

1 **For submission to Bulletin of Entomological Research**

2 **Running title: Zhao et al., Seasonal migration of *Heliothis virescens***

3

4 ***Is Heliothis virescens* (Lepidoptera: Noctuidae) a long-distance**
5 **migrant?**

6 Xiao-yang Zhao¹, Xiao-wei Fu¹, Abid Ali¹, Kenneth Wilson², Kong-ming

7 Wu¹ *

8 *1. State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of*

9 *Plant Protection, Chinese Academy of Agricultural Sciences, No. 2 West*

10 *Yuanmingyuan Road, Beijing, 100193, China.*

11 *2. Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK.*

12

13 *** Corresponding author:**

14 Mailing address: Institute of Plant Protection, Chinese Academy of Agricultural

15 Sciences, No. 2 West Yuanmingyuan Road, Beijing, 100193, China.

16 Tel: +86-010-82105551.

17 E-mail: wukongming@caas.cn

18

19 **Abstract** *Heliothis virescens* (Hüfnagel) (Lepidoptera: Noctuidae) is an important
20 polyphagous pest of beans, cotton, maize, and alfalfa worldwide. Whether *H.*
21 *virescens* is a long-distance migrant, and if so, what pattern of seasonal migration this
22 species exhibits in northern China remains unknown. In this study, in order to
23 determine the seasonal migration of *H. virescens* in northern China, the combination
24 of searchlight trapping and ovarian dissection was carried out on an isolated small
25 island in the center of the Bohai Strait during 2003-2014. The results confirmed that
26 *H. virescens* undertakes long-distance migration on the prevailing winds of the East
27 Asian monsoon airflows. This species exhibited a regular pattern of seasonal
28 migration across the sea from May to October, but there was considerable yearly and
29 monthly variation in the trapped numbers, with the majority being trapped in summer
30 ($67.99 \pm 6.54\%$). The mean period when migration was detectable at the island was
31 116.5 ± 5.6 days from 2003 to 2014, with the shortest time span of 74 days in 2013
32 and the longest of 144 days in 2005. Trapped females in May and June showed a
33 relatively higher mating rates and some degree of ovarian development when
34 compared with July, August, and September, suggesting the migration of this species
35 is not completely bound by the 'oogenesis-flight syndrome'. These findings will be
36 helpful to improve the forecasting system and managing strategies of *H. virescens*.

37 **Keywords:** *Heliothis virescens*, seasonal pattern, searchlight trapping, sexual
38 maturation, trans-regional migration

39

40 **Introduction**

41 Insects, with the most species and abundant biodiversity, have evolved two
42 general strategies to cope with habitat changes: diapause and migration, which have
43 been referred to as the ‘here later’ and ‘there now’ strategies (Dingle, 2014).
44 Long-distance migration, a seasonal to and from movement of insects between
45 regions where conditions are favorable or unfavorable, plays a key role in the
46 life-cycle of many insect species (Dingle & Drake, 2007). Billions of insects migrate
47 (over land, or through air, or across water) within and between continents every year,
48 often responsible for sudden outbreaks of crop pests and insect-vectored plant
49 diseases (Chapman *et al.*, 2011, 2015). A good understanding of insect migration
50 facilitates the development of forecasting systems and management strategies,
51 however the general patterns of how populations migrate across different regions and
52 seasons are largely unknown in most insect species (Stefanescu *et al.*, 2013).

53 *Heliothis virescens* (Hüfnagel) (Lepidoptera: Noctuidae), one of the major crop
54 pests in the world, is widely distributed in Europe, Africa, and Asia (Kravchenko *et al.*
55 *et al.*, 2005), occupying climates ranging from tropical to temperate (Weigand, 1996;
56 Kahrarian, 2012). In China, *H. virescens* is widely distributed from northeastern
57 through central to the Tibetan Plateau, and occasionally the occurrence range can
58 extend to southeastern provinces. There are 2-4 generations of this species each year,
59 increasing as the effective accumulative temperature increases from north to south
60 (He *et al.*, 1997). *H. virescens* larvae are polyphagous with 78 host plants including >
61 20 cultivated crops. They mainly damage peas in spring; cotton, maize and soybean in
62 summer; alfalfa, sunflower and sugar beet in autumn; and overwinter as pupae in the
63 soil (Cui *et al.*, 1997; He *et al.*, 1997; Liu *et al.*, 2010). It is hard to prevent the
64 damage and to control this pest species because it can silk and roll plant leaves, and it
65 has also developed resistance to chemical pesticides (Mu *et al.*, 2004). In the past
66 decade, a series of major outbreaks of *H. virescens* has been reported in Asian soybean,
67 maize, and chickpea fields, and severe infestations commonly reduce yields by 40-90%
68 (Mu *et al.*, 2004; Liu *et al.*, 2010; Kahrarian *et al.* 2012).

69 Although it is commonly accepted that the wide distribution of *H. viriplaca* is
70 due to its strong flight ability (He *et al.*, 1997), so far there is no direct evidence that
71 this species is a long-distance migrant. And if so, it is still unclear (1) whether the
72 migration of this species is a regular occurrence, and (2) what the pattern and
73 physiological states of seasonal migration is in this species. In the current study, the
74 combination of searchlight trapping and ovarian dissection was used to monitor
75 wind-borne migration of *H. viriplaca* for 12 consecutive years on a small isolated
76 island located in the center of the Bohai Strait, China. Findings from this study will be
77 helpful in developing sound management strategies against *H. viriplaca*.

78

79 **1. Materials and Methods**

80 **1.1 Searchlight Trapping and Field Observation**

81 The searchlight trapping studies were carried out each year from April to October
82 2003-2014 on Beihuang island (BH, 38°24'N, 120°55'E), the northern most island of
83 Changdao county in Shandong province. BH (≈ 2.5 km²) is located in the center of
84 the Bohai Strait at a distance of ≈ 60 km from the mainland to the south and ≈ 40
85 km to the north (Fig. 1). A vertical-pointing searchlight trap was placed on a platform
86 ≈ 8 m above sea level, and was used to attract and capture high-altitude migrants (up
87 to ≈ 500 m above the ground level; Feng *et al.* 2009). The trap was equipped with a
88 1,000 W metal halide lamp (model JLZ1000BT; Shanghai Yaming Lighting Co. Ltd.,
89 Shanghai, China), which produces a vertical beam of light with a luminous flux of
90 105,000 lm, a color temperature of 4,000 K, and a color rendering index of 65.

