Population Ecology

Population ecology and egg laying strategy in the 'cruciata' ecotype of the endangered butterfly Maculinea alcon (Lepidoptera: Lycaenidae)
--Manuscript Draft--

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Abstract:	Population dynamics studies in insects mostly focus on a specific life stage of a species and seldom consider different stages. In the framework of our research we studied the population demography of a protected Maculinea alcon 'cruciata' population and the factors that could influence the distribution of eggs. The results of the mark-recapture survey showed a relatively short flight period between mid-June and mid-July with clearly marked early peak period. Unlike in many other butterflies, proterandry was not strong. The total population of M. alcon 'cruciata' was estimated at 699 individuals. The survival rate, and consequently the average life span, was relatively low. Generally, males proved to be more mobile than females. Eggs showed a highly aggregated pattern, and egg numbers was positively related to general shoot size, while the number of flower buds and the features of the surrounding vegetation did not display any effect on egg laying. Based on our findings the studied population appears viable, but specific management techniques could ensure optimal conditions for egg laying in this protected butterfly.
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2 **endangered butterfly *Maculinea alcon* (Lepidoptera: Lycaenidae)**

3

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27

28   **Abstract**

29   Population dynamics studies in insects mostly focus on a specific life stage of a species

30   and seldom consider different stages. In the framework of our research we studied the

31   population demography of a protected *Maculinea alcon 'cruciata'* population and the

32   factors that could influence the distribution of eggs. The results of the mark-recapture

33   survey showed a relatively short flight period between mid-June and mid-July with

34   clearly marked early peak period. Unlike in many other butterflies, proterandry was not

35   strong. The total population of *M. alcon 'cruciata'* was estimated at 699 individuals.

36   The survival rate, and consequently the average life span, was relatively low. Generally,

37   males proved to be more mobile than females. Eggs showed a highly aggregated

38   pattern, and egg numbers was positively related to general shoot size, while the number

39   of flower buds and the features of the surrounding vegetation did not display any effect

40   on egg laying. Based on our findings the studied population appears viable, but specific

41   management techniques could ensure optimal conditions for egg laying in this protected

42   butterfly.

43

2

Introduction

Dynamics of insect populations, mostly in the case of pests, and more recently also in protected species, has been the subject of wide range of studies (Hassell et al. 1991, Way and Heong 1994, Hunter 2001, Yamamura et al. 2006, Thomas et al. 2009). Most of these studies though concentrate on a single life stage of an insect (e.g., adults, larvae), while usually neglecting the parallel investigations into other developmental stages, or the connection between them (Jones and Sullivan 1982, Elkinton and Liebhold 1990, Yamamura et al. 2006, Ordano et al. 2015). Admittedly, it is much easier, and therefore much more practical to determine the viability of any population based solely on the abundance of adults, consequently many pest control and species conservation actions primarily rely on such information (Jones and Sullivan 1982, Katsoyannos 1992, Steytler and Samways 1995, Sunderland and Samu 2000, Thomas et al. 2009, Vrezec et al. 2012). However, linking the dynamics of adults with e.g., egg laying patterns can offer a more precise picture of the sustainability of certain populations in a given area, since the viability of a population is primarily determined by the number of offspring produced in the study area, i.e., in the case of insects by the number of eggs and/or larvae (Begon et al. 1996). In winged insects, such as butterflies, which disperse very efficiently, this combined information is vital, since the mere presence of adults might not imply the persistence of a population in that area at all, it could merely be a sign of efficient dispersal of adults.

The population dynamics of adult butterflies is frequently connected to weather conditions and environmental stochasticity (Melbourne and Hastings 2008, Nowicki et al. 2009, Cormont et al. 2013), while adult egg laying decisions, thus the fate of their

70   offspring primarily relies on the condition of host plants, the strength of intraspecific

71   competition, predatory pressure or other habitat parameters (Stamp 1980, Wiklund

72   1984, Bergman 2001, Czekes et al. 2014). Ovipositing females have to choose the

73   optimal site for their offspring, as well as the best available host plant within the site.

74   Additionally, the survival of the offspring can also be affected by the host plants' direct

75   or indirect responses to the presence of eggs and/or larvae as well (see Hilker and

76   Fatouros 2015 for a review). In the present study we investigated the within-season

77   dynamics of adult butterflies in the '*cruciata*' ecotype of the endangered *Maculinea*

78   *alcon* (featured in many former studies as *Maculinea rebeli*) while linking it to egg

79   laying patterns and preferences.

80   Large Blue butterflies of the genus *Maculinea* Van Eecke, 1915 (synonymised

81   lately with *Phengaris* Doherty, 1891) are one of the most intensively studied butterfly

82   groups in Europe, being considered flagship and umbrella species in nature

83   conservation. They are highly sensitive to habitat changes, and the conservation of their

84   habitats is beneficial to many other threatened species (Thomas et al. 1998a, Thomas

85   and Settele 2004, Nowicki et al. 2005a, Settele et al. 2005). In the past decades severe

86   declines were recorded in most of their Western European populations due to habitat

87   fragmentation and intensification of agriculture (Van Swaay and Warren 1999, Van

88   Swaay et al. 2010). They also raise specific scientific interest due to the intriguing

89   obligate myrmecophylic lifestyle of their larvae (see Witek et al. 2010). Most

90   *Maculinea* populations are small and isolated (Thomas et al. 1998b, Meyer-Hozak

91   2000), characterized by density dependent regulation due to intra-specific competition

92   between larvae on host plants and/or in host ant colonies (Hochberg et al. 1992,

93   Nowicki et al. 2009). Long-term surveys have already shown the importance of weather

4

94 patterns (Roy et al. 2001, Cormont et al. 2013), but *Maculinea* populations are also

95 affected by general habitat characteristics (Nowicki et al. 2007), and human activities

96 (e.g., changes in agricultural practices) (Schmitt and Rákosy 2007).

