Oecanthus nigricornis (Orthoptera: Gryllidae) as the first known host of *Stylogaster neglecta* (Diptera: Conopidae)

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1   **Abstract**

2   The conopid fly *Stylogaster neglecta* Williston (Diptera: Conopidae) is a parasitoid with no

3   known host. We report this species as the first recorded dipteran parasitoid of *Oecanthus*

4   *nigricornis* Walker (Orthoptera: Gryllidae) (blackhorned tree crickets)*.* We reared field-collected

5   *O. nigricornis* juveniles over several months in 2017 and found that larval *S. neglecta* emerged

6   from them during late July into August. We estimated the incubation period for *S. neglecta*

7   larvae to be around 30 days based on the length of time it took for them to emerge from the host

8   and pupate (subsequently all hosts died). We documented several cases of multiple parasitism. In

9   2018, we dissected *O. nigricornis* sampled from four sites across southern Ontario, Canada and

10   upstate New York, United States of America and found that the percentage of juvenile *O.*

11   *nigricornis* parasitised ranged from 2–39%. Further sampling will be necessary to determine

12   whether this variation represents consistent population differences or between year variation in

13   parasitism.

Introduction

15   Conopidae (Diptera) larvae are obligate endoparasitoids (Gibson and Skevington 2013;

16   Gibson *et al*. 2013). *Stylogaster* Macquart (Diptera: Conopidae) is the sister group to other

17   conopids (Gibson and Skevington 2013; Marshall 2012). *Stylogaster* species target nymphs and

18   adult Gryllidae (Orthoptera) and Blattodea, whereas other conopid genera use adult aculeate

19   Hymenoptera (Freeman 1966; Kotrba 1997; Woodley and Judd 1998; Schmid-Hempel 2001;

20   Rasmussen and Cameron 2004; Marshall 2012; Gibson *et al*. 2013). *Stylogaster* eggs have been

21   found on other species, such as other Diptera, but the lack of egg development indicates that

22   these may be accidental ovipositions (Couri *et al*. 2019; Couri and Barros 2010; Stuke 2012).

23   *Stylogaster* species have been studied mainly in Africa and the Neotropics and are

24   associated with army ants (Hymenoptera: Formicidae), using hosts that have been flushed out by

25   the ants (Lopes 1937; Rettenmyer 1961; Burt *et al*. 2015). The flies are thought to either stab

26   their ovipositors into the abdomen of the host and insert the egg under a sclerite, or shoot the egg

27   from the ovipositor via a flipping motion of the abdomen (Kotrba 1997; Woodley and Judd

28   1998). While most studies have focussed on tropical species, *Stylogaster neglecta, S. biannulata*

29   (Say), and *S. beresfordi* Burt are found in the Nearctic region (including Canada), typically in

30   forest understoreys where adults feed on yellow/white flowers (Burt *et al*. 2015). Only *S.*

31   *biannulata* has a recorded host, *Gryllus rubens* Scudder (Orthoptera: Gryllidae) (Woodley and

32   Judd 1998). While incubation times were not examined, Woodley and Judd (1998) found that in

33   the few cases were adult flies emerged, it was 19–25 days after the puparia were formed. Little is

34   known of the life history of *Stylogaster*. *Sicus* Latreille, and *Physocephala* Schiner (Diptera:

35   Conopidae), which parasitise *Bombus* Latreille (Hymenoptera: Apidae) in Europe, North

36   America, and Japan, oviposit during periods of host reproduction (Schmid-Hempel 2001) from

37 July until mid-September (Macfarