Model selection and averaging in the estimation of population parameters of *Bemisia tabaci* (Gennadius) from stage frequency data in sweet pepper plants

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Abstract

Bemisia tabaci is a significant pest for many crops, but there are few population studies of this insect on sweet pepper (*Capsicum annuum*). In this study, stage frequency data were generated with *B. tabaci* in sweet pepper plants in various situations, and the Bellows and Birley method was used to obtain population parameters from the data. The Akaike Information Criterion (AIC) was used to select the best option of the Bellows and Birley method and, in some cases, to estimate the parameters of the population using model averaging. The ratios estimated/observed for each population parameter were calculated to assess bias and were used to correct the estimations if the ratios were different from 1. The effects of different factors on the estimations of population parameters were analysed. The total duration of development was affected by the experimental conditions (laboratory vs. greenhouse) and temperature, but it had the highest precision. The final survival rate was affected by temperature, and the estimation of individuals entering each stage was affected only by the options included in the Bellows and Birley method. AIC helped to detect differences in the daily survival rate among the different experiments between N1 (first instar) (range 0.842-0.923), and the egg (range 0.989-1.0) and N4 (fourth instar) (0.990). The methodology used can be employed in field population studies. For example, the final survival rate in the

25 greenhouse experiments varied between 0.624 and 0.097, depending on if the parasitoids were

26 present or not, and the total development varied between 420.6 and 440.7 degree-days.

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Introduction

The whitefly, *Bemisia tabaci* (Gennadius), is a significant pest in many crops around the world (Oliveira et al. 2001). In regions where there is a great density of vegetable crops cultivated in greenhouses, as is found in the southeast of Spain, the whitefly becomes a serious threat in terms of the increase of its population and the potential transmission of several viral diseases (Navas-Castillo et al. 2000; Segundo et al. 2004; Ruiz et al. 2006). Crops such as sweet peppers, tomatoes, melons, cucumbers, green beans and others may be seriously affected by this pest. Many studies have focused on the biology of this species in different crops and on the analysis of life tables to investigate different parameters of the population or the key factors that regulate its population (Von Arx et al. 1983; Horowitz et al. 1984; Baumgartner et al. 1986; Baumgartner and Yano 1990; Naranjo and Ellsworth 2005; Asiimwe et al. 2007). Several of these studies have compared different models. The biology of *B. tabaci* has been studied in sweet peppers (*Capsicum annuum*) under controlled (laboratory) conditions (González-Zamora and Gallardo 1999; Muñiz 2000; Muñiz et al. 2002), but no studies have been presented on the biology of this species with sweet peppers under field conditions.

Stage frequency data are analysed in different ways to obtain information on populations. One way is to use a model or models, which can be as simple or as complicated as needed under the circumstances (for a review see Manly 1990; Southwood and Henderson 2000). If different models are used to analyse the data, the results must be compared to select the most suitable one. Different biological conclusions may be drawn from the data depending upon the final model selected, and therefore, it is important to have a method that selects the best model and measures the strength of the evidence for each one. The Akaike Information Criterion (AIC) is widely used in biological studies to select the best model due to the advantages it has over other criteria, and it is used to estimate parameters by model averaging (Burham and Anderson 2002; Johnson and Omland 2004;

60 Posada and Buckley 2004). In the field of entomology, the application of AIC or other information

61 criteria is generally used to select models that help explain different aspects of the biology and

62 behaviour of insects and to select models that can be used in the field of crop protection (Luh and

63 Croft 1999; Hansen et al. 2001; Hemerik and van der Hoeven 2003; Umble and Fisher 2003; Sileshi

64 2006; Takeuchi 2006; Saint-Germain et al. 2007). A study undertaken by Sileshi (2006) is one of

65 few examples of the use of AIC for insect count data or applications for life table analyses. Model

66 averaging is applied when none of the set of models is clearly the best, and several can be used. In

67 such case, the parameters of interest are estimated based on the relative importance (or weight) of

68 the models. To date, no examples have been found on the use of model averaging to estimate

69 population parameters.

70

71 This work had different objectives corresponding to the information that can be obtained from stage

72 frequency data of *B. tabaci* in sweet peppers, both from the laboratory and field. We studied the bias

73 generated after using a model (in this case, the Bellows and Birley method), comparing the

74 observed and estimated parameters, and how different factors can influence this bias. The other

75 objective of this study was to demonstrate the application of model selection and averaging with the

76 AIC to accurately estimate population parameters. The Bellows and Birley method produces

77 different parameters from stage frequency data and, with the help of the AIC, it can be of great

78 interest in population studies due the information generated, such as, for example, survival rates,

79 development time, number of entering stages, and others. Finally, population parameters from field

80 studies are presented to show the potential of this methodology.

81

82 **Materials and Methods**

83

84 Experimental conditions

85   The study was carried out in the facilities of the I.F.A.P.A. (Instituto para la Formación Agraria y

86   Pesquera de Andalucia) of "La Mojonera-La Cañada" (36º47'18.57" N and 2º42'13.87'' W) in

87   Almería (southeast Spain). The experiments were conducted under laboratory conditions with

88   potted plants and in a plastic greenhouse using sweet pepper plants (*Capsicum annum*) cv.

89   "Espartaco". The pots had a diameter of 13.8 cm and a volume of 1.2 L. The substratum was

90   coconut fibre, and the plants were periodically fertilised with Multi Poli-Feed[®] (Haifa Chemical).

91

92   A 600-m^2 plastic greenhouse was used for the greenhouse conditions. The sweet pepper plants were

93   transplanted to the ground in August 1995. The normal agricultural practice in the area for this crop

94   was followed during the period of cultivation, with the spraying of pesticides on the upper part of

95   the plants to control certain diseases and pests, such as powdery mildew (*Leveillula taurica* (Lev.)