97   Despite a relatively large number of both field and modelling studies into the

98 ecology of *M. alcon* 'cruciata' (e.g., Hochberg et al. 1992, Meyer-Hozak 2000, Árnyas

99 et al. 2006, Oskinis 2012, Timuş et al. 2013, Czekes et al. 2014), hardly any of them

100 investigated the adult population size and their egg laying behaviour at the same time

101 (Meyer-Hozak 2000, Kőrösi et al. 2008). Furthermore, none of these studies combined

102 the information from both sources in a joint analysis. Despite the need for complex

103 information on populations of protected butterflies, such studies are generally rare in

104 case of other butterfly species as well (see Bergman 2001). Consequently, the aims of

105 our research were to (a) study the within-season dynamics of a *M. alcon* 'cruciata'

106 population, while also (b) examining the temporal changes in the deposition of eggs,

107 and (c) identifying the factors influencing the distribution of eggs.

108

109 **Materials and methods**

110

111 <u>Study species and site</u>

112   Two major ecotypes of the butterfly *M. alcon* are differentiated based on their

113 host plant: the hygrophilous form feeding on *Gentiana pneumonanthe* (previously

114 treated as *M. alcon*), and the more xerophilous form feeding on *G. cruciata* (previously

115 treated as *M. rebeli*, hereafter referred to as *M. alcon* 'cruciata'). Recent molecular

116 studies showed that the two forms cannot be regarded as different species (Als et al.

117 2004, Bereczki et al. 2005, Steiner et al. 2006, Pecsenye et al. 2007). Nevertheless, in

118 addition to habitat and host plant segregation, they typically use different host ant

5

119 species, and they also have different flight periods (Bereczki et al. 2005, Pech et al.

120 2004, Sielezniew et al. 2012). *M. alcon* '*cruciata*' prefers semi-natural calcareous

121 grasslands (Bálint 1994, Pech et al. 2004, Rákosy and Vodă 2008), and it uses quite a

122 wide range of host ant species from the genus *Myrmica* Latreille, 1804, which adopt

123 them due to their efficient chemical and acoustical mimicry (see Fiedler 2006 and Witek

124 et al. 2014 for a review). Their development continues inside the ant nest, where they

125 are fed by the ant workers (Elmes et al. 1991). The flight period of adult butterflies is

126 from mid-June to mid-July (Meyer-Hozak 2000, Kőrösi et al. 2008, Timuş et al. 2013).

127 The conservation status of *M. alcon* is Least Concern according to the IUCN Red List in

128 Europe and Near Threatened in the European Union (Van Swaay et al. 2010).

129   The field study was performed on a 9252 m^2 semi-natural calcareous dry

130 grassland of southeastern exposure in the surroundings of Rimetea village

131 (N46°27'51.45", E23°33'46.26", ca. 620 m a.s.l., Romania). The grassland is a plant

132 species-rich meadow dominated by *Brachypodium pinnatum*, *Carex humilis* and

133 *Festuca rupicola* with other characteristic species like *Dorycnium pentaphyllum*,

134 *Cytisus albus*, *Hieracium bauhinii*, *Teucrium montanum* and *Thymus serpyllum*, and it

135 is intensively grazed by goats and sheep. The meadow is partially surrounded by a

136 mixed forest and shrubs of *Crataegus monogyna*, *Prunus spinosa*, *Pyrus pyraster* and

137 *Rosa canina*. The site constitutes a part of the ROSCI0253 'Trascău' Natura 2000

138 protected site.

139

140 Data collection

141 *a) Population dynamics survey*

142   A mark-recapture study of adult *M. alcon 'cruciata'* butterflies was conducted

143   between 15 June and 16 July 2012 covering the entire flight period. The survey plan

144   followed the requirements of the Pollock's Robust Design approach (Pollock 1982;

145   Pollock et al. 1990), i.e. relatively infrequent but highly intensive capture days were

146   established, which constituted primary sampling periods. The sampling took place on

147   every fourth day, with a single exceptional case in which the interval between

148   consecutive capture days was reduced to three days due to the forecast of unfavourable

149   weather conditions on the following days. Butterflies were surveyed between 10 AM

150   and 5 PM during five one-hour capture sessions, regarded as secondary sampling

151   periods, and were separated by 30 min breaks to allow free mixing of butterflies

152   between the secondary sampling periods. Captured individuals were marked on the

153   underside of their hind-wing with unique identity numbers using a fine-tipped

154   waterproof pen (© Schneider GmbH), and then immediately released at the place of

155   capture. For each capture we recorded the date, the exact time and the position of each

156   capture (GPS coordinates), as well as the identity number and the sex of the adult.

157

158   *b) Distribution of butterfly eggs*

159   Prior to the adult butterfly survey we randomly placed out 22 sampling plots

160   within the study site. The plots were circles of 2 m radius, as generally applied in the

161   case of *Maculinea* species based on the average foraging radius of the host ant *Myrmica*

162   (see Elmes 1975, Elmes et al. 1998), with a focal *G. cruciata* plant in the middle.

163   Within the plots we recorded the number of all *G. cruciata* host plants, and the number

164   of their shoots. Shoots were considered to belong to the same plant when they were

165   obviously connected either above the soil surface. In order to minimise disturbance, we

166 recorded the number of eggs on the focal host plant within each plot (n = 22) only at the

167 end of each mark-recapture sampling day. At the end of the whole study period we

168 counted all eggs found on all host plant shoots within the sampling plots in addition to

169 the characteristics of the host plants and general vegetation features. The following

170 parameters were recorded: (a) the total number of butterfly eggs laid on the host plant

171 shoots, and separately on different verticils, (b) shoot height as the length of the shoot

172 (cm), (c) number of shoot leaves, and (d) number of flowers (only flower buds with

173 coloured sepals were taken into account since small green flower buds are impossible to

174 count sometimes) on separate verticils of shoots, (e) the number of host plants in each

175 plot, (f) the maximum height of the surrounding vegetation (cm), and (g) the proportion

176 of vegetation cover visually estimated to the nearest 5%.

