120 a (224.3%)	0.0909 ± 0.0380 a (417.3%)
The finite rate of increase λ (days^{-1})	1.145 ± 0.007 a (6%)	1.105 ± 0.013 a (11.6%)	1.110 ± 0.017 a (15.1%)	1.094 ± 0.021 a (19.5%)	1.098 ± 0.023 a (20.7%)	1.094 ± 0.040 a (36.9%)
Gross reproductive rate (*GRR*) (offspring)	636.3 ± 129.6 a (203.6%)	426.5 ± 159.5 a (374.6%)	322.4 ± 120.0 a (372.1%)	119.3 ± 56.4 a (473.0%)	146.5 ± 94.7 a (646.3%)	868.61 ± 484.84 a (558.2%)
The net reproductive rate R_0 (offspring/individual)	206.3 ± 44.8 a (217.3%)	66.0 ± 26.3 b (398.0%)	27.7 ± 11.7 b (423.5%)	10.1 ± 4.9 b (482.4%)	17.5 ± 10.5 b (602.5%)	11.4 ± 8.8 b (776.4%)
The mean generation time T (days)	39.5 ± 0.8 a (19.1%)	42.6 ± 1.5 a (34.3%)	32.8 ± 1.5 a (45.7%)	27.2 ± 2.3 b (83.2%)	34.0 ± 3.9 a (113.4%)	35.0 ± 7.4 a (212.2%)

527 Means in the same row followed by the same letter are not significantly different ($P > 0.05$) using the Tukey-Kramer procedure.

528 Figure captions

529 Fig. 1. Age-stage specific survival rate (s_{xj}) of *Bactrocera cucurbitae* for

530 different treatments.

531 Fig. 2. Age-specific survival rate (l_x), female age-specific fecundity (f_{x2}),

532 age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of *Bactrocera cucurbitae*
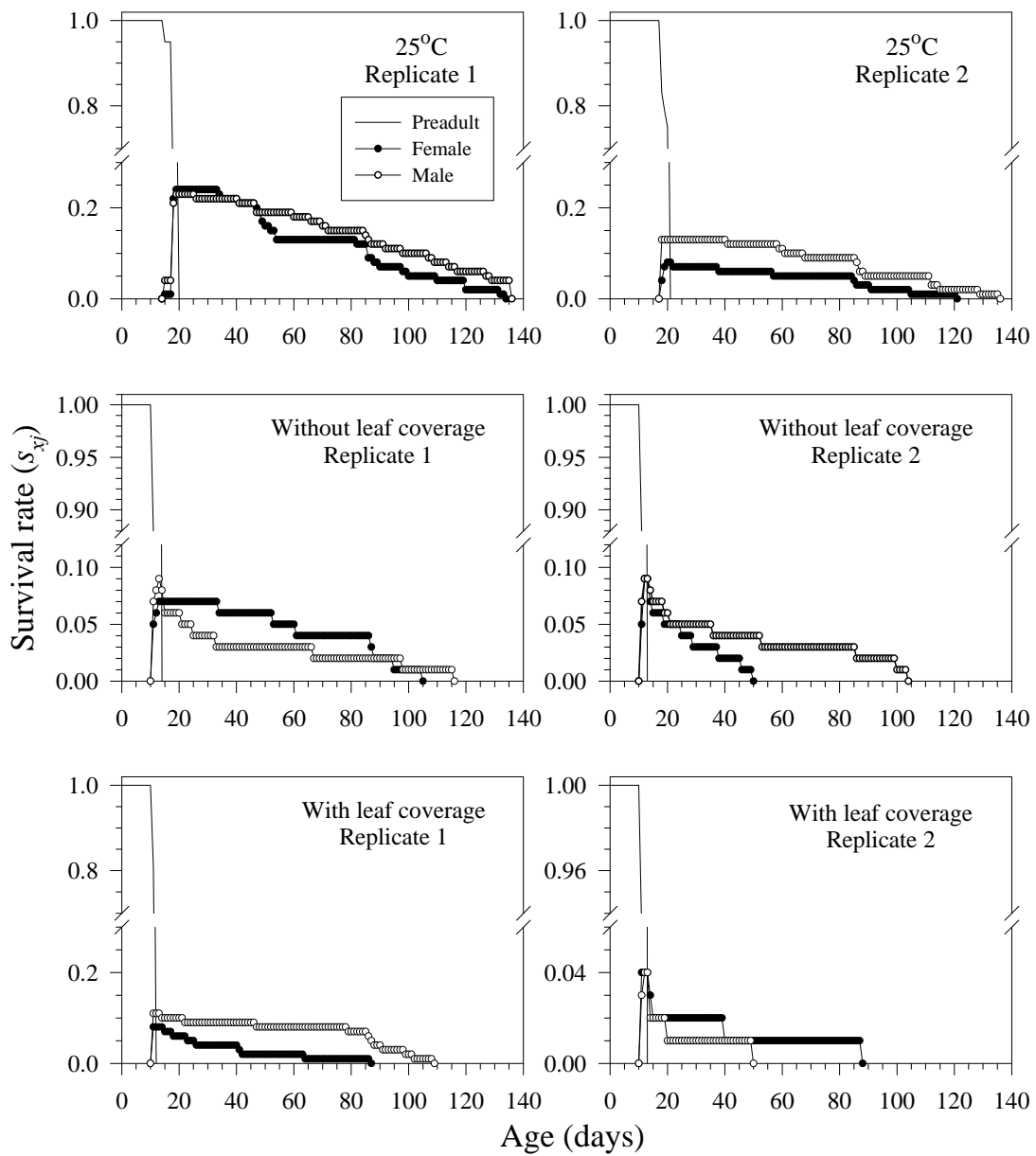
533 for different treatments.