96   Arnaud (Perisporales: Erysiphaceae)) with dinocap and bupirimate; beet armyworm (*Spodoptera*

97   *exigua* (Hübner) (Lepidoptera: Noctuidae)) with *Bacillus thuringiensis* and trichlorfon mixed with

98   wheat bran; and broad mite (*Poliphagotarsonemus latus* (Banks) (Acari: Tarsonemidae)) with

99   bromopropylate and avermectin. Care was taken to avoid products harmful to whiteflies and their

100   natural enemies.

101

102   The adults of *B. tabaci* that were used to lay the eggs were collected from a different greenhouse

103   planted with peppers (cv. "Espartaco"), where a colony of *B. tabaci* was constantly reared.

104

105   Three trials were carried out in different situations to generate stage frequency data that could be

106   used for the posterior analysis of model selection and model averaging to obtain population

107   parameters. The experiments were carried out under the following two experimental conditions:

108   controlled temperature (laboratory conditions in Trials 1 and 2) vs. uncontrolled temperature (field

109   conditions in Trial 3). There were also two scales of observation: individual counts (in Trial 1) vs.

110   grouped counts (in Trials 2 and 3). The three trials were as follows:

111

112   1) Trial 1 (individual counts and controlled temperature). Assays were carried out at 20 ± 1, 25 ± 1

113   and 30 ± 1 °C in a growth chamber (KOXKA model MEC-185/F) with 4,000 lux, a 16:8

114   photoperiod (light:dark) and a relative humidity of 75 ± 10%; and in a breeding chamber at 25 ±

115   2°C with 6,000 lux, a 16:8 photoperiod (light:dark) and a relative humidity of 65 ± 10%. Each of

116   the studies consisted of one or two potted plants with six to eight leaves each. The plants were

117   infested with high numbers of *B. tabaci* adults. The adults were confined to one or two leaves per

118   plant by means of a cloth bag for 24 h at the different temperatures defined above. After this time,

119   the adults were eliminated, and the eggs were counted. This time point was considered the initial

120   moment, or zero time point, for the study of development. The eggs were observed and counted

121   daily. When nymphs of the first instar emerged, we waited until they fixed on the leaf, and then

122   their positions were marked with a soft marker (Lumocolor[®], Staedtler, Germany). Daily counts of

123   each individual took place until the whitefly adults emerged.

124

125   2) Trial 2 (grouped counts and controlled temperature). Assays were carried out at 20 ± 1 and 30 ± 1

126   °C in a growth chamber (KOXKA model MEC-185/F) with 4,000 lux, a 16:8 photoperiod

127   (light:dark) and a relative humidity of 75 ± 10%; and in a breeding chamber at 25 ± 2°C with 6,000

128   lux, a 16:8 photoperiod (light:dark) and a relative humidity of 65 ± 10%. Two replicates were done

129   at each temperature. The plant infestation was initiated following the same procedure as described

130   in Trial 1. Once the adults were eliminated, the leaves where the adults had been confined were

131   observed daily. The eggs and individuals that emerged were counted and grouped according to their

132   developmental stage, but they were not marked. The daily counts took place until the adults

133   emerged.

134

135   3) Trial 3 (grouped counts with uncontrolled temperature in a plastic greenhouse). Three

136   experiments were carried out at several time periods throughout the year, as follows: September 19,

137   1995 to October 23, 1995 (experiment 1); December 1, 1995 to February 26, 1996 (experiment 2);

138   and March 6, 1996 to April 30, 1996 (experiment 3). In each experiment, six to ten plants were

139   selected, and a leaf from each plant was isolated with a cloth bag. Large numbers of adult *B. tabaci*

140   were introduced into each bag and left for 24 h. The eggs that were laid were counted, and this was

141   considered the starting point for the developmental study. The population was counted daily except

142   in experiment 1, where it was counted every two days until all of the adults had emerged.

143   Individuals were counted and grouped according to their developmental stage. The temperature and

144   relative humidity were registered daily during the experiments, with mean temperatures (and

145   ranges) of 24.9 ºC (12 - 37 ºC), 15.9 ºC (4 - 30 ºC) and 18.9 ºC (8 - 33 ºC) for experiments 1, 2, and

146   3, respectively. Time was measured using degree days (DDs). The DDs were calculated using the

147   maximal and minimal temperatures of two periods in the day (from 00.00 to 12.00 h and from 12.00

148   to 24.00 h), and 10 °C was the minimum development threshold temperature (Zalom et al. 1985).

149   The following equation was used to calculate DD:

150
$$DD = \frac{\dfrac{\left(T_{\max} + T_{\min}\right)_{0-12}}{2} + \dfrac{\left(T_{\max} + T_{\min}\right)_{12-24}}{2}}{2} - 10 \quad ,$$

151   where *T* is temperature.

152

153   In Trials 1 and 2, the different developmental stages, from egg to fourth instar (N4), were observed

154   in the laboratory with a stereobinocular microscope (9x and 45x magnification) by turning the leaf

155   under the microscope. The developmental stages were distinguished as a function of size. The first

156   instar (N1) was the smallest, and the fourth (N4) was the largest. In Trial 3, the different

157   developmental stages from egg to N4 were distinguished using a field lens (8x magnification), and

158   they were separated according to their relative size. In the first greenhouse experiment, the nymphs

159   of the first, second and third instars were counted together.