177

178 Data analysis

179 Mark-recapture data was analysed with the use of Mark 7.0 program (White and

180 Burnham 1999) applying the Robust Design (RD) model (Pollock 1982; Kendall et al.

181 1995). The RD model allows relatively high precision of population estimates, and it

182 has proved its applicability in butterfly population studies (Nowicki et al. 2008). The

183 analyses were conducted separately for males and females, because sex-specific

184 population parameters were of interest for our study. The data from capture sessions

185 (i.e. secondary periods of the RD model) within sampling days were used to estimate

186 daily population sizes for these days (N_i). In the estimation we accounted for individual

187 heterogeneity in capture probabilities, since its existence was revealed by the tests for

188 violations to equal catchability assumption (Otis et al. 1978; Chao 1988). In turn, the

189 data pooled together within capture days (i.e. primary periods of the RD model) were

8

190 used for assessing survival rate between these days (φ_i). The model variant assuming no

191 time variation in survival rate performed the best as indicated by its lowest value of the

192 Akaike Information Criterion corrected for small sample (AIC$_c$; Hurvich and Tsai

193 1989), which implies that adult survivorship was fairly constant throughout the flight

194 period. Subsequently, we calculated the average adult lifespan as $e = (1 - \varphi)^{-1} - 0.5$

195 (Nowicki et al. 2005b).

196   Based on the estimates of daily population sizes and survival rates, we also

197 estimated the recruitment (B_i), i.e. the numbers of individuals eclosing from pupae and

198 entering the adult population during the intervals between consecutive capture days. As

199 the adult life span was relatively short when compared with the length of these intervals

200 (d_i), we used the formula of Nowicki et al. (2005a; see this reference for the rationale),

201 which accounts for the individuals eclosing and dying within the same intervals: $B_i' = d$

202 $\times (N_{i+1} - N_i \cdot \varphi^d) \times (\varphi - 1) / (\varphi^d - 1)$. The sum of recruitment for the entire flight period

203 makes up seasonal population size (N_{total}). In a similar way, by summing female

204 recruitments prior to each capture day, we derived the total numbers of females present

205 until these days.

206   To compare the distances covered by female and male butterflies we measured

207 the distance between the two furthermost points where an individual was captured. We

208 also measured the area of the polygon marked by the capture points of an individual in

209 order to compare the area covered by female and male butterflies. The measurements

210 were based on recorded GPS coordinates and conducted using Garmin Mapsource

211 software (version 6.16.3, Garmin Ltd. 1999-2010). The flight distances and areas could

212 be quantified only in the case of individuals which were captured at least twice (for

213 distance), and three times (for area), therefore, due to the low recapture rate, a relatively

9

214   small data set was available for analysis (n = 11 females and 59 males for distance; n = 5

215   females and 28 males for area). Wilcoxon signed rank test were used for the comparison

216   of flight distances between males and females. Due to the low sample size a similar

217   analysis was not performed for the area covered.

218   Poulin's discrepancy index (Rózsa et al. 2000) was used to characterize the

219   distribution of eggs on all host plants within sampling plots recorded at the end of the

220   study period. Biases in the distribution of eggs among different host plant verticils were

221   checked with Generalized Linear Mixed Model approach (GLMM, Poisson error,

222   maximum likelihood approximation; n = 133). The number of eggs laid on different

223   verticils of egg bearing plant shoots was introduced as dependent variable, while the ID

224   of verticil as independent factor. Sampling plot and plant IDs were introduced as nested

225   random factors to handle dependency of data. Only egg data regarding the top four

226   verticils were taken into account since no eggs were recorded on lower verticils.

227   We tested the relationship between the estimated number of females present

228   before each sampling day, and the total number of eggs laid in the same period (n = 8)

229   in order to reveal whether the number of eggs laid is related to the number of female

230   butterflies. Spearman rank correlation analysis was applied due to the lack of normality

231   of both variables. In addition, the effect of the abundance of eggs already present on

232   oviposition was checked by testing the relationship between the number of eggs present

233   and the number of newly laid eggs in the following period for seven consecutive periods

234   between the eight sampling days. Again, Spearman rank correlation analysis was

235   applied in this case.

236

237   The effects of host plant and vegetation characteristics on egg distribution were

238   analyzed with the use of GLMM approach (Poisson error, maximum likelihood

239   approximation; n = 410). Correlation between host plant characteristics were checked

240   using Spearman rank correlation analysis due to non-normality of datasets. A principal

241   component analysis (PCA) was applied to obtained uncorrelated derived variables for

242   plant characteristics, and the principal components were used as independent variables

243   in the GLMM analysis. The number of eggs laid on each focal host plant was

244   introduced as a dependent variable, while independent variables were the host plant

245   morphological characteristics (PC1 [correlated plant height and number of leaves] and

246   PC2 [correlated number of flower buds]), the number of host plants in sample plots, the

247   maximum height of the surrounding vegetation, and vegetation cover. Sampling plot

248   and host plant IDs were introduced as random factors to handle dependencies.

249   Automated model selection procedure was carried out, and the effects of different

250   explanatory variables were averaged across the supported models with delta $AIC_c < 4$,

251   i.e. those with the AIC_c differing by less than 4 from the best model (see Grueber et al.,

252   2011).

253   All statistical analyses were carried out using the R 3.1.1 Statistical Environment

254   (R Development Core Team 2014) and Quantitative Parasitology 3.0 (Rózsa et al.,

255   2000). Normality of datasets was regularly checked with the Shapiro-Wilk test. *Relevel*

256   function was used in order to carry out post-hoc sequential comparisons among factor

257   levels when performing GLMM. GLMMs were carried out with the use of *glmer*

258   function in *lme4* package (Bates et al. 2014), and *dredge* function in *MuMIn* package

259   (Barton 2015) was applied for automated model selection. Table-wide Bonferroni-Holm

260   correction was applied in the case of sequential comparisons, such as Spearman rank

261 correlations and comparison of factor levels in the GLMM analysis concerning the

262 location of eggs on different verticils.