534 Fig. 3. Age-stage specific life expectancy (e_{xj}) of *Bactrocera cucurbitae* for

535 different treatments.

536 Fig. 4. Age-stage specific reproductive value (v_{xj}) of *Bactrocera cucurbitae* for

537 different treatments.

538 Fig. 5. Frequency distribution of pseudo-R_0 grouped for different treatments.

539 Each bar represents the number of pseudo-R_0 between two ticks. The bar at zero

540 represents the frequency of pseudo-R_0 zero.
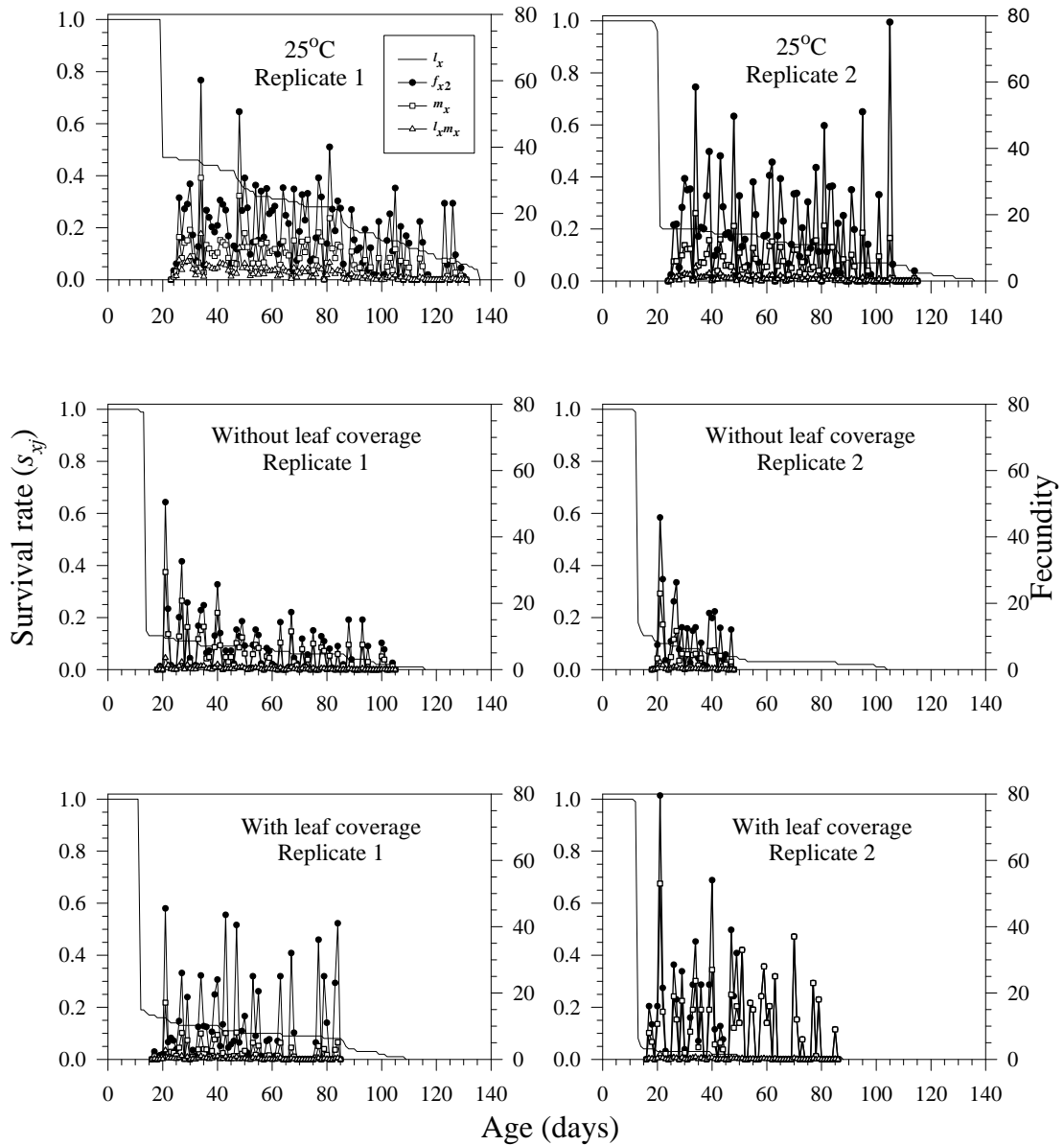
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544   Fig. 1.   Age-stage specific survival rate (s_{xj}) of *Bactrocera cucurbitae* for
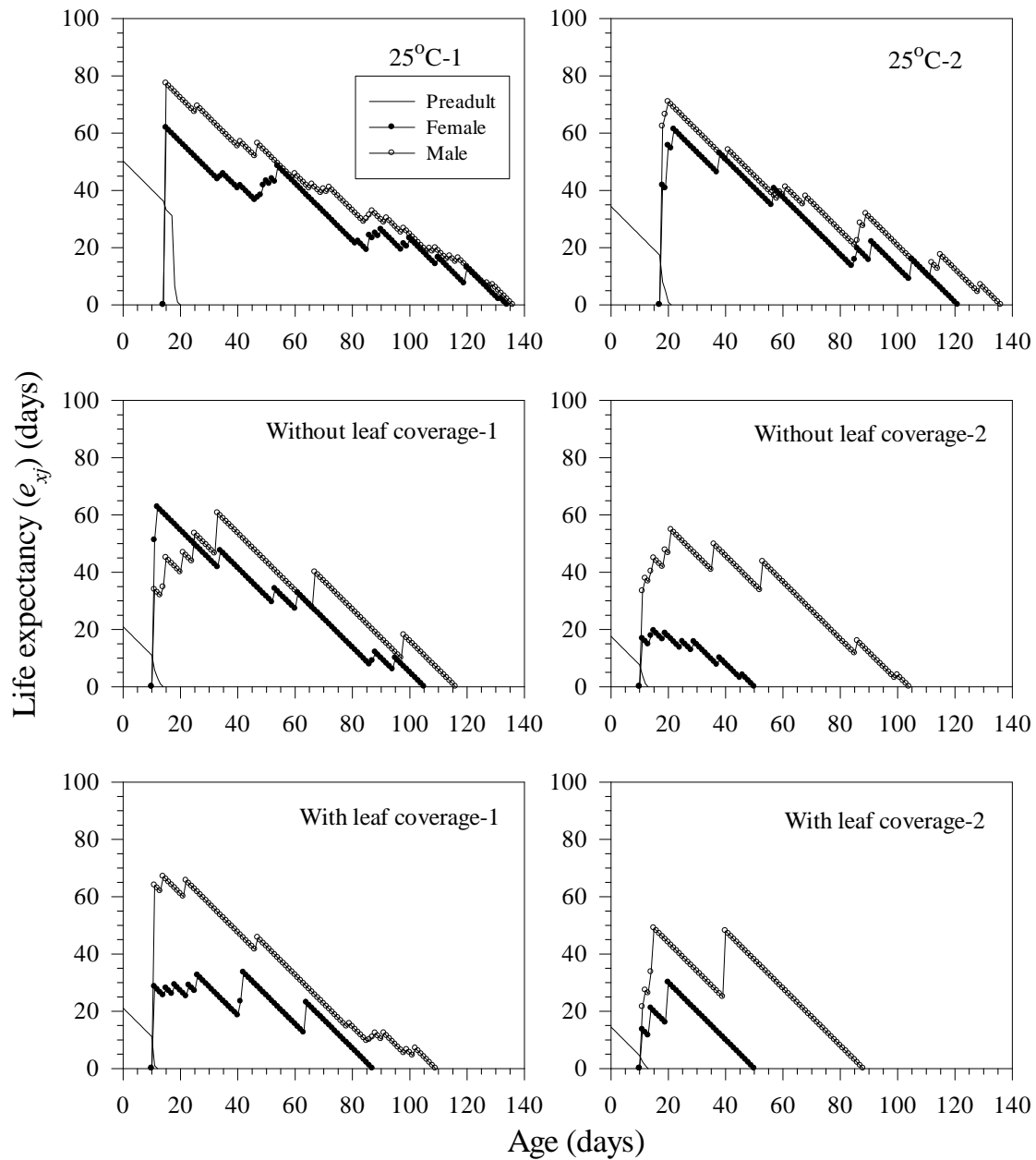
545   different treatments.