160

161   In the individual counts (Trial 1), the fate of each individual was recorded. Thus, it was possible to

162   calculate different parameters, such as the number of individuals entering each instar, the daily

163   survival rate of each instar, the survival rate of each developmental stage, the duration of each

164   instar, the final survival rate of the population and the total development period (González-Zamora

165   and Gallardo 1996). In contrast, in the grouped counts (Trials 2 and 3), only the number of

166   individuals found at each instar was recorded daily. In the grouped counts, the initial number of

167   eggs and the final number of adults that emerged from the empty pupal cases was known. With

168   these data, most of the previous parameters could not be calculated except for the final survival rate

169   of the population and the total development period. Therefore, the other parameters had to be

170   estimated with the help of a model. With individual counts, it was possible to compare the observed

171   values of all parameters with their estimations and to establish the bias and validity of the model

172   used. With Trials 2 and 3, the bias was identified using fewer parameters, such as individuals

173   entering the egg and adult stage, the final survival rate and the total development.

174

175   Model Fitting

176   The P1f software package (Manly 1994) was used to analyse the life tables, and it was specifically

177   designed to analyse data from stage-structured populations with different models. In model

178   selection, it is important to have a group of models that are relevant to the data and to the objectives

179   of the analysis, representing a plausible research hypothesis (Burham and Anderson 2002). The

180   Bellows and Birley method (Bellows and Birley 1981) is the most flexible method because it allows

181   estimation of the duration of each stage, the unit time survival rate, the final survival rate, and the

182 numbers entering each stage. This method also allows for different assumptions when different

183 survival parameters for each stage or time of entry in stage 1 are considered (Manly 1990).

184

185 All of the experiments were performed using a single cohort, and therefore, the initial number

186 entering stage 1 was known, and no entering distribution was necessary. The Weibull distribution

187 was also used to model the distribution function of each stage. The Weibull distribution function is

188 as follows:

189
$$f(t) = 1 - \exp\left[-\left(\frac{t}{\lambda}\right)^{\alpha}\right] \tag{3}$$

190 where alpha (α) is the shape parameter, and lambda (λ) determines the spread of the curve along the

191 X axis. Lambda is also an estimate of the mean duration of each stage.

192

193 The P1f program allows for different combinations of the unit time survival rate (needed in the

194 Bellows and Birley method) and the shape parameter (α) of the Weibull distribution, which may be

195 different for each stage in the Bellows and Birley method. The combinations of these two

196 parameters produce the following four options in the program: 1) different survival and shape

197 parameters for each stage; 2) the same survival parameters but different shape parameters for each

198 stage; 3) different survival parameters but the same shape parameters for the stages; and 4) the same

199 survival parameters and shape parameters for all stages. These four options of the Bellows and

200 Birley method produced different estimations of the same population parameters along with fitting

201 of the model to the data as expressed in the log *likelihood* for each option. For this reason, the four

202 options were considered in this study as models to be selected with a given criterion.

203

204 The output estimates produced by the Bellows and Birley method were as follows: a) individuals

205 entering into each stage (egg, N1, N2, N3, N4 and adult); b) the stage-specific survival rate (SSSR),

206 which is the survival of a given stage; and c) duration, which is the developmental time for each

207 stage considered. The P1f program generated the standard deviation for the duration of each stage,

208 but not for the individuals entering the stage or for the SSSR. Two other estimates were calculated

209 using the results of the program as follows: a) the SR_f, which is the final survival rate from egg to

210 adult; and b) the $Duration_t$, which is the duration of the total developmental period, from egg to

211 adult. However, neither of these two last estimates had an associated standard deviation. The shape

212 parameter (α) of the Weibull distribution and the unit time (daily) survival rate (ϕ) were also

213 estimated in the four options of the Bellows and Birley method. Both of these parameters could be

214 considered equal or different for each stage, and both of them had a standard deviation produced by

215 the P1f program.

216

217 Statistical analyses

218 The output estimates produced by the Bellows and Birley method, such as the individuals entering

219 each stage, the SSSR, the duration of each immature stage, the final survival rate (SR_f) and the total

220 duration ($Duration_t$), were compared with the observed values of the same parameters, which were

221 obtained mainly from Trial 1, but also from Trials 2 and 3, to obtain the estimated/observed ratios.

222 The ratios were used to identify the bias of the estimates and to determine if the bias was affected

223 by different factors.

224

225 The previous parameters, expressed by relative values in the ratios, were considered as variables

226 that could be affected by different factors. These factors and their levels were as follows: a) *Scale of*

227 *observation*, with two levels, including individual counts (with data coming from the experiments

228 of Trial 1) and grouped counts (with data coming from the experiments of Trial 2); b) *Experimental*

229 *conditions*, with two levels, including controlled temperatures (with data coming from the

230 experiments of Trial 2) and uncontrolled temperatures (with data coming from the experiments of

231 Trial 3); c) *Temperatures*, with the three temperatures used in controlled temperatures (with data

232 coming from the experiments of Trials 1 and 2); d) *Options*, with the four options of the Bellows

233 and Birley method supported by the P1f program (with the available data from Trials 1, 2 and 3).

234

235 The ratios were not transformed in any way, and they were first analysed to test the homogeneity of

236 the variances within factors using Cochran's C contrast, Bartlett's contrast and Levene's tests. If the

237 probability associated with any of them was less than 0.05, the Kruskall-Wallis test was used to

238 analyse the data. In contrast, if the *p*-value was greater than 0.05 in all of them, a one-way ANOVA

239 was used to analyse the data. If the *p*-value of the Kruskall-Wallis statistic was less than 0.05, the

240 means of the different levels within the factor were separated using Mann-Whitney's U test (Steel

241 and Torrie 1988). If the *p*-value of the ANOVA test was less than 0.05, the means of the different

242 levels within the factor were separated using Tukey's honestly significant difference (HSD) test at *p*

243 = 0.05. The ratios were then tested to determine whether they differed from 1 using the contrast

244 hypothesis test, with *p* = 0.05. All analyses were performed using the Statgraphics package

245 (Statistical Graphics 2000).