263

264 **Results**

265

266 <u>Demography of adult butterflies</u>

267 During the entire study we captured and marked 152 (67.5%) males and 73

268 (32.5%) females, out of which 85 males and 14 females, respectively, were recaptured

269 at least once. The total adult population was assessed at 699 individuals, with a

270 relatively balanced sex ratio (55% males vs. 45% females) (Table 1). The estimated

271 survival was fairly low, which translates in rather short adult lifespan of ca. 2 days with

272 no major inter-sexual difference (Table 1).

273 The butterfly had a relatively short flight period between mid-June and mid-

274 July, with a clearly pronounced peak occurrence in the early part of the period (Fig. 1).

275 More than 50% of individuals emerged within the first week, and more than 80% within

276 the first two weeks (Fig. 1). Besides, in comparison to many other species of butterfly,

277 we found rather weak proterandry (cf. Pfeifer et al. 2000; Nowicki et al. 2005b): the

278 number of females peaked only three days after the peak of males.

279 Most of the butterflies clearly preferred the close proximity of shrubs (Fig. 2).

280 The mean distance covered by males was 81.61 m (SD = ±56.99, min = 9, max = 217),

281 and the mean area was 1766.98 m^2 (SD = ±2260.67, min = 25, max = 8091). Females

282 were less mobile, with a mean flight distance of 53.9 m (SD = ±57.72, min = 14, max =

283 213), and with a mean area of 193 m^2 (SD = ±289.19, min = 5, max = 684). Males

284 covered significantly longer distances, than females (Wilcoxon signed rank test W =

285 454, p < 0.05).

286

Egg laying dynamics and preferences

At the end of the study altogether 94 eggs were recorded on a total of 410 *G. cruciata* shoots of 201 plants within the 22 study plots. More than 90% of the shoots lacked eggs, and the maximum number of eggs was 23 on a single shoot. The overall mean egg density was 0.47 eggs/plant, and 0.23 eggs/shoot (4.48 eggs/plant and 4.09 eggs/shoot only for plants with eggs); while the mean host plant density was 0.72 plants/m^2 (9.05 plants/plot), and 1.48 shoots/m^2 (18.6 shoots/plot). The distribution of eggs on plants showed a highly aggregated pattern (Fig. 3) as indicated by Poulin's discrepancy index (D = 0.97). Eggs were laid only on the top four verticils of the plants. Most eggs were laid on the 2nd verticil (33.93% of total), but no significant differences were revealed between the number of eggs on the different verticils (GLMM, z ≤ 1.487, p = NS, n = 133).

Eggs were recorded even during the first part of the study period on the focal host plants of the sampling plots (n = 22), even if less than 10% of the focal plants bore eggs on the 2nd sampling day (22.06). By the 6th sampling day (08.07) 63% of the plants had eggs, after this the percentage of egg bearing plants decreased (Fig 4.). The number of eggs laid before each capture period did not correlate with the number of females recruited in the same period (Spearman r = 0.53, p = 0.13, n = 8). In turn, the number of newly laid eggs correlated negatively with the number of eggs already present on host plants, the negative correlations between the two variables reached statistical significance level during all but two sampling periods (Table 2).

Host plant morphological characteristics were mostly correlated according to the results of the Spearman rank-correlation analysis (n = 410): height vs. number of leaves

310   r = 0.5, p < 0.001; number of leaves vs. number of flower buds r = 0.25, p < 0.001;

311   height vs. number of flower buds r = 0.10, p = 0.050. The PCA yielded 1st (PC1) and 2nd

312   (PC2) principal components that explained 52% and 31% of the variance, respectively.

313   PC1 represented plant height and number of leaves with loadings of 0.66 and 0.68,

314   respectively, as a measure of general shoot size, while PC2 reflected the number of

315   flower buds with a loading of 0.94. All input variables were retained in the best average

316   GLMM model for egg laying preferences (Table 3), but only the general shoot size

317   (PC1) had a significant positive effect on the number of eggs laid (z = 4.59, p < 0.001;

318   Fig. 5), while none of the other variables displayed any significant effects (z ≤ 1.63, p =

319   NS)

320

321   **Discussion**

322

323   The results of the present study show that the studied butterfly population

324   appears fairly viable based on the comparison with other studies concerning the size of

325   *M. alcon 'cruciata'* populations (Árnyas et al. 2005, Timuş et al. 2013). During a three

326   year long MRR study Árnyas et al. (2005) found that on a 0.75 ha site the studied *M.*

327   *alcon 'cruciata'* population was stable with nearly 1000 individuals, while Timuş et al.

328   (2013) estimated the size of another population in Romania to 1073 individuals for a 40

329   ha site. In comparison, the size of our studied population (699 individuals on ~1ha)

330   suggests that the population is relatively big. Generally, *Maculinea alcon* populations

331   show very small fluctuations (Hochberg et al. 1994, Elmes et al. 1996), thus there is a

332   considerable chance that our studied population is stable.

333   Similarly to other studies (Meyer-Hozak 2000, Árnyas et al. 2005), we found

334   that the butterflies fly from mid-June to mid-July. In some cases the flight period takes

14

less than one month (Timuş et al. 2013), which can reflect differences in habitat or/and

meteorological conditions of different populations. Although we found a relatively

weak indication of proterandry, the peak emergence of males still preceded that of

females. This phenomenon is in fact common for all *Maculinea* species and for

butterflies in general. According to Elmes and Thomas (1987) the males pupate a few

days before females, and thus during the initial part of the flight period the population is

dominated by males. During the entire study we caught roughly twice as many male

individuals as female, but the estimated sex ratio was relatively balanced, which

corresponds with results of other studies (Árnyas et al. 2005, Timuş et al. 2013).