91 The searchlight trap was turned on at sunset and turned off at sunrise on all nights
92 from April to October (Zhai, 2004). Incomplete data sets caused by power cuts or
93 heavy rains were excluded from the analysis, while those nights in which the light
94 trapping was carried out normally but no *H. viriplaca* was captured were given a 'zero'
95 count in the analysis. Trapped insects were collected with a nylon net bag (60 mesh)
96 beneath the trap, which was changed manually every 2 h each night. The trapped
97 insects were kept in a freezer at -20°C for 4 h before being identified and *H. viriplaca*

98 females were dissected.

99 There are some pine trees and graminaceous weeds on BH, but no arable lands or
100 host crops of *H. viriplaca*. To confirm whether there is a local population of *H.*
101 *viriplaca* (e.g. on the weeds), visual observations were carried out daily to detect
102 larvae of this species on any potential wild host plants from spring throughout autumn
103 2003-2014.

104 **1.2 Ovarian Dissection**

105 To test the hypothesis of an ‘oogenesis-flight syndrome’, a subsample of 20 *H.*
106 *viriplaca* females (or all individuals if the total capture of females was < 20) was
107 randomly taken each night, and was dissected under a stereomicroscope (model
108 JNOEC-Jsz4; Motic China Group Co.Ltd., Xiamen, China) to determine the
109 development level of the ovaries from 2009-2014. The level of ovarian development
110 1-5 was estimated according to the criteria described in [Table 1](#). These data were used
111 to generate an average monthly level of ovarian development (i.e., the sum of
112 individual levels of ovarian development divided by the number of females dissected).
113 Females with ovarian development level 1-2 were regarded as “sexually immature
114 individuals”, and others with level 3-5 were regarded as “sexually mature individuals”
115 ([Zhang et al., 1979](#)). Moreover, mating frequency and mating occurrences of *H.*
116 *viriplaca* were determined by the number of spermatophores in the female
117 spermatheca ([Zhang et al., 1979](#)).

118 **1.3 Meteorological Data**

119 Daily wind directions on Bohai Strait from May to October 2003-2014 were
120 obtained from China Meteorological Data Sharing Service System
121 (<http://cdc.cma.gov.cn/>).

122 **1.4 Data Analysis**

123 Dates of trap catches reported in this paper indicate the period from sunset of that
124 day to sunrise of the next day. Differences in the number of *H. viriplaca* captured in
125 the searchlight trap, the monthly mean proportion of females, mated females, and
126 sexually mature females (the proportion data were arcsine square root transformed),
127 were analyzed by using generalized linear mixed models (GLMMS), with month as

128 the fixed effect and year as the random effect (Chaves, 2010; Tang, 2010; Tang &
129 Zhang, 2013). If the ANOVA indicated a significant difference between months,
130 Tukey's HSD (honestly significant difference) test was employed to distinguish
131 significantly different monthly means. Sex ratio (females: males = 1:1) in each month
132 from 2009 to 2014 was compared using chi-square tests. Differences of the mean
133 proportion between mated and unmated females, sexually mature and immature
134 females, were compared by using *t*-test (the proportion data were arcsine square root
135 transformed). In order to distinguish mass or weak invasion years, the annual total
136 catches of *H. viriplaca* were analyzed by hierarchical cluster analysis (clustering
137 distance: Euclidean distance; clustering method: nearest-neighbor method) (Zhang et
138 al., 2015). All statistical analysis was performed by SPSS software (SPSS, 1989),
139 except for the sex ratio which was analyzed by SAS software (SAS Institute, 1990).

140

141 **2. Results**

142 **2.1 Annual and Seasonal Pattern of Migration**

143 During the study period of 2003-2014, no *H. viriplaca* larvae were found on BH
144 by field investigations although some graminaceous weeds were available as potential
145 wild host plants. However, *H. viriplaca* moths were regularly captured in the
146 searchlight trap, which strongly suggests that these moths immigrate from the
147 mainland rather than emerging locally, and that they migrated at least 40-60 km (and
148 probably much greater distances) to reach the trapping site across the Bohai Strait.
149 The strength of this over-sea migration did not differ significantly across years ($F_{11,}$
150 $_{1836} = 1.78, p = 0.052$; Table 2), but month \times year interaction ($F_{55, 1836} = 1.75, p <$
151 0.001 ; Table 2) was significant. The results of the hierarchical cluster analysis
152 indicated that the annual total trap catches could be divided into three groups – 2005,
153 2008, and the other ten years clustered together (Table 3). Specifically, mass
154 migrations occurred in 2005 and 2008 (with the annual total catches reaching 1,363
155 and 1,144 individuals, respectively), while weak migrations occurred in the other
156 years (with the annual total catches of *H. viriplaca* ranging between 40 and 250

157 individuals; Fig. 2).

158 The number of *H. viriplaca* captured in the searchlight trap was not significantly
159 different across months ($F_{5, 1836} = 1.21, p = 0.317$; Table 2 and Fig. 3), but month \times
160 year interaction ($F_{55, 1836} = 1.75, p < 0.001$; Table 2) was significant. Throughout the
161 early summer (May to July), southerly winds (ESE to WSW, $65.4 \pm 1.6\%$) were the
162 prevailing airstream over the Bohai Strait (Fig. 4), and the mean proportion of *H.*
163 *viriplaca* trapped in this period was $39.83 \pm 7.48\%$. In contrast, throughout the late
164 summer and the autumn (August to October), northerly winds (WNW to ENE, $51.0 \pm$
165 2.2%) became the prevailing airstream (Fig. 4), and the mean proportion of *H.*
166 *viriplaca* trapped in this period reached to $60.2 \pm 7.5\%$.

167 The mean period when over-sea migration was detectable on the island was 116.5
168 ± 5.6 days (ranged from 74 to 144 d) during 2003-2014, with the earliest and latest
169 trapping occurred on 1st May and 4th October 2005, respectively (Table 4).

170 2.2 Sex Ratio, Mating Frequency, and Ovarian Development

171 From May to September 2009-2014, the vast majority of trapped *H. viriplaca*
172 were females (Fig. 5A), and the proportion of trapped females was significantly
173 greater than that of males in each month (chi-square tests: May: $60.1 \pm 6.8\%$, $\chi^2 =$
174 $11.76, df = 1, p < 0.01$; June: $57.9 \pm 3.8\%$, $\chi^2 = 13.13, df = 1, p < 0.01$; July: $66.8 \pm$
175 1.1% , $\chi^2 = 32.76, df = 1, p < 0.01$; August: $66.7 \pm 2.37\%$, $\chi^2 = 34.57, df = 1, p < 0.01$;
176 September: $62.2 \pm 1.75\%$, $\chi^2 = 21.62, df = 1, p < 0.01$) (Fig. 5B). The monthly mean
177 proportion of *H. viriplaca* females captured in the searchlight trap did not differ
178 significantly across months ($F_{4, 141} = 0.44, p = 0.780$; Table 5) or years ($F_{5, 141} = 0.80,$
179 $p = 0.550$; Table 5), and there was no significant month \times year interaction ($F_{17, 141} =$
180 $1.55, p = 0.085$; Table 5) during 2009-2014 (Fig. 5B).