246

247 Model selection

248 There are different ways of comparing models to select the most appropriate one. This study used

249 the AIC, which is a powerful method for model selection and the inference of ecological data

250 (Burham and Anderson 2002). With AIC, the goal is to select the model with the least number of

251 parameters that represents the data adequately (i.e., the principle of parsimony) (Franklin et al.

252 2001; Mazerolle 2004). The AIC was used to select the best option of the Bellows and Birley

253 method, and it is defined as follows:

254 $$AIC = 2k - 2\ln(L)$$

255 In this equation, *K* is the number of estimated parameters included in each model (or the options of

256 the Bellows and Birley method in this study). The log-likelihood of the model given the data are

257 readily available in the statistical output, and reflects the overall fit of the model. When there was a

258 comparison of models, the model with the smallest AIC was selected. With count data, as was the

259 case here, it is normal to find overdispersion. Therefore, the AIC was modified to obtain $QAIC_c$

260 (Burham and Anderson 2002).

261

262 Two measures, delta AIC (Δ) and Akaike weights (w), associated with the AIC and equally with

263 $QAIC_c$ were used to compare models (Burham and Anderson 2002). The delta AIC is a measure of

264 each model relative to the best model. As a rule of thumb, when Δ_i is less than two, it suggests

265 substantial evidence in support of the model. When the values are between three and seven, it

266 indicates that the model has considerably less support. When Δ_i is greater than ten, it indicates that

267 the model is unlikely. Akaike weights provide another measure of the strength of evidence for each

268 model, and they represent the ratio of delta AIC (Δ_i) values for each model relative to the whole set

269 of candidate models (the four options of the Bellows and Birley model). Akaike weights also

270 indicate the probability that the model is the best among the set of candidate models.

271

272 Selecting a model from a set of candidate models may produce a new problem. When no single

273 model is clearly the best, predictions cannot be based on the model ranked in first place. In some

274 cases, the best model may have competitors for the top rank (e.g., when $\Delta_i < 2$). A solution to this

275 problem is to base the inference on the entire set of models, an approach called "multimodel

276 inference" or "model averaging" (Burham and Anderson 2002; Johnson and Omland 2004; Posada

277 and Buckley 2004). When this situation happened in the present study, a weighted average of the

278 estimates was computed using the Akaike weights.

279

280 To conduct model averaging, the estimate of the parameter for each model was weighted by the

281 Akaike weights as follows:

282 $$\overline{\hat{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta}_i,$$

283 where $\hat{\theta}_i$ denotes the estimate for model i. Similarly, the precision (as standard error, SE) of the

284 model averaged estimate may also be computed and is called the unconditional SE (Burham and

285 Anderson 2002). In many cases, model averaging reduces bias and increases precision, which are

286 desirable properties (Burham and Anderson 2002). Once the model averaged estimates and SE were

287 calculated, confidence intervals were used to assess the magnitude of the effect. After using AIC, or

288 model averaging if needed, the observed parameters and their final estimates were used to calculate

289 the coefficients of determination R^2.

290

291 **Results**

292

293 Differences among the observed parameters and their estimates from the Bellows and Birley

294 method in its different options were observed. The discrepancies were measured by calculating the

295 estimated/observed ratios (Table 1), which were used to identify the bias of the method in the

296 different parameters and to assess the effect of the factors on estimations of the same parameters.

297 The ratios were less than one in most cases, but some were close to one. Table 2 shows the statistics

298 obtained for the analyses and their significance. There were no differences in the ratios of each

299 variable studied within the *scale of observation* (individual counts vs. grouped counts), although the

300 *experimental conditions* (controlled temperature vs. uncontrolled temperature) showed a significant

301 difference in the ratios only in the total duration of development. The *temperature* factor displayed

302 differences only in the final survival rate and total duration. Finally, the *option* factor, which must

303 be considered as appertaining to the Bellows and Birley method, demonstrated significant

differences within each factor only in the entering individuals. The estimated/observed ratios were used to correct the estimated parameters in each situation, but only when the ratio was significantly different from one, by dividing the estimated parameter by the ratio value. This correction was used to obtained the final values of each parameter, but it was not used to select the best option with the AIC.

The different parameters of the AIC analysis for each Trial (Table 3) indicated that the data were overdispersed (c between 1 and 5; Burham and Anderson 2002). Each trial comprised its own set of data, and therefore, the results are shown separately. The four options supported by the P1f program with the Bellows and Birley method were compared with the delta AIC (Δ) and the Akaike weights (w). The first option (i.e., different daily survival rates for the stages) was selected as the best with the experiments carried out at the lowest temperature under controlled conditions (20ºC in both individual and grouped counts, Trials 1 and 2, respectively). In contrast, the second option (i.e., the same daily survival rate for all stages) was selected as the best at the intermediate temperature (25ºC in both individual and grouped counts, Trials 1 and 2, respectively). At the higher temperature (30ºC in both individual and grouped counts, Trials 1 and 2, respectively), the selection was not as clear, but the options with the same survival rate for the stages (options 2 and 4) generally had higher weights. Similar selections of options occurred in the experiments carried out in the greenhouse (Trial 3). In the experiment carried out in winter (experiment 2 with a mean temperature of 15.9ºC), the first option (i.e., different daily survival rates for the stages) was clearly selected. In experiment 3 (mean temperature of 18.9 ºC and at the beginning of spring), the third option (i.e., different daily survival rate for each stage) was the most important. In experiment 1, under greenhouse conditions (warm temperatures with a mean of 24.9ºC and at the beginning of autumn), the second and fourth options (both with the same daily survival rate for each stage) were more important.