Considerably higher capture and recapture rates of males may be attributed also to the

fact that they fly more often and higher searching for the less mobile females. The latter

tend to fly lower because they are searching for food plants in the undergrowth (Árnyas

et al. 2005).

Earlier mark-recapture and individual tracking studies suggested that *Maculinea*

butterflies are highly sedentary (Hovestadt and Nowicki 2008, Kőrösi et al. 2008,

Hovestadt el al. 2011, Skórka et al. 2013). Our results concerning adult mobility also

support this fact. Keeping close to the place of eclosion can be an adaptation of these

butterflies to myrmecophily (Hovestadt and Nowicki 2008). Inter-sexual differences

were revealed by our study: males proved to be more mobile than females. On the other

hand, similar research on other *Maculinea* species showed higher mobility in females

(Kőrösi et al. 2012, Skórka et al. 2013), which could be attributed to females trying to

decrease intra-specific competitive pressure among their offsprings (Nowicki and

Vrabec 2011). However, all these studies were carried out on *M. teleius* and *M.*

nausithous, i.e. species with more restricted habitat requirements (wet meadows) and

359   higher population densities in comparison to *M. alcon 'cruciata'*, which prefers semi-

360   dry grasslands and has lower population densities (Meyer-Hozak 2000, Nowicki et al.

361   2007). In our population the higher mobility of males is likely to stem from the high

362   male/female ratio due to which males may need to cover larger areas in order to find

363   mating partners. Therefore, male mobility may play a crucial role in gene flow in our

364   population (Piaggio et al. 2009, Solmsen et al. 2011).

365   Phytophagous butterfly species mostly lay their eggs separately one by one or in

366   clusters (Stamp 1980 for a review, Vulinec 1990, Dixon and Guo 1993). Both strategies

367   can influence positively the survival of eggs and larvae. Females can lower the chances

368   of predation and competition for their offspring by depositing their eggs individually. In

369   these cases eggs are usually cryptic (light yellow or green) and are laid on protected

370   parts of the host plants (see Stamp 1980). Laying eggs in clusters can be advantageous

371   when other factors can affect negatively the reproduction, like the patchy distribution of

372   host plants, the scarcity of resources for larvae and adults, low population density or

373   unfavorable weather conditions (Stamp 1980, Karlsson and Johansson 2008,. Karlsson

374   et al. 2008). Besides, as clusters of eggs and larvae are more protected from desiccation

375   when clumped together, clusters can ensure higher survivability through lower

376   sensitivity to ambient conditions (Stamp 1980, Clark and Faeth 1998). During our study

377   we found a low mean egg density per host plants (0.47 eggs/plant) compared to that

378   recorded by Czekes et al. (2014) in another population (8.89 eggs/plant). In addition, the

379   distribution of eggs among host plants showed a clearly aggregated pattern, thus most of

380   the eggs were concentrated only on a few host plants. This could suggest the patchy

381   distribution of host ants, however there is no convincing evidence yet that ovipositing

382 females can detect the presence of host ants (Van Dyck et al. 2000, Thomas and Elmes

383 2001, Nowicki et al. 2005a, Fürst and Nash 2010, Wynhoff et al. 2015).

384   The number of females did not explain the number of new eggs laid, which can

385 also be attributed to the emigration of females. It is possible that some of the females

386 present in the study area laid their eggs in the surrounding land fragments. Another

387 cause of this result could be the perishing of a large amount of eggs during the egg

388 laying season which can be attributed to an increased level of predation (Bergman

389 2001), but also to meteorological factors and grazing of host plants. There was a

390 negative relationship between the number of eggs already present on the plants and the

391 quantity of newly laid eggs. This result could indicate that females would prefer laying

392 eggs on empty plants or at least with a small amount of eggs present only. However,

393 this evidence is very circumstantial, specifically designed study could only clear the

394 effect of egg abundance on female ovipositing behaviour (see e.g. Kőrösi et al. 2008).

395   Earlier studies about egg laying preferences showed that the most important

396 factors influencing oviposition are the morphological characteristics of host plants, such

397 as the height of the plant, the number, the size and the phenology of buds, and the

398 number of leaves (Dolek et al. 1998, Nowicki et al. 2005a, Árnyas et al. 2006, 2009,

399 Czekes et al. 2014, Wynhoff et al. 2015). In concordance with the aforementioned

400 studies, our research suggests that females preferred the taller shoots with many leaves

401 for oviposition. A visually conspicuous host plant (i.e. tall ones with many leaves) may

402 be more attractive or more perceptible for females than smaller ones (Nowicki et al.

403 2005a, Van Dyck and Regniers 2010, Czekes et al. 2014, Arnaldo et al. 2014, Wynhoff

404 et al. 2015). The large number of eggs on tall plants with a high number of leaves can

405 be beneficial for the butterflies due to an increased egg laying surface, decreased larval

406 competition, or even better climatic conditions. Wynhoff et al. (2015) suggested that

407 larger host plants might provide high quantities of food for the caterpillars because of

408 bearing later many fully developed flower buds. *Maculinea alcon 'cruciata'* females

409 laid their eggs exclusively on the four top verticils of their host plants, which could be

410 attractive sites for oviposition presumably also because of the lower predation risk for

411 adult females (Van Dyck and Regniers 2010) and the better microclimate for larval

412 development (Alonso 2003). In addition, ovipositing mostly on the 2nd verticil from the

413 top, as suggested by our results, could ensure better climatic conditions to eggs through

414 reduced exposure to sun and wind.