181 In May and June, most of the trapped *H. viriplaca* females were mated
182 individuals (May: $90.3 \pm 4.0\%$, $t = 5.19, df = 6, p < 0.01$; June: $76.2 \pm 6.4\%$, $t =$
183 $2.59, df = 8, p < 0.01$). There was no significant difference between the proportion of
184 mated ($45.3 \pm 4.1\%$) and unmated ($54.71 \pm 4.1\%$) females in July ($t = 0.71; df = 8; p$
185 $= 0.50$). However, in August and September, the majority of the trapped *H. viriplaca*
186 females was unmated individuals (August: $90.4 \pm 1.5\%$, $t = 9.49, df = 10, p < 0.01$;

187 September: $93.1 \pm 1.0\%$, $t = 10.61$, $df = 10$, $p < 0.01$). The monthly mean proportion
188 of mated females was not significantly different across months ($F_{4, 141} = 0.01$, $p =$
189 0.999 ; Table 6) or years ($F_{5, 141} = 1.32$, $p = 0.261$; Table 6), but month \times year
190 interaction ($F_{17, 141} = 2.18$, $p = 0.007$; Table 6) was significant. Overall, the seasonal
191 variation in the mean proportion of mated females showed a significant downward
192 trend from May to September (logistic regression model: $y =$
193 $96.18/(1+6.01E-05*e^{1.41})$, $R^2 = 0.94$, $n = 5$, $F = 33.02$, $p = 0.03$) (Fig. 5D). The
194 majority ($65.1 \pm 6.7\%$) of the mated females had mated once, about a third ($33.5 \pm$
195 6.6%) had mated twice, only a small proportion ($1.4 \pm 0.8\%$) had mated three times,
196 and no individuals mated more than this (Fig. 6).

197 In May and June, the vast majority of the trapped *H. viriplaca* females were
198 sexually mature individuals (May: $77.4 \pm 7.5\%$, $t = 2.52$, $df = 6$, $p = 0.04$; June: $85.8 \pm$
199 3.2% , $t = 4.90$, $df = 8$, $p < 0.01$). There was no significant difference between the
200 proportion of sexually mature ($53.2 \pm 3.8\%$) and immature ($56.8 \pm 3.8\%$) females in
201 July ($t = 0.55$; $df = 8$; $p = 0.60$). However, in August and September, most of the
202 trapped *H. viriplaca* females was sexually immature individuals (August: $77.3 \pm 2.5\%$,
203 $t = 6.14$, $df = 10$, $p < 0.01$; September: $86.6 \pm 1.8\%$, $t = 6.45$, $df = 10$, $p < 0.01$). The
204 monthly mean proportion of sexually mature females was not significantly different
205 across months ($F_{4, 141} = 0.04$, $p = 0.996$; Table 7) or years ($F_{5, 141} = 1.60$, $p = 0.165$;
206 Table 7), but month \times year interaction ($F_{17, 141} = 2.61$, $p = 0.001$; Table 7) was
207 significant. Overall, the seasonal variation on the mean proportion of sexually mature
208 females showed a significant downward trend (logistic regression model: $y =$
209 $170.43/(1+0.032*e^{0.65})$, $n = 5$, $F = 173.56$, $p < 0.01$, $R^2 = 0.99$) from May to September
210 2009-2014 (Fig. 5F).

211

212 4 Discussion

213 Migratory insects have been studied for many years because of their economic and
214 ecological importance, and a better understanding of the migration behavior of crop
215 pests is essential for the development of forecasting systems and sustainable IPM

216 strategies (Irwin 1999, Wu & Guo 2005, Wu *et al.* 2006). *H. virescens* is one of the
217 most destructive crop pests in East Asia, and there has been a long debate about
218 whether this species is a migrant or not (Wu *et al.*, 1998). In the present long-term
219 study, the results from the combination of searchlight trapping, field investigations
220 and ovarian dissection on BH Island provide direct evidence that *H. virescens* is a
221 long-distance migrant. The seasonal population dynamics of this species observed in
222 this study was similar to previous observations for other migratory insects in the
223 orders of Lepidoptera, Odonata and Coleoptera made over the sea (Feng *et al.*, 2003,
224 2004a, b, 2005, 2006, 2008, 2009; Wu *et al.*, 1998, 2006).

225 The East Asian monsoon airflows in temperate regions provide an advantageous
226 carrier for long-distance insect migration (Drake & Farrow, 1988). In the semi-arid
227 temperate climate zone (Liaoning province, which is located to the north of BH), the
228 average of daily minimum temperature in April is generally <6°C. Given the low
229 temperature, *H. virescens* moths cannot overwinter or produce a new generation in
230 spring (Kahrarian *et al.*, 2012). In the current study, *H. virescens* moths could be
231 captured on BH island as early as May, and considering the prevailing southerly
232 winds during this season, these individuals should be coming from the mainland in
233 south of BH by windborne migration, in order to exploit temporary habitats in
234 northeastern agricultural regions of China, while the spring maize and soybean widely
235 planted there plays an important role in the survival of *H. virescens* larvae. Similar
236 wind-related migration has been observed in *Helicoverpa armigera* (Hübner),
237 *Spodoptera exigua* Hübner, *Mythimna separata* (Walker), and *Loxostege sticticalis* L.
238 at the same site (Feng *et al.*, 2004a, b, 2005, 2008, 2009).

239 In autumn (August to October), prevailing northerly winds, caused by the
240 prevailing temperature gradient, blowing from east Siberia to northern China, and the
241 updraft airflows that generally occur in the northeastern agricultural region of China,
242 promote large number of offspring produced by summer breeders emigrating to the
243 south. Characteristics of the backward migration observed in the present study were
244 rather similar to those windborne migrations of *Empoasca fabae* (Harris) (Taylor &
245 Relling, 1986), *Nilaparvata lugens* (Stål) (Riley *et al.*, 1994), *Cnaphalocrocis*

246 *medinalis* Guenée (Riley *et al.*, 1995), *Agrotis ipsilon* (Rottemberg) (Shower, 1997),
247 *Vanessa atalanta* (L.) (Mikkola, 2003), *M. separata* (Feng *et al.*, 2008), *H. armigera*
248 (Feng *et al.*, 2009), and *Autographa gamma* (L.) (Chapman *et al.*, 2012), and it has
249 been postulated that this behavior facilitated return movements to the southern
250 overwintering areas of these species. Understanding the seasonal migration pattern of
251 *H. virescens* is also of economic importance, as this species becomes a major pest in
252 many Asian crop fields during outbreak years. Just how representative *H. virescens* is
253 of other migrant insects is a matter for further study, but given the similarities in the
254 migration strategies of *H. virescens* to those of other insects in Asia, it is very likely
255 that the results of this study will be applicable to a wide range of migrants.

256 The monthly mean proportion of mated females and that of sexually mature
257 females showed a significant downward trend from May to September 2009-2014.
258 Trapped females in May and June showed a relatively higher mating rates and some
259 degree of ovarian development when compared with July, August, and September,
260 which might be due to these moths emigrating from sites far away from the trapping
261 site and therefore having several successive nights of migration. This trend was
262 similar to previous observations in *M. separata* (Zhao *et al.*, 2009), *Athetis lepigone*
263 (Fu *et al.*, 2014), *S. litura* (Fu *et al.*, 2015), *A. ipsilon* (Liu *et al.*, 2015), *Agrotis*
264 *segetum* (Guo *et al.*, 2015), *Mamestra brassicae* (Wu *et al.*, 2015) and *Ctenoplia*
265 *agnata* (Li *et al.*, 2015) at the same site. However, the majority of the trapped *H.*
266 *virescens* females from August to September have little or no ovarian development,
267 supporting the idea that the onset of migration is initiated by sexually immature
268 individuals (Riley *et al.*, 1995). The relationship between long-duration flight and the
269 state of oogenesis appears to be similar to that of *A. ipsilon* in North America
270 (Showers 1997). Here the northward-moving spring migrants developed
271 reproductively, and it was suggested that there was no need to shut down reproductive
272 development because the movement takes place rapidly, aided by the low-level jet
273 stream. The southward movement in autumn is generally much slower (8–15 nights)
274 due to the slow-speed winds, and in this case the moths may enter reproductive
275 diapause (Showers 1997).

276 The current study provides direct evidence that *H. viriplaca* can migrate across the
277 Bohai Strait, thus the hypothesis that *H. viriplaca* is a long-distance migrant is
278 confirmed. These findings will contribute to a better understanding of the occurrence
279 of this species in northern China, and also to make managing this pest more efficient.
280 However, further study is needed to characterize the population dynamics of *H.*
281 *viriplaca* on the Chinese mainland. In addition, migration behavior in high-altitude
282 and trajectory analysis would be beneficial to determine the seasonal pathway of this
283 pest.

284

285 **Acknowledgments**

286 The authors thank Jianglong Guo, Xiao Wu, Hong Chang, and Limei He from
287 Institute of Plant Protection, Chinese Academy of Agricultural Sciences; Ning Liu,
288 HaoHao Li from College of Plant Protection, Henan Agricultural University; and
289 Congzheng Yuan, Shengyuan Zhao from College of Agronomy and Plant Protection,
290 Qingdao Agricultural University, for their contributions in field investigation. This
291 research was supported by Special Fund for Agro-scientific Research in the Public
292 Interest of China (grant number 201403031).

293

294 **References**

- 295 **Chapman, J.W., Bell, J.R., Burgin, L.E., Reynolds, D.R., Pettersson, L.B., Hill,**
296 **J.K., Bonsall, M.B. & Thomas, J.A.** (2012) Seasonal migration to high latitudes
297 results in major reproductive benefits in an insect. *Proceedings of the National*
298 *Academy of Sciences* **109**, 14924-14929.
- 299 **Chapman, J.W., Drake, V.A. & Reynolds, D.R.** (2011) Recent insights from radar
300 studies of insect flight. *Annual Review of Entomology* **56**, 337-356.
- 301 **Chapman, J.W., Reynolds, D.R. & Wilson, K.** (2015) Long-range seasonal
302 migration in insects: mechanisms, evolutionary driver and ecological
303 consequences. *Ecology Letters* **18**, 287-302.
- 304 **Chaves, L.F.** (2010) An entomologist guide to demystify pseudoreplication: data
305 analysis of field studies with design constraints. *Journal of Medical Entomology*
306 **47**, 291-298.
- 307 **Cui, Z.-L., Gai, Y.-J., Ji, D.-F. & Ren, Z.-J.** (1997) A study on leaf-feeding insect
308 species on soybeans in Nanjing area. *Soybean Science* **16**, 12-20.
- 309 **Dingle, H. & Drake, V.A.** (2007) What is migration? *BioScience* **57**, 113-121.
- 310 **Dingle, H.** (2014). *Migration: the biology of life on the move* (2nd end.). New York,
311 Oxford University Press, 352pp.
- 312 **Drake, V.A. & Farrow, R.A.** (1988) The influence of atmospheric structure and
313 motions on insect migration. *Annual Review of Entomology* **33**, 183-210.
- 314 **Feng, H.-Q., Wu, K.-M. Cheng, D.-F. & Guo, Y.-Y.** (2003) Radar observations of
315 the autumn migration of the beet armyworm *Spodoptera exigua* (Lepidoptera:

316 Noctuidae) and other moths in northern China. *Bulletin of Entomological*
317 *Research* **93**, 115-124.

318 **Feng, H.-Q., Wu, K.-M. Cheng, D.-F. & Guo, Y.-Y.** (2004a) Northward migration of
319 *Helicoverpa armigera* (Lepidoptera: Noctuidae) and other moths in early
320 summer observed with radar in northern China. *Journal of Economic*
321 *Entomology* **97**, 1874-1883.

322 **Feng, H.-Q., Wu, K.-M. Cheng, D.-F. & Guo, Y.-Y.** (2004b) Spring migration and
323 summer dispersal of *Loxostege sticticalis* (Lepidoptera: Pyralidae) and other
324 insects observed with radar in northern China. *Environmental Entomology* **33**,
325 1253-1265.

326 **Feng, H.-Q., Wu, K.-M. Ni, Y.-X. Cheng, D.-F. & Guo, Y.-Y.** (2005) High-altitude
327 windborne transport of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in
328 mid-summer in northern China. *Journal of Insect Behavior* **18**, 335-349.

329 **Feng, H.-Q., Wu, K.-M., Ni, Y.-X., Cheng, D.-F. & Guo, Y.-Y.** (2006) Nocturnal
330 migration of dragonflies over the Bohai Sea in northern China. *Ecological*
331 *Entomology* **31**, 511-520.