329

330   Finally, the final population parameters for each experiment (with their own standard errors), were

331   obtained using multimodel inference when necessary, according to the *w* factor of Table 3. The

332   coefficients of determination R^2 between the observed and estimated parameters (corrected with the

333   ratio if necessary) were calculated as follows: 0.909 (41), 0.925 (20), 0.988 (20), 0.985 (12) and

334   0.999 (13) for the individuals entering the different stages, the stage specific survival rate (SSSR),

335   the duration of development in the different stages, the final survival rate, and the duration of total

336   development period, respectively (the numbers between brackets are the number of points used to

337   calculate the coefficient of determination in each case).

338

339   In 6 out of 13 experiments, the first and/or third option of the Bellows and Birley method (i.e., in

340   which the daily survival rates were considered differently for each instar) produced higher Akaike

341   weights (Table 4). Three of the experiments demonstrated a clear difference with non-overlapping

342   confidence intervals between the daily survival rates of the egg and N1 stages, and in one

343   experiment between the N1 and N4 stages (Table 4). In several cases, there was only a light overlap

344   in the confidence intervals of the daily survival rate of the N4 with the egg stage. Also, the estimates

345   of the daily survival rate with the different options in the individual counts (Trial 1) were similar to

346   the observed daily survival rates, which were included in the 95% confidence intervals of the

347   estimates (Table 4). The observed values of daily survival rate showed statistical differences in the

348   stage and temperature factors and their interaction ($F_{4,5} = 68.5$, p < 0.001; $F_{2,5} = 113.8$, $p < 0.001$;

349   and $F_{8,5} = 16.6$, $p = 0.003$, respectively). The differences between stages within the temperature

350   were consistent with the results from the estimations and their confidence intervals at 20ºC (N1 was

351   different from egg and N4; Table 4). At 30ºC and 25ºC, however, differences were found between

352   the egg stage and the remaining instar stages (Table 4 and data not shown).

353

354   The final estimates obtained for the greenhouse experiments are presented in Table 5, and they

355   show the type of output obtained using the AIC and the multimodel inference. From the results, the

356   similarity of the total duration among the three experiments (ranging from 420.6 to 440.7 DD) was

357   significant, whereas the final survival rates (ranging from 0.097 to 0.624) indicate that the

358   environmental conditions in the three experiments were different.

359

360   **Discussion**

361

362   The study presented in this paper had two objectives. The first objective was to show the potential

363   of the Bellows and Birley method to estimate parameters from stage frequency data. As in any

364   estimation, the parameters estimated may differ from the observed values of the same parameters.

365   The observed parameters are not always known. In this study, however, the observed parameters

366   were known in most of the cases, and they were used to identify the bias of the Bellows and Birley

367   method as presented by the software P1f program. The second objective was to use a procedure to

368   select a model that provides the best trade-off between bias and accuracy (i.e., AIC selected the

369   most parsimonious model from those used to adjust the data). If different models support the data

370   similarly, a multimodel inference (e.g., model averaging) can be considered to obtain a precision

371   estimator for the different parameters.

372

373   The Bellows and Birley method produced several estimates that were different from the observed

374   values, as shown by the ratios in Table 1. The ratios of the estimated/observed parameters are useful

375   for identifying the bias of the estimates and for determining if this bias is affected by the different

376   factors considered. It is of particular interest that no difference of the ratios within the *scale of*

377   *observation* (individual vs. grouped counts) was observed in the variables estimated. However,

378   there were statistical differences in the ratios within the *experimental conditions* and *temperatures*,

379   which affected variables representing general values (i.e., final survival rate and total duration of

380   development). There were differences among the experiments carried out in the greenhouses and

381   among the different temperatures in the laboratory. However, there was a remarkably high precision

382   in several of the estimated variables, such as the total duration of development, across all factors.

383

384   The *option* factor was associated with the Bellows and Birley method of the P1f program, and it had

385   a significant effect on one of the studied variables. The second option of the Bellows and Birley

386   method (i.e., same survival parameter but different shape parameter for each stage) had a

387   remarkable effect on the estimations of entering individuals, with a ratio close to 0.5 (Table 1).

388

389   With the analysis presented herein, we have a tool to help answer the question of whether there are

390   different daily survival rates at each stage. The options of the Bellows and Birley method with

391   different daily survival rates in each stage (options 1 and 3) obtained better support at lower

392   temperatures (both in controlled conditions and the plastic greenhouse), whereas the options with

393   equal survival rates (options 2 and 4) were selected at medium and higher temperatures. The factors

394   that affect mortality in each situation may be different and may change in other experiments, but

395   their identification and quantification may only be answered with an adequate sampling

396   methodology that identifies them and relates them to the results of the analysis.

397

398   The daily survival rates of the stages was of particular interest (Table 4). The observed values of the

399   daily survival rates in the experiments of Trial 1 fell within the confidence interval of their

400   estimations, reflecting their accuracy. It may be assumed that the estimations in the other

401   experiments shown in Table 4, where no observed values were generated, were equally accurate.

402   Although the daily survival rates were different among some stages within the temperatures, as

403   confirmed by the ANOVA of the observed values (even though these results must be considered

404 with caution due the low number of replications of the observed data), this was not confirmed with

405 the Bellows and Birley method in some cases (e.g., the experiment performed at 25ºC, not shown in

406 Table 4, the experiment performed at 30ºC in Trial 1, shown in Table 4, or one of the experiments

407 performed at 20ºC in Trial 2, shown in Table 4).

408

409 For differences among stages, studies that relate this variation to environmental variables, such as

410 climate, number of predators, number of parasitoids, food availability or any other variable, may

411 help to explain these differences (Manly 1990). In experiments conducted at a controlled

412 temperature at 20ºC, the temperature and possible manipulations under the stereomicroscope may

413 be considered as factors affecting the survival of N1. Other factors may have produced these

414 differences in the experiments carried out with uncontrolled temperatures (Trial 3 in the

415 greenhouse).