415   Linking population demography data to oviposition preferences could help the

416 protection of the focal butterfly species not only by offering data to nature

417 conservationists, but also by revealing that specific management techniques could

418 ensure better conditions for egg laying. Specifically, sustaining a low grazing pressure

419 could have a positive effect on the butterfly population (WallisDeVries and Raemakers

420 2001), and it would also keep shrubs from invading the grassland.

421

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423

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715   **Table 1.** Basic parameters of the investigated *Maculinea alcon* '*cruciata*' population as

716   revealed by the MRR study (95% confidence intervals in brackets).

	Captured individuals	Seasonal population	Survival rate $[day^{-1}]$	Adult lifespan [days]
Males	152	382 (305–496)	0.63 (0.57–0.69)	2.2 (1.8–2.8)
Females	73	317 (219–480)	0.57 (0.34–0.77)	1.8 (1.0–3.8)
All	225	699 (565–884)	0.62 (0.56–0.68)	2.1 (1.8–2.6)

717

718 **Table 2.** Spearman rank correlations (n = 22 in all cases) between the number of eggs

719 present and the number of newly laid eggs on host plants on different capture dates.

720 Statistically significant values are bolded.

capture date	Spearman r	p
19.06	-0.73	**0.001**
22.06	-0.21	0.731
26.06	-0.51	**0.006**
30.06	-0.89	**< 0.001**
04.07	0.04	0.861
08.07	-0.74	**< 0.001**
12.07	-0.91	**<0.001**

721

722 **Table 3.** The supported models according to the results of the automated model

723 selection procedure. See the text for the explanations of the model variables.

Model	df	logLik	AICc	ΔAICc	weight
PC1+PC2	5	-119.61	249.37	0.00	0.25
PC1+PC2+Height	6	-119.30	250.80	1.43	0.12
PC1	4	-121.47	251.03	1.66	0.11
Cover+PC1+PC2	6	-119.51	251.23	1.87	0.10
Density+PC1+PC2	6	-119.56	251.33	1.96	0.10
Density+PC1	5	-121.14	252.43	3.06	0.06
Cover+PC1+PC2+Height	7	-119.16	252.61	3.27	0.05
PC1+Height	5	-121.28	252.72	3.35	0.05
Density+PC1+PC2+Height	7	-119.26	252.79	3.43	0.05
Cover+PC1	5	-121.37	252.89	3.52	0.05
Cover+Density+PC1+PC2	7	-119.46	253.20	3.84	0.04

724

725

726   **Fig. 1.** Dynamics of male and female adult butterflies throughout the study period based

727   on mark-recapture estimates. Error bars represent 95% confidence intervals.

728   **Fig. 2.** The (a) outline of the study site and the (b) distribution of male (black) and

729   female (white) butterfly captures (recaptures included).

730   **Fig. 3.** The frequency distribution of eggs on host plant shoots.

731   **Fig. 4.** Temporal dynamics of eggs laid on the host plants during the flight period. Error

732   bars represent Standard Deviations.

733   **Fig. 5.** The number of butterfly eggs laid on host plants in relation to the host plant

734   height and number of leaves (the circle area is proportional to the number of eggs laid).

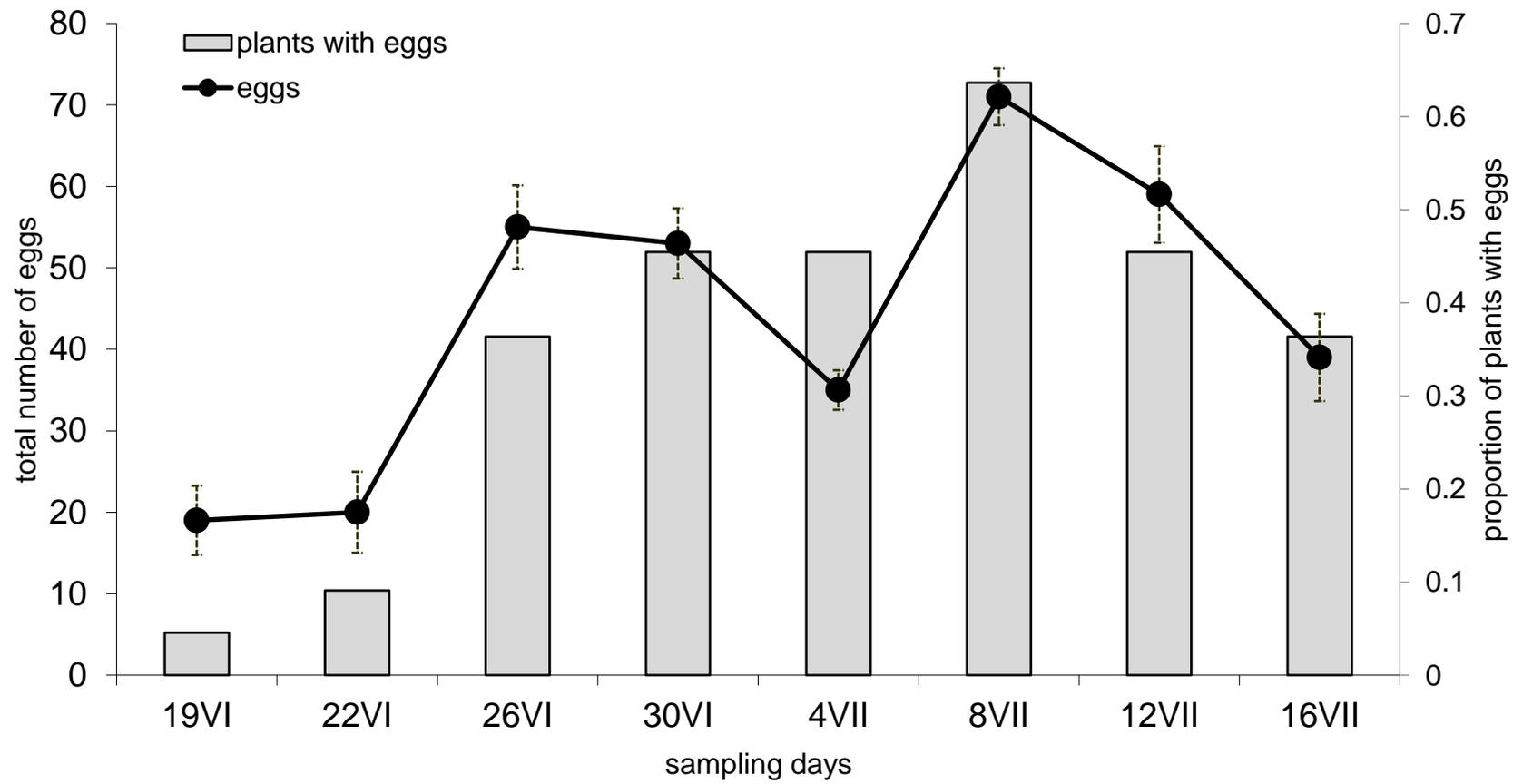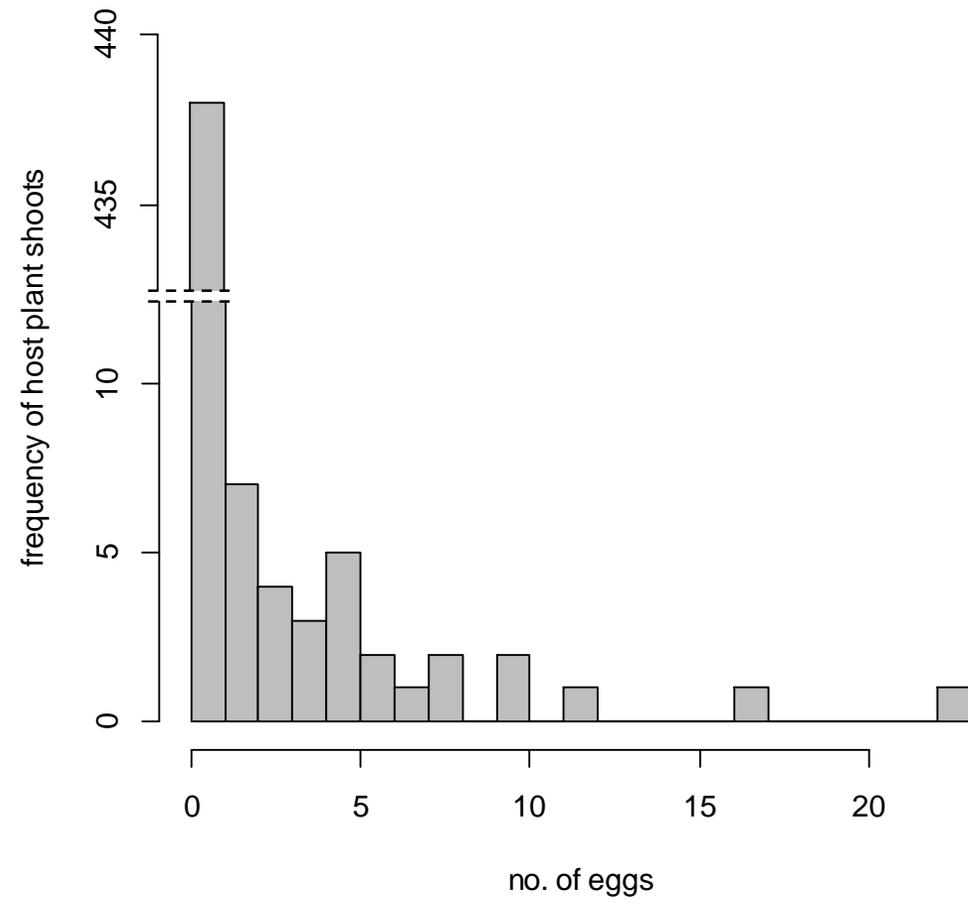Figure 1