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Fig. 2.   Age-specific survival rate (l_x), female age-specific fecundity (f_{x2}),

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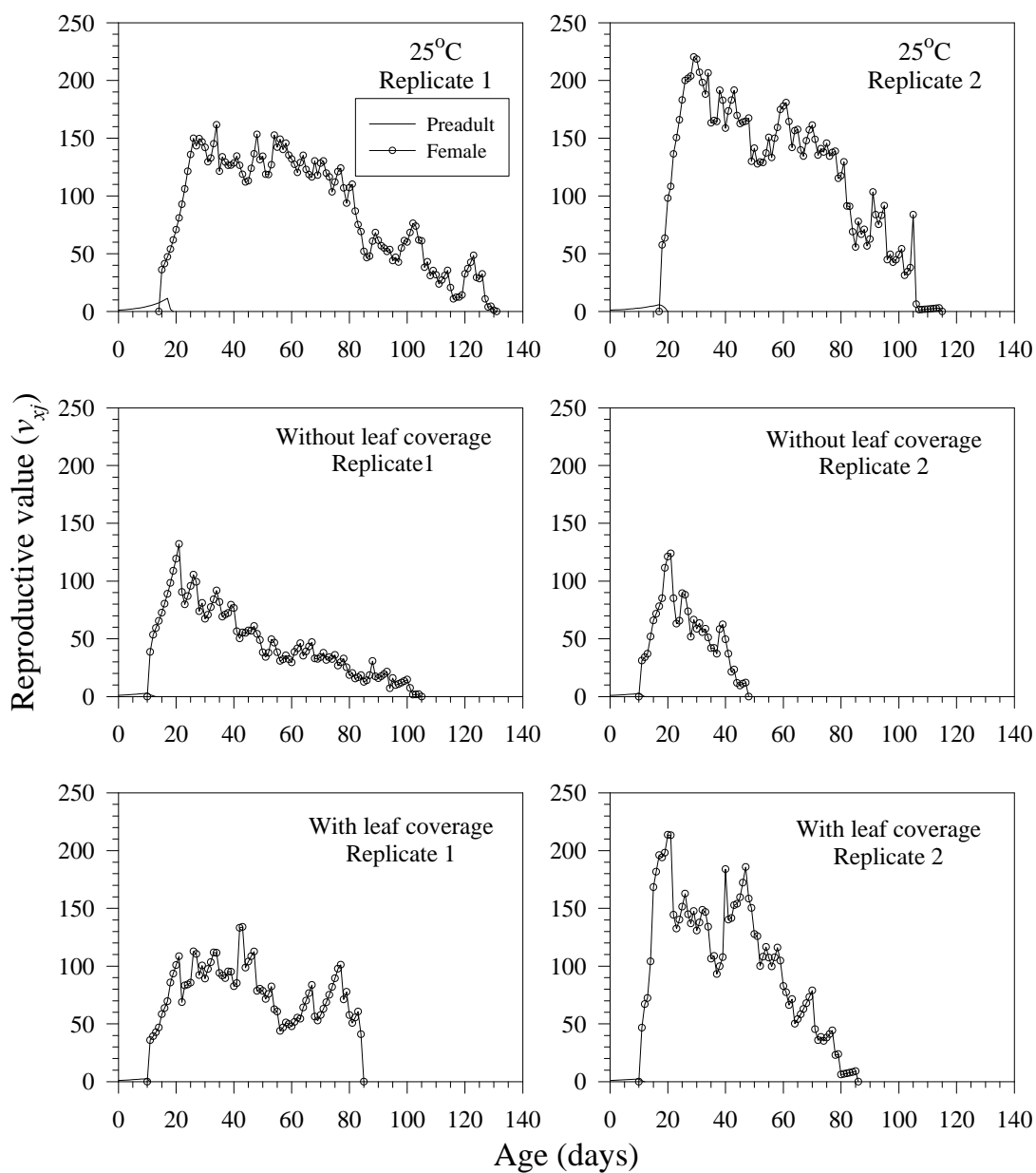
for different treatments.