416

417 The egg and N1 and N4 instar stages had the greatest effect on the *B. tabaci* population in the life

418 table analysis in different locations and crops (Horowitz et al. 1984; Naranjo and Ellsworth 2005;

419 Asiimwe et al. 2007). Predation (Naranjo and Ellsworth 2005) and parasitisation (Asiimwe et al.

420 2007) were the principal factors responsible for decreasing populations, affecting mainly the N4

421 instar, and dislodgement was second in most of the previous studies. In general, these conclusions

422 agree with the results obtained in the present study for the greenhouse experiments (although with

423 only three experiments), where N1 and N4 had the highest mortalities, with estimated survival rates

424 of 0.758 and 0.474, respectively, in experiment 2, and 0.372 and 0.515, respectively, in experiment

425 3 (Table 5). In greenhouses, the N1 instar is the most exposed to environmental factors, such as

426 peaks of high temperature and low humidity typical of greenhouses in southeast Spain and low

427 temperatures in some periods of the year. The N1 instar is also subject to other factors related to the

428 plant itself, such as nutritional factors and cuticle thickness (Byrne and Bellows 1991). Predation by

429 lacewings or beetles on whiteflies was not observed in Trial 3 (greenhouses). However,

430 *Eretmocerus mundus* Mercet adults, which are the main parasitoid of *B. tabaci* in greenhouses in

431 Almería (Rodríguez-Rodríguez et al. 1994), and subsequently, parasitised N4, were detected. The

432 high mortality found in N4 (mainly from parasitism but also from direct feeding) and the low final

433 survival rates recorded in experiments 2 and 3 (SR_f = 0.143 and SR_f = 0.097, respectively) (Table 5)

434 were due to *E. mundus* in contrast to the values obtained in the first experiment in which no *E.*

435 *mundus* was detected.

436

437 The level of parasitism due to *E. mundus* in the N4 instar may be high (González-Zamora et al.

438 1996; Téllez et al. 2003; Stansly et al. 2005). Predation by *E. mundus* adults on different instars of

439 the whitefly *B. tabaci* is well known and has been evaluated (Gerling and Fried 2000; Urbaneja et

440 al. 2007), and is considered an important factor in population regulation (Téllez et al. 2003; Zang

441 and Liu 2008).

442

443 The methodology used in this work allowed the bias of the Bellows and Birley method to be

444 identified in different experimental situations (laboratory vs. greenhouse and individual vs. grouped

445 counts) and with the use of the P1f program. The final estimates obtained from the best option of

446 the Bellows and Birley method selected with the AIC or with model averaging, when it was needed,

447 include the correction with the estimated/observed ratio when the ratios were different from one.

448 The estimations may be used to analyse life tables to, for example, study the key factors that affect

449 the survival of a population with a high enough number of generations (Southwood and Henderson

450 2000). However, this was not the objective of the present work. The final estimates for all of the

451 experiments were compared with the observed values, obtaining, in general, a good agreement

452 between them, as reflected in the coefficient of determination R^2. It is especially remarkable that the

453 total duration of development had an R^2 = 0.999, which reflects the robustness of its estimation in

454   both experimental conditions (Table 1). The duration of development of each stage and the final

455   survival rates also had high values of R^2 (0.988 and 0.985, respectively). The high similarity

456   between the observed and final estimated parameters with the field experiments in greenhouses is

457   shown in Table 5.

458

459   The final estimates for the experiments carried out in the greenhouses (Table 5) are of particular

460   interest for their implications in population studies in field conditions. The final estimation of the

461   total duration of development may be compared with other studies, such as those carried out in

462   cotton, to study the developmental time of *B. tabaci* (Zalom et al. 1985; Zalom and Natwick 1987).

463   The mean generation time of *B. tabaci* in cotton was found to be between 316.0 DD and 369.5 DD,

464   which differs from the values obtained for sweet peppers in the present study. The duration of each

465   instar also indicates the difference among instars. The development times of the egg and N4 stages

466   were longer than the other instars, in agreement with results from laboratory studies on sweet

467   peppers and other crops (González-Zamora and Gallardo 1996, Muñiz 2000).

468

469   In conclusion, the methodology used in this paper allowed the bias of the estimations obtained from

470   the model (the Bellows and Birley method) to be identified. This methodology also permitted the

471   selection of the best model from a set of models (applying model averaging when necessary) to

472   analyse stage frequency data in life tables to shed light on important aspects of a population, which

473   was presented in this study for the whitefly *B. tabaci* in sweet pepper plants.

474

475

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487

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Table 1 Mean value ± the standard error of the estimated/observed ratios of the different population parameters with the factors used

FACTORS	POPULATION PARAMETERS				
	Individuals Entering	SSSR	Duration	SR_f	$Duration_t$
Scale of observation [1]					
Individual	0.913±0.026	-	-	1.010±0.030	0.878±0.008
Group	0.902±0.034	-	-	1.037±0.044	0.891±0.005
Experimental conditions[2]					
Controlled temperature	0.902±0.034	-	-	1.037±0.044	0.891±0.005 a
Greenhouse	1.028±0.101	-	-	1.253±0.191	0.931±0.006 b
Temperature[3]					
20º C	0.914±0.047	1.020±0.075	0.891±0.006	0.971±0.067 a	0.923±0.001 b
25º C	0.877±0.027	1.015±0.027	0.856±0.015	0.944±0.023 a	0.866±0.003 a
30º C	0.955±0.036	1.039±0.043	0.825±0.028	1.189±0.031 b	0.875±0.005 a
Option[4]					
Opt 1	1.024±0.026 b	1.033±0.053	0.869±0.019	1.085±0.073	0.900±0.009
Opt 2	0.548±0.024 a	1.019±0.054	0.850±0.023	1.090±0.104	0.893±0.010
Opt 3	1.039±0.027 b	1.025±0.045	0.857±0.025	1.046±0.079	0.897±0.008
Opt 4	1.084±0.032 b	1.013±0.053	0.852±0.023	1.033±0.073	0.894±0.009

Means in the same column within a factor followed by different letter differ significantly (Tukey's honestly significant difference test, $p = 0.05$).