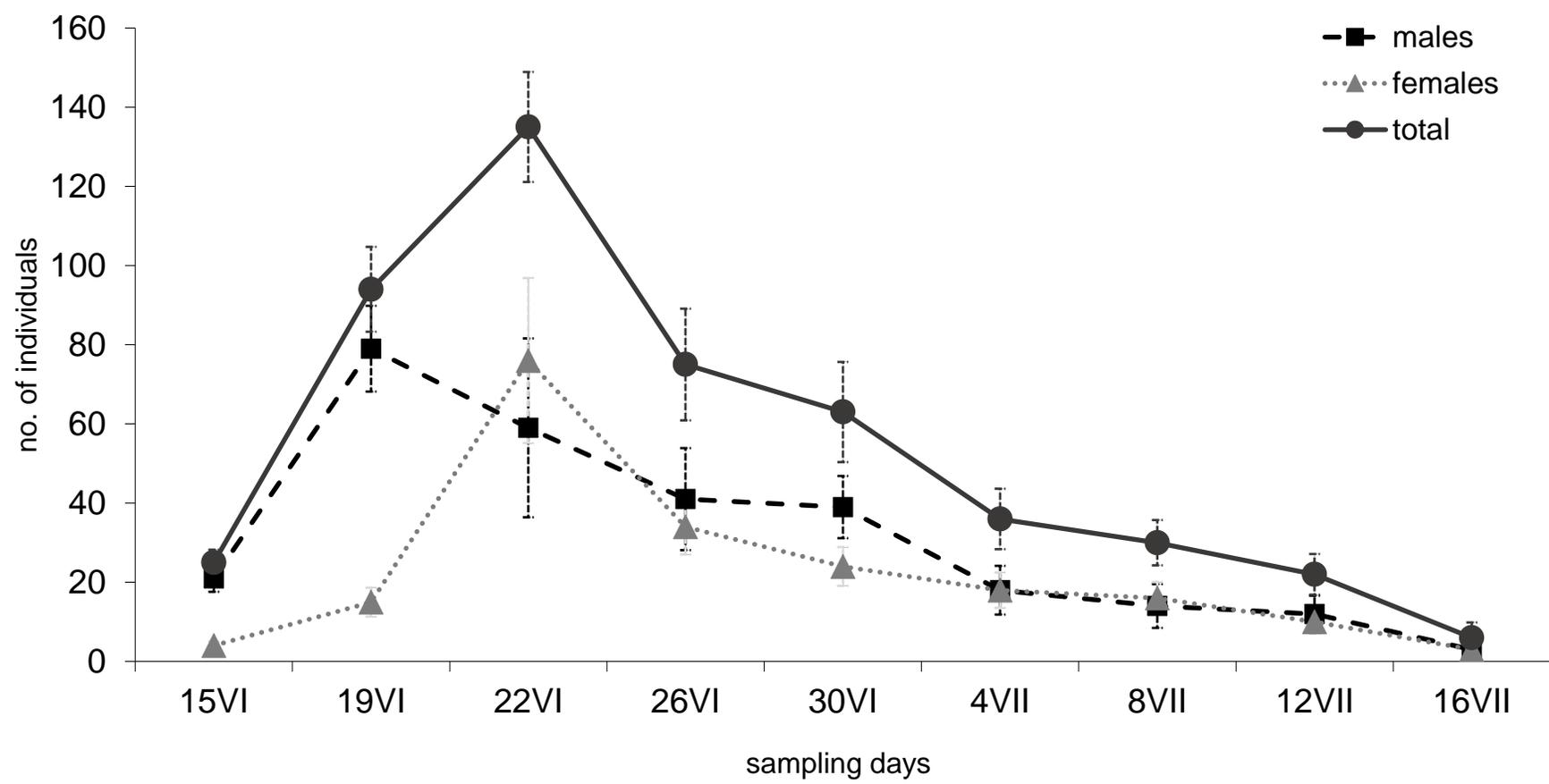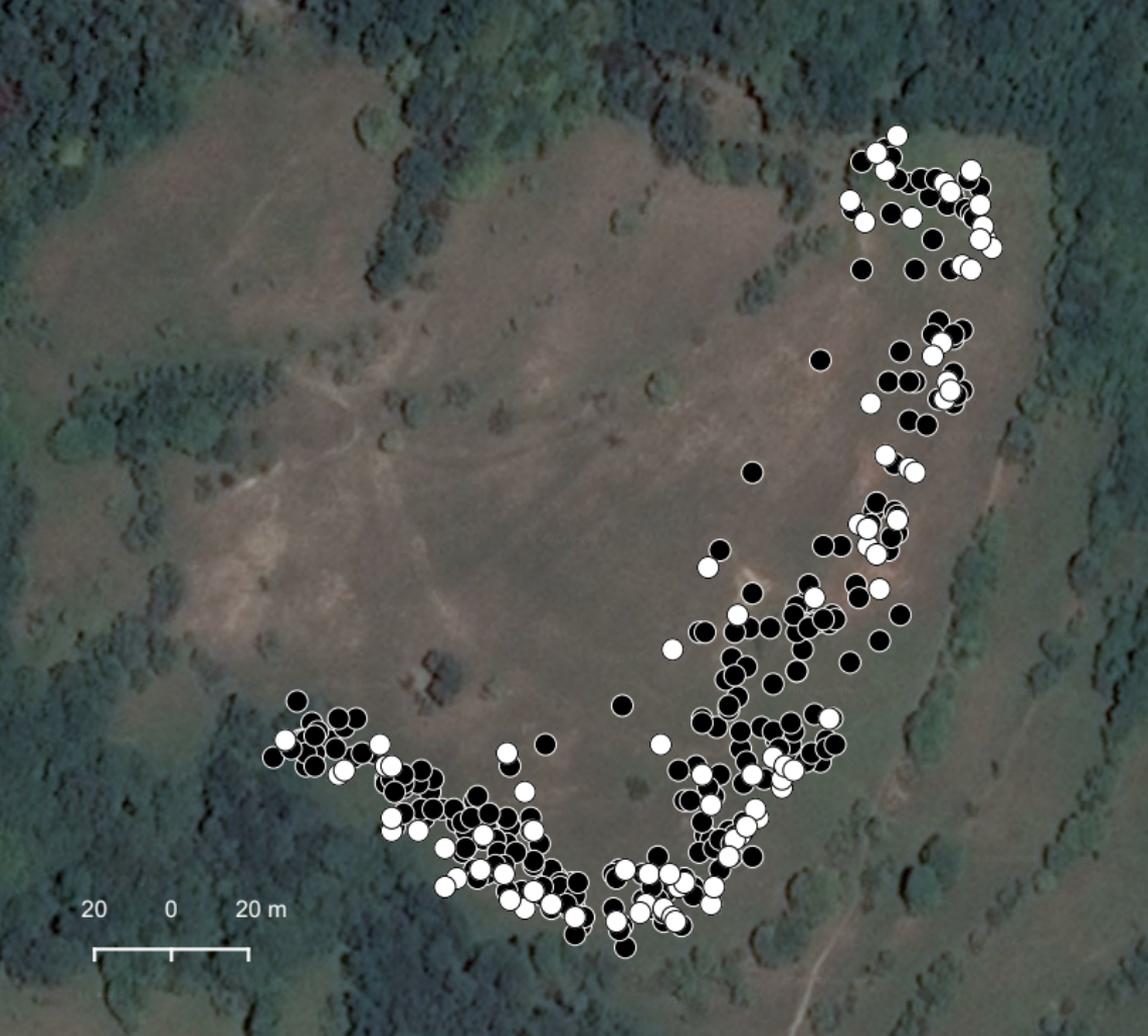
20   0   20 m

Figure 3

Figure 4

Figure 5