332 **Feng, H.-Q., Wu, X.-F., Wu, B. & Wu, K.-M.** (2009) Seasonal migration of
333 *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai Sea. *Journal of*
334 *Economic Entomology* **102**, 95-104.

335 **Feng, H.-Q., Zhao, X.-C., Wu, X.-F., Wu, B. & Wu, K.-M.** (2008) Autumn
336 migration of *Mythimna separate* (Lepidoptera: Noctuidae) over the Bohai Sea in
337 Northern China. *Environmental Entomology* **37**, 774-781.

- 338 **Fu, X.-W., Liu, Y.-Q., Li, Y.-H., Ali, A. & Wu, K.-M.** (2014) Does *Athetis lepigone*
339 moth (Lepidoptera: Noctuidae) take a long-distance migration? *Journal of*
340 *Economic Entomology* **107**, 995-1002.
- 341 **Fu, X.-W., Zhao, X.-Y., Xie, B.-T., Ali, A. & Wu, K.-M.** (2015) Seasonal pattern of
342 *Spodoptera litura* (Lepidoptera: Noctuidae) migration across the Bohai Strait in
343 northern China. *Journal of Economic Entomology* **108**, 525-538.
- 344 **Guo, J.-L., Fu, X.-W., Wu, X., Zhao, X.-C. & Wu, K.-M.** (2015) Annual migration
345 of *Agrotis segetum* (Lepidoptera: Noctuidae): observed on a small isolated island
346 in northern China. *PloS ONE* **10**, e1031639.
- 347 **He, Z.-C., Zhang, Z.-L., Huang, F., & Jiang Y.-W.** (1997) *A Colored Pictorial*
348 *Handbook of Agricultural Pests in Northern China*. Shenyang, Liaoning Science
349 and Technology Press, 473pp.
- 350 **IBM SPSS Statistics 20 Brief Guide.** (2011) IBM Corporation 1989.
- 351 **Irwin, M.E.** (1999) Implications of movement in developing and deploying
352 integrated pest management strategies. *Agricultural and Forest Meteorology* **97**,
353 235-248.
- 354 **Kahrarian, M., Ebadi, R., Seyedol Eslami, H., & Tohidi, M.T.** (2012) Study on
355 biology and behavior of pod borer *Heliothis virescens* Hüfn. (Lep. Noctuidae)
356 laboratory conditions. *Journal of Entomological Research* **4**, 309-318.
- 357 **Kravchenko, V.D., Orlova, O.B., Fibiger, M., Ronkay, L., Mooser, J., Li, C. &**
358 **Muller, G.C.** (2005) The *Heliothina* of Israel (Lepidoptera: Noctuidae). SHILAP
359 *Revista de Lepidopterologia* **33**, 365-77.

- 360 **Li, C., Fu, X.-W., Feng, H.-Q., Ali, A., Li, C.-R. & Wu, K.-M.** (2014) Seasonal
361 migration of *Ctenopplusia agnata* (Lepidoptera: Noctuidae) over the Bohai Sea in
362 northern China. *Journal of Economic Entomology* **107**, 1003-1008.
- 363 **Liu, H.-G., Zhang, X.-Y., Li, S., Su, S.-X., Wu, X.-G., & Zhang, Y.** (2010) The
364 occurrence rules of *Heliothis virescens* and effective prevention and test in
365 *Scutellaria baicalensis*. *China Plant Protection* **30**, 30-31.
- 366 **Liu, Y.-Q., Fu, X.-W., Feng, H.-Q., Liu, Z.-F. & Wu, K.-M.** (2015) Trans-regional
367 migration of *Agrotis ipsilon* (Lepidoptera: Noctuidae) in north-east Asia. *Annals*
368 *of the Entomological Society of America* **108**, 519-527.
- 369 **Mikkola, K.** (2003) Red admirals *Vanessa atalanta* (Lepidoptera: Nymphalidae)
370 select northern winds on southward migration. *Entomologica Fennica* **14**, 15-24.
- 371 **Mu, W., Liu, F., Zhao, D. & Wu, K.-M.** (2004) The toxicities of 14 kinds of
372 insecticide to *Heliothis virescens*. *Acta Phytopharmacologica Sinica* **31**, 333-334.
- 373 **Riley, J.R., Reynolds, D.R., Smith, A.D., Rosenberg, L.J., Cheng, X.-N., Zhang,**
374 **X.-X., Xu, G.-M., Cheng, J.-Y., Bao, A.-D., Zhai, B.-P., & Wang, H.-K.** (1994)
375 Observations on the autumn migration of *Nilaparvata lugens* (Homoptera:
376 Delphacidae) and other pests in east central China. *Bulletin of Entomological*
377 *Research* **84**, 389-402.
- 378 **Riley, J.R., Reynolds, D.R., Smith, A.D., Edwards, A.S., Zhang, X.-X., Cheng,**
379 **X.-N., Wang, H.-K., Cheng, J.-Y. & Zhai, B.-P.** (1995) Observations of the
380 autumn migration of the rice leaf roller *Cnaphalocrocis medinalis* (Lepidoptera:
381 Pyralidae) and other moths in eastern China. *Bulletin of Entomological Research*

382 **85**, 397-414.

383 **SAS Institute.** (1990) SAS/STAT user's guide. SAS Institute, Cary, NC.

384 **Showers, W.B.** (1997) Migratory ecology of the black cutworm. *Annual Review of*
385 *Entomology* **42**, 393-425.

386 **Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T.,**
387 **Carnicer, J., Cassar, L.F., Fox, R., Heliölä, J., Hill, J.K., Hirneisen, N.,**
388 **Kjellén, N., Kühn, E., Kuussaari, M., Leskinen, M., Liechti, F., Musche, M.,**
389 **Regan, E.C., Reynolds, D.R., Roy, D.B., Ryrholm, N., Schmaljohann, H.,**
390 **Settele, J., Thomas, C.D., Swaay, C., Chapman, J.W.** (2013)
391 Multi-generational long-distance migration of insects: Studying the painted lady
392 butterfly in the western Palearctic. *Ecography* **36**, 474-486.

393 **Tang, Q.-Y.** (2010) *Data Processing System-Experimental Design, Statistical*
394 *Analysis and Data Mining (Second Edition)*. Beijing, Science Press, 1172pp.

395 **Tang, Q.-Y. & Zhang, C.-X.** (2013) Data processing system (DPS) software with
396 experimental design, statistical analysis and data mining developed for use in
397 entomological research. *Insect Science* **20**, 254-260.

398 **Taylor, R.A.J. & Reiling D.** (1986) Preferred wind direction of long distance
399 leafhopper (*Empoasca fabae*) migrants and its relevance to the return migration
400 of small insects. *Journal of Animal Ecology* **55**, 1103-1114.