[1] In controlled conditions (laboratory), with Trials 1 and 2.

[2] With grouped counts, Trials 2 and 3.

[3] With the three temperatures used in the laboratory trials, Trials 1 and 2.

[4] With the four options of the Bellows and Birley method supported in the P1f software package, using Trials 1, 2 and 3.

Table 2 Statistical analyses of the population parameters studied with the factors used and their significance

FACTORS	Individuals entering		SSSR		Duration		SR_f		$Duration_t$	
		P		*P*		*P*		*P*		*P*
Scale of observation	F^a=0.05	0.815	-	-	-	-	K-W^b=0.37	0.544	F=2.10	0.156
Experimental conditions	K-W=0.22	0.638	-	-	-	-	K-W=0.32	0.572	F=23.24	<0.001
Temperature	K-W=3.02	0.220	K-W=1.16	0.561	K-W=3.86	0.145	K-W=18.84	<0.001	K-W=25.82	<0.001
Option	F=84.69	<0.001	F=0.03	0.990	F=0.14	0.938	F=0.11	0.951	F=0.13	0.941

[a] F statistic obtained by one-way ANOVA
[b] Kruskall-Wallis statistic

Table 3 Values of the Akaike Information Criterion (AIC) in the different trials and options of the Bellows and Birley method

		N	K	Deviance	Residuals d.f.	c	QAICc	Δ	w
Trial 1 (Individual counts with controlled temperature)									
20 ºC	Option 1	72	16	78.8	55	1.43	99.93	0.00	0.999
	Option 2	72	11	121.4	60	2.02	113.81	13.88	0.001
	Option 3	72	12	124.6	59	2.11	119.05	19.12	0.000
	Option 4	72	7	169.2	64	2.64	136.31	36.38	0.000
25º(I)	Option 1	64	16	138.4	47	2.94	93.75	11.84	0.003
	Option 2	64	11	153.2	52	2.95	81.91	0.00	0.997
	Option 3	64	12	325.3	51	6.38	143.46	61.55	0.000
	Option 4	64	7	326.0	56	5.82	129.25	47.34	0.000
25 º(II)	Option 1	57	16	132.7	40	3.32	88.93	16.18	0.000
	Option 2	57	11	139.2	45	3.09	72.74	0.00	1.000
	Option 3	57	12	267.8	44	6.09	114.84	42.10	0.000
	Option 4	57	7	265.5	49	5.42	98.94	26.19	0.000
30 ºC	Option 1	57	16	13.7	40	0.34	88.93	0.00	0.737
	Option 2	57	11	20.7	45	0.46	90.99	2.06	0.263
	Option 3	57	12	52.4	44	1.19	186.61	97.68	0.000
	Option 4	57	7	59.0	49	1.20	190.64	101.71	0.000
Trial 2 (Grouped counts with controlled temperature)									
20ºC(I)	Option 1	79	16	295.5	62	4.77	105.71	0.00	0.972
	Option 2	79	11	530.3	67	7.91	139.84	34.13	0.000
	Option 3	79	12	398.8	66	6.04	115.09	9.38	0.009
	Option 4	79	7	455.5	71	6.42	113.56	7.85	0.019
20ºC(II)	Option 1	91	16	190.3	74	2.57	116.16	0.00	0.999
	Option 2	91	11	260.7	79	3.30	129.25	13.09	0.001
	Option 3	91	12	393.4	78	5.04	183.55	67.39	0.000
	Option 4	91	7	420.2	83	5.06	181.10	64.94	0.000
25ºC(I)	Option 1	67	16	172.4	50	3.45	96.00	10.27	0.006
	Option 2	67	11	193.6	55	3.52	85.73	0.00	0.994
	Option 3	67	12	265.6	54	4.92	109.65	23.92	0.000
	Option 4	67	7	291.2	59	4.93	102.83	17.11	0.000
25ºC(II)	Option 1	61	16	114.8	44	2.61	91.60	8.15	0.017
	Option 2	61	11	138.9	49	2.83	83.45	0.00	0.983
	Option 3	61	12	191.7	48	3.99	106.89	23.44	0.000
	Option 4	61	7	223.2	53	4.21	104.20	20.76	0.000
30ºC(I)	Option 1	67	16	56.1	50	1.12	96.00	12.89	0.002
	Option 2	67	11	60.1	55	1.09	83.11	0.00	0.998
	Option 3	67	12	149.8	54	2.77	166.01	82.90	0.000
	Option 4	67	7	156.2	59	2.65	157.54	74.44	0.000
30ºC(II)	Option 1	64	16	178.9	47	3.81	93.75	5.24	0.050
	Option 2	64	11	223.2	52	4.29	88.51	0.00	0.692
	Option 3	64	12	234.5	51	4.60	94.59	6.08	0.033
	Option 4	64	7	275.0	56	4.91	90.76	2.25	0.225
Trial 3 (Grouped counts with uncontrolled temperatures (greenhouse))									
EXP-1	Option 1	46	9	94.8	36	2.63	61.95	6.02	0.032
	Option 2	46	7	101.2	38	2.66	58.13	2.21	0.213
	Option 3	46	8	96.5	37	2.61	59.38	3.45	0.114
	Option 4	46	6	103.0	39	2.64	55.93	0.00	0.641
EXP-2	Option 1	72	16	43.2	55	0.79	99.93	0.00	1.000
	Option 2	72	11	73.7	60	1.23	122.90	22.97	0.000
	Option 3	72	12	176.7	59	2.99	256.82	156.90	0.000
	Option 4	72	7	199.4	64	3.12	271.82	171.89	0.000
EXP-3	Option 1	51	16	82.9	34	2.44	85.49	10.12	0.006
	Option 2	51	11	171.6	39	4.40	102.16	26.79	0.000
	Option 3	51	12	97.6	38	2.57	75.37	0.00	0.994
	Option 4	51	7	185.6	43	4.32	95.38	20.01	0.000