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554   Fig. 3.   Age-stage specific life expectancy (e_{xj}) of *Bactrocera cucurbitae* for
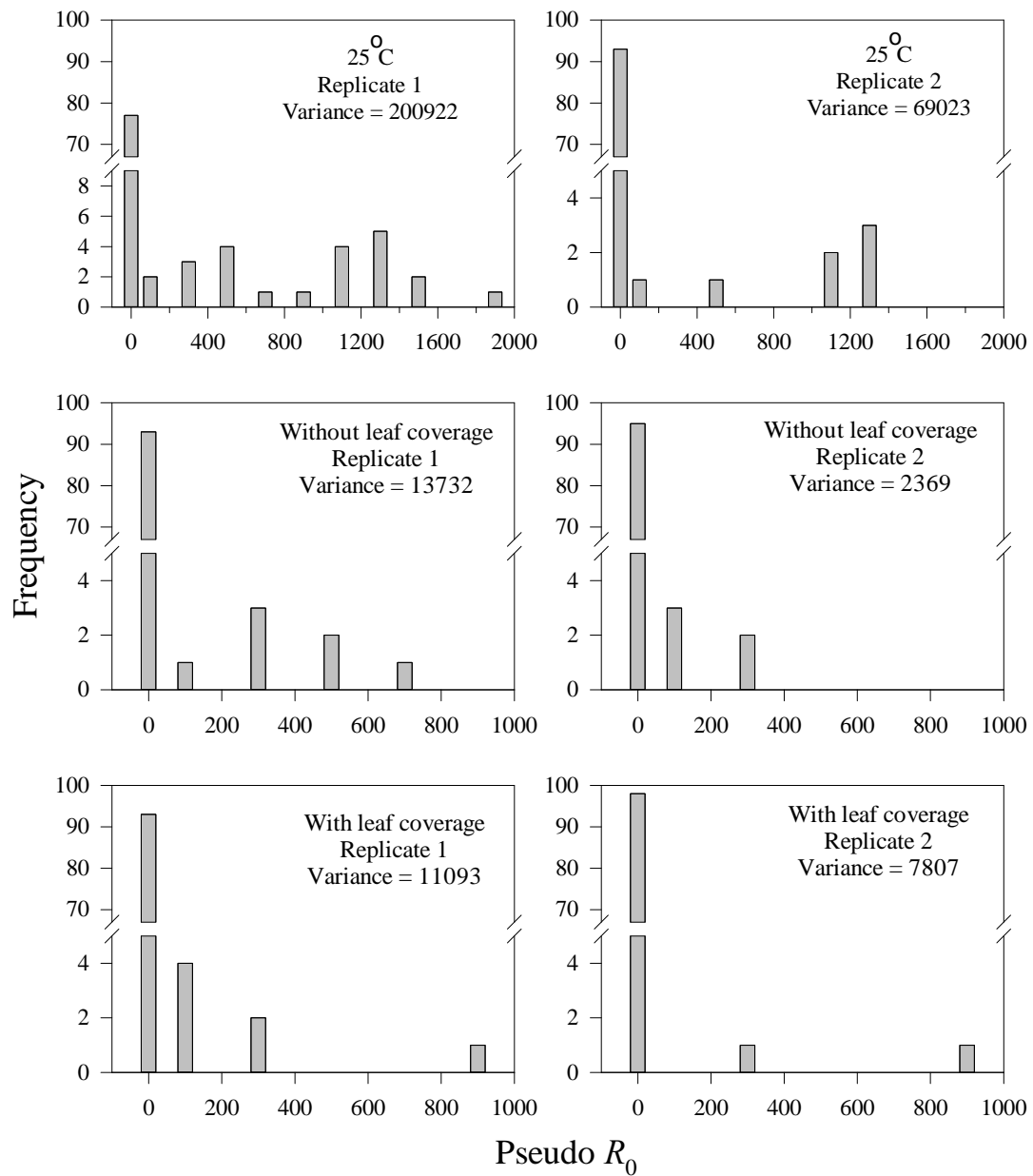
555   different treatments.

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Fig. 4.   Age-stage specific reproductive value (v_{xj}) of *Bactrocera cucurbitae* for different treatments.

561

562   Fig. 5.   Frequency distribution of pseudo-R_0 grouped for different treatments.

563   Each bar represents the number of pseudo-R_0 between two ticks.   The bar at zero

564   represents the frequency of pseudo-R_0 zero.