401 **Weigand, S.** (1996) Chickpea Insect Pests: Distribution, Importance, and
402 Management Strategy in WANA and SAT. International Center for Agricultural
403 Research in the Dry Areas (ICARDA).

404 **Wu, K.-M. & Guo, Y.-Y.** (2005). The evolution of cotton pest management practices
405 in China. *Annual Review of Entomology* **50**, 31-52.

406 **Wu, K.-M., Xu, G. & Guo, Y.-Y.** (1998) Observations on migratory activity of cotton
407 bollworm moths across the Bohai Gulf in China. *Acta Phytophylacica Sinica* **25**,
408 337-340.

409 **Wu, K.-M., Zhai, B.-P., Feng, H.-Q., Cheng, D.-F., & Guo, Y.-Y.** (2006) Radar
410 observations on the migratory behavior of the second generation cotton
411 bollworm moths in the north part of northern China. *Acta Phytophylacica Sinica*
412 **33**, 163-167.

413 **Wu, X., Fu, X.-W., Guo, J.-L., Zhao, X.-C. & Wu, K.-M.** (2015) Annual migration
414 of cabbage moth, *Mamestra brassicae* L. (Lepidoptera: Noctuidae), over the sea
415 in northern China. *PloS ONE* **10**, e1032904.

416 **Zhai, B.-P.** (2004). Computing the day length for programming insect behavior.
417 *Entomological Knowledge*, **41**, 178-184.

418 **Zhang, X.-M., Li, Q., Chen, G.-H., Shi, A.-X. & Song, J.-X.** (2015) Fuzzy
419 clustering analysis of insect community structure in a *Zanthoxylum bungeanum*
420 garden. *Chinese Journal of Applied Entomology*, **52**, 237-248.

421 **Zhang, X.-X., Lu, Z.-Q. & Geng, J.-G.** (1979) Application of ovarian dissection of
422 female *Cnaphalocrocis medinalis* moths in prediction and forecasting system.
423 *Entomological Knowledge* **16**, 97-99.

424 **Zhao, X.-C., Feng, H.-Q., Wu, B., Wu, X.-F., Liu, Z.-F., Wu, K.-M., & McNeil,**
425 **J.N.** (2009). Does the onset of sexual maturation terminate the expression of

426 migratory behavior in moths? A study of the oriental armyworm, *Mythimna*
427 *separata*. *Journal of Insect Physiology* **55**, 1039-1043.

428

429 **Figure legends**

430 **Figure 1.** Maps showing the position of Beihuang (BH) Island, the searchlight
431 trapping site, relative to the Bohai and Yellow Sea.

432

433 **Figure 2.** Annual number of *H. viriplaca* captured in the searchlight trap on BH from
434 2003 to 2014.

435

436 **Figure 3.** Nightly catch (A) and annually mean number (B) of *H. viriplaca* in the
437 searchlight trap on BH from April to October during 2003 to 2014.

438

439 **Figure 4.** Frequency distribution of wind direction on BH during 2003-2014.
440 Concentric circles indicate the frequency of wind direction, and each circle
441 means difference value of 4% in May, 7% in June, 8% in July, 6% in August,
442 4% in September, and 3% in October.

443

444 **Figure 5.** Proportion of females (A-B), mated females (C-D) and sexually mature
445 females (E-F) of *H. viriplaca* captured in the searchlight trap from May to
446 September 2009-2014. The histograms in A and C indicate the mean
447 proportion in each month. The histograms in E indicate the mean ovarian
448 development level in each month. Vertical bars in A, C, and E, represent
449 standard errors between days in that month. Dots in B, D, and F indicate the
450 monthly mean proportion from 2009 to 2014. Vertical bars in B, D, and F

451 represent standard errors between years in that month. Single asterisk (*)
452 above a bar in B indicates the sex ratio (female: male) was greater than 1:1
453 in that month at the 5% level of significance as determined by chi-squared
454 test. Single asterisk (*) above a bar in D and F, indicates there was
455 significant difference between the monthly mean proportion of mated and
456 unmated females, and that of sexually mature and immature females at the 5%
457 level of significance as determined by *t*-test in D and F.

458

459 **Figure 6.** Proportion of mating occurrences of *H. viriplaca* females captured in the
460 searchlight trap on BH from May to September 2009-2014.

461

462

463 **Tables**

464

465 **Table 1. Criteria of ovarian development level of *H. viriplaca* moths.**

Development level	Characteristics of ovary
1	Undeveloped thin and short oviducts, with transparent and light milky white ovary
2	Developed longer oviducts and ovarioles, with developing oocytes but no mature eggs
3	Well-developed yellowish green ovary with 1-3 chorionated eggs stored in the egg calyx
4	Well-developed the biggest oviducts, some eggs have been laid and interspaces appeared among mature eggs
5	The ovary has atrophied and contains no eggs

466

467 **Table 2. Two-way ANOVA analysis on the number of *H. viriplaca* captured in the searchlight**
 468 **trap on BH from May to October 2003-2014.**

Source	Type III sum of squares	df	Mean squares	F-values	P
Month	5560.80	5	1112.1605	1.21	0.317
Year	10315.71	11	937.79	1.78	0.052
Month × Year	50573.04	55	919.51	1.75	<0.001
Error	964810.97	1836	525.50		
Total	1036388.81	1907			

469

470 **Table 3. Hierarchical clustering analysis on the annual total numbers of *H. viriplaca***
 471 **captured in the searchlight trap on BH from May to October 2003-2014.**

Group	Year	Observed value	Distance to the center	Group mean	SD
First group	2003	120	9	129.0	38.8
	2004	165	36		
	2006	250	121		
	2007	54	75		
	2009	163	34		
	2010	92	37		
	2011	193	64		
	2012	41	88		
	2013	148	19		
	2014	64	65		

Second group	2008	1144	0	1144.0	--
Third group	2005	1363	0	1363.0	--
R ²	0.98				
Pseudo_F	236.28				
<i>p</i>	< 0.001				

472

473 **Table 4. Duration and peak catches of *H. viriplaca* moths caught in the searchlight trap on**