Table 4 Unit time (daily) survival rates estimated and observed, and their confidence intervals, for the experiments in which the Akaike Information Criterion selected the option with different daily survival rates for the stages

		ESTIMATED		OBSERVED	
		Survival	95% CI	Survival	95% CI[1]
Trial 1 (Individual counts with controlled temperature)					
20ºC	Egg	1.000 a[2]	0.978 - 1.023	0.997	0.991-1.000
	N1	0.880 b	0.829 - 0.931	0.857	0.828-0.885
	N2	0.928	0.755 - 1.101	0.962	0.944-0.976
	N3	0.932	0.767 - 1.098	0.948	0.928-0.964
	N4	0.990 a	0.928 - 1.052	0.987	0.977-0.995
	Adult	0.990	0.868 - 1.112	--	
30ºC	Egg	0.983	0.914 - 1.052	0.986	0.975-0.994
	N1	0.960	0.892 - 1.029	0.941	0.920-0.959
	N2	0.963	0.767 - 1.160	0.956	0.937-0.971
	N3	0.936	0.678 - 1.195	0.941	0.920-0.959
	N4	0.941	0.862 - 1.020	0.941	0.921-0.959
	Adult	0.981	0.895 - 1.067	--	
Trial 2 (Grouped counts with controlled temperature)					
20ºC(I)	Egg	0.996	0.973 - 1.019		
	N1	0.964	0.902 - 1.027		
	N2	0.952	0.800 - 1.103		
	N3	0.921	0.751 - 1.091		
	N4	0.972	0.899 - 1.044		
	Adult	0.982	(-7.620) - 9.584		
20ºC(II)	Egg	0.989 a	0.972 - 1.006		
	N1	0.923 b	0.876 - 0.970		
	N2	0.999	0.870 - 1.128		
	N3	0.977	0.855 - 1.099		
	N4	0.976	0.934 - 1.018		
	Adult	1.018	(-0.404) - 2.440		
Trial 3 (Grouped counts with uncontrolled temperatures (greenhouse))					
EXP-2	Egg	0.992 a?[3]	0.973 - 1.011		
	N1	0.945	0.878 - 1.012		
	N2	0.976	0.873 - 1.078		
	N3	0.972	0.889 - 1.055		
	N4	0.953 b?	0.919 - 0.987		
	Adult	0.830	(-5.179) - 6.839		
EXP-3	Egg	0.995 a	0.972 - 1.018		
	N1	0.842 b	0.756 - 0.927		
	N2	0.890	0.678 - 1.102		
	N3	0.923	0.737 - 1.110		
	N4	0.961	0.884 - 1.038		
	Adult	1.063	0.727 - 1.400		

The AIC (and model averaging if it was needed) was used to obtain the mean (m) and standard error (s.e.) needed to calculate the 95% confidence intervals of the estimated values. The standard error was corrected with the c of the most complex model (option) of the Bellows and Birley method.

[1] Standard errors needed to calculate confidence intervals were obtained from pooled data.

[2] Different letters in each experiment indicates differences between the stages when comparing the intervals, which do not overlap.

[3] The confidence intervals of egg and N4 overlapp slightly in this experiment.

Table 5 Final estimates of population parameters with their standard errors obtained from the three experiments carried out in the plastic greenhouse

	Individuals entering		SSSR		Duration[a]	
	m	s.e.	m	s.e.	m	s.e.
EXP-1						
Egg					132.3	0.0
N123	145.1	14.1	0.746	0.024	178.6	37.2
N4	107.9	9.7	0.836	0.010	110.0	19.3
Adult	90.2	8.4				
	(97)[b]		**0.624**[c]	0.026	**420.7**[d]	0.5
					(420.2)	
EXP-2						
Egg	56.8	0.0	0.901	0.000	128.7	4.9
	(59)					
N1	51.2	0.0	0.758	0.000	47.2	21.5
N2	38.8	0.0	0.892	0.000	43.5	4.8
N3	34.6	0.0	0.865	0.000	48.2	6.8
N4	29.9	0.0	0.474	0.000	153.1	16.5
Adult	14.2	0.0				
	(8)		**0.143**[c]	0.000	**420.6**[d]	0.0
			(0.136)		*(422.2)*	
EXP-3						
Egg	120.3	0.0	0.933	0.000	142.3	31.7
	(126)					
N1	112.3	0.0	0.372	0.001	56.9	13.4
N2	41.8	0.1	0.625	0.001	38.3	9.8
N3	26.0	0.0	0.640	0.001	50.3	12.1
N4	17.3	0.0	0.515	0.003	152.6	33.9
Adult	8.9	0.0				
	(12)		**0.097**[c]	0.000	**440.7**[d]	0.1
			(0.095)		*(440.2)*	

The AIC was used to select the best option of the Bellows and Birley method, and model averaging was used to obtain the parameters of the experiment 1, accordingly with the w values of Table 3. The estimated parameters have been corrected with the estimated/observed ratio. The standard error was corrected with the c of the most complex model (option) of the Bellows and Birley method.

[a] Duration is expressed in degree days (DD)

[b] Numbers in italics between brackets are the observed values.

[c] Final survival rate (SR_f).

[d] Duration of total development ($Duration_t$). It is also expressed in degree days (DD).