474 **BH from May to October 2003-2014.**

Year	Date of first capture (no.)	Date of final capture (no.)	Duration (d)	Date of peak catches (no.)
2003	29 May (2)	17 Sep. (1)	112	25 Aug. (52)
2004	26 Jun. (4)	19 Sep. (15)	86	09 Sep. (81)
2005	01 May (1)	04 Oct. (1)	144	29 Jul. (880)
2006	27 May (1)	29 Sep. (1)	126	24 Aug. (40)
2007	21 May (2)	13 Sep. (1)	116	10 Sep. (11)
2008	30 May (3)	19 Sep. (1)	113	03 Aug. (380)
2009	13 May (1)	15 Sep. (1)	126	01 Jun. (40)
2010	08 May (1)	13 Sep. (2)	129	15 Jul. and 02 Sep. (11)
2011	18 May (1)	09 Sep. (1)	116	02 Sep. (58)
2012	04 May (3)	13 Sep. (1)	133	20 Aug. (11)
2013	17 Jul. (1)	29 Sep. (1)	74	26 Jul. (42)
2014	22 May (1)	21 Sep. (2)	123	06 Aug. and 16 Sep. (8)

475

476 **Table 5. Two-way ANOVA analysis on the monthly mean proportion of *H. viriplaca* females**

477 **captured in the searchlight trap on BH from May to September 2009-2014 (the proportions**

478 **were arcsine square root transformed).**

Source	Type III sum of squares	<i>df</i>	Mean squares	<i>F</i> values	<i>P</i>
Month	12.70	4	3.18	0.44	0.7797
Year	18.74	5	3.75	0.80	0.5502
Month×Year	123.38	17	7.26	1.55	0.0853
Error	659.32	141	4.68		
Total	802.11	167			

479

480 **Table 6. Two-way ANOVA analysis on the monthly mean proportion of mated *H. viriplaca***

481 females captured in the searchlight trap on BH from May to October 2009-2014 (the
 482 proportions were arcsine square root transformed).

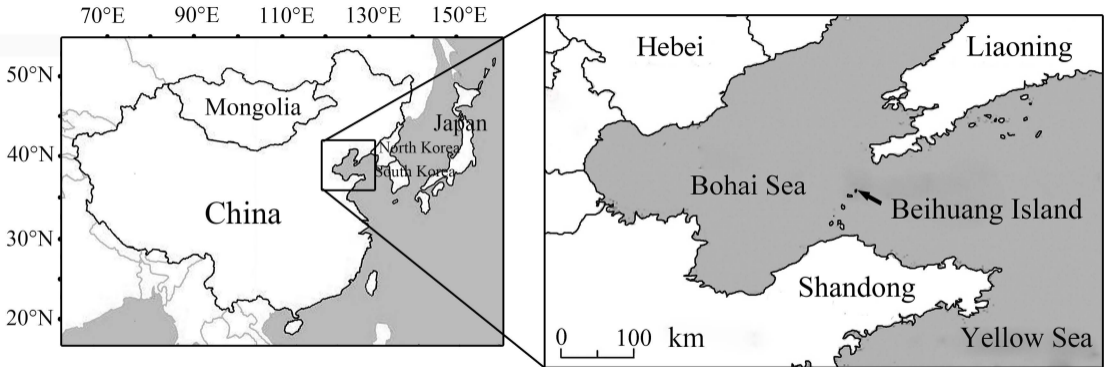
Source	Type III sum of squares	<i>df</i>	Mean squares	<i>F</i> values	<i>P</i>
Month	0.26	4	0.07	0.01	0.9998
Year	19.53	5	3.91	1.32	0.2605
Month × Year	109.72	17	6.45	2.18	0.0072
Error	418.29	141	2.97		
Total	761.20	167			

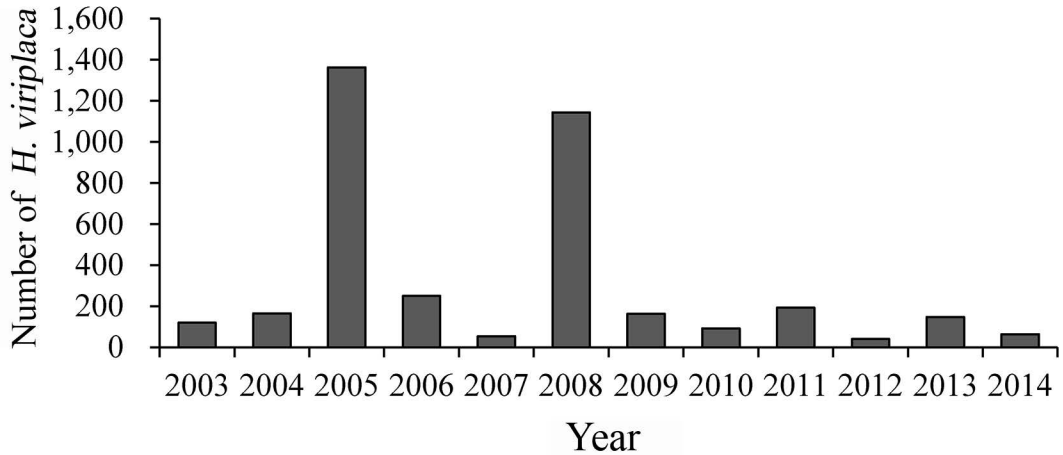
483

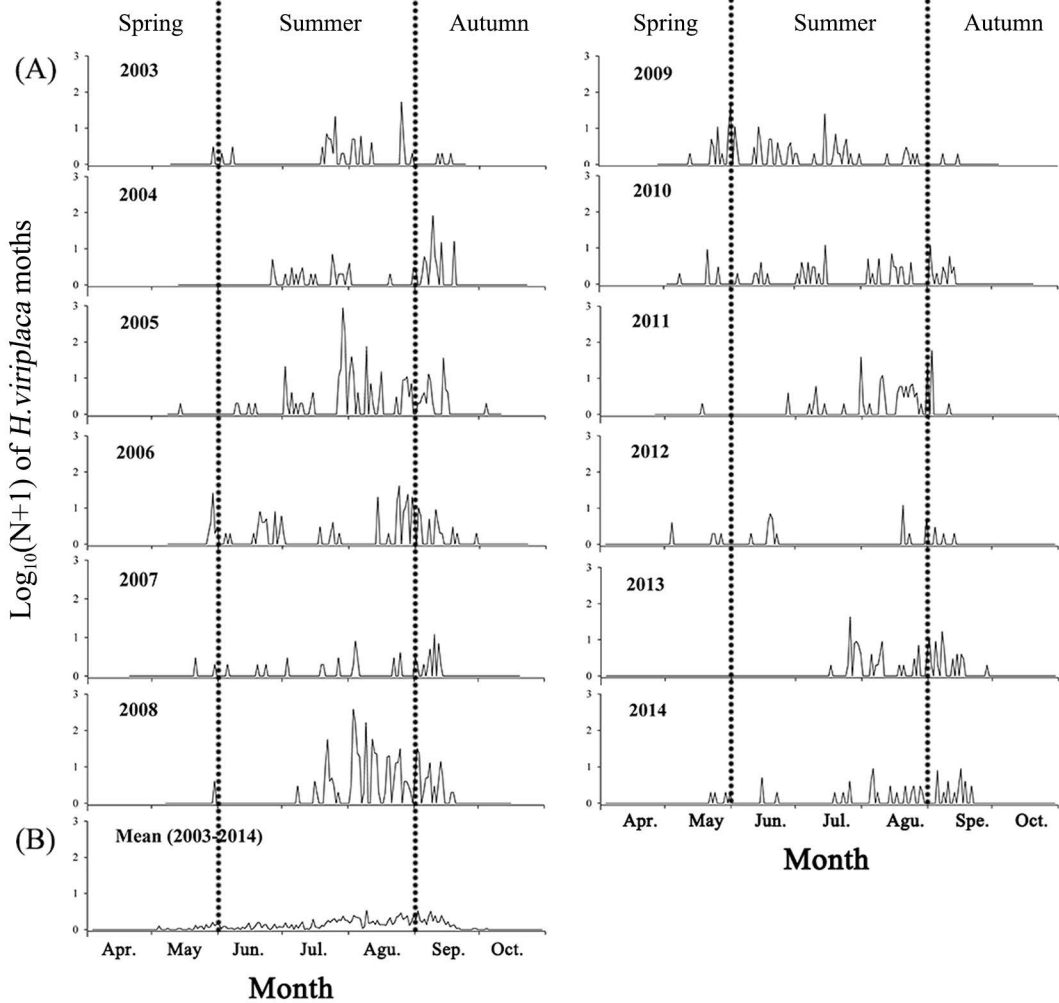
484 Table 7. Two-way ANOVA analysis on the monthly mean proportion of sexually mature *H.*
 485 *viriplaca* females captured in the searchlight trap on BH from May to October 2009-2014
 486 (the proportions were arcsine square root transformed).

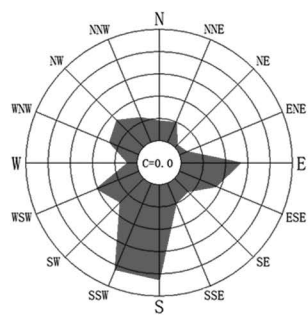
Source	Type III sum of squares	<i>df</i>	Mean squares	<i>F</i> values	<i>P</i>
Month	1.27	4	0.32	0.04	0.9963
Year	23.09	5	4.62	1.60	0.1651
Month × Year	128.39	17	7.55	2.61	0.0011
Error	408.07	141	2.89		
Total	731.87	167			

487

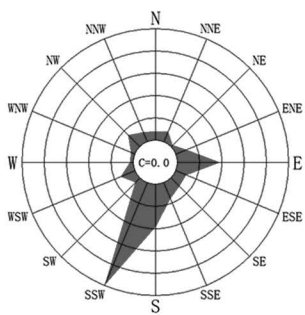




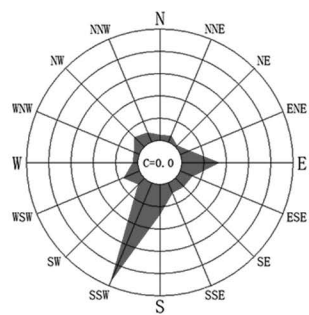




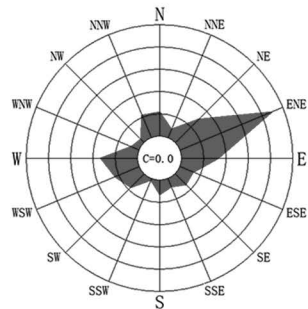
May



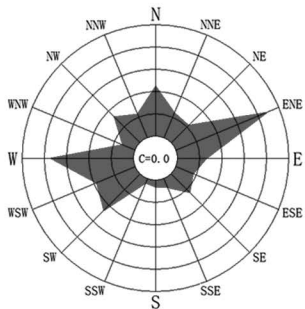
June



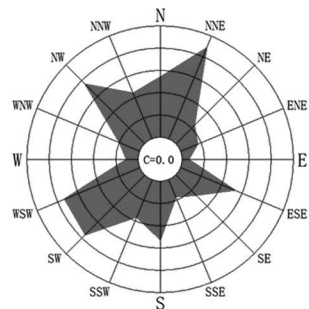
July



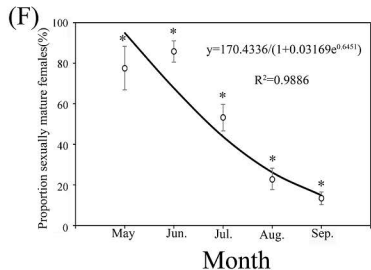
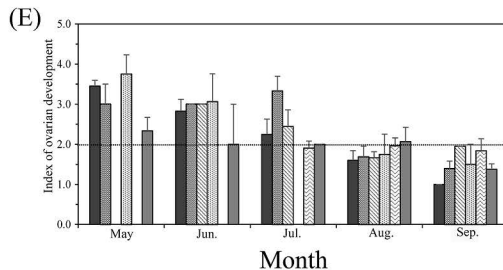
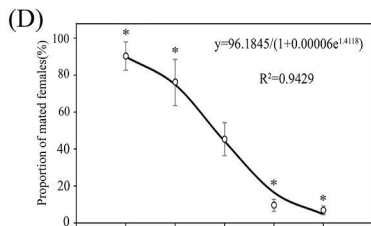
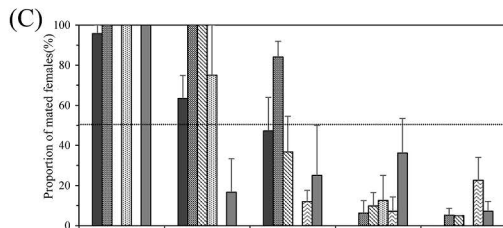
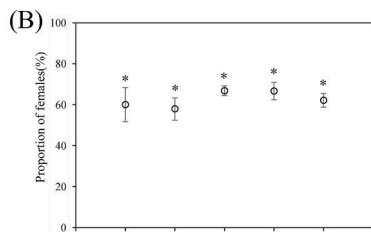
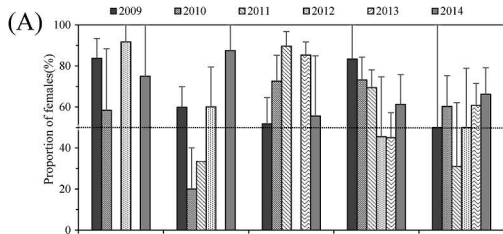
August



September



October



Proportion of mating occurrences(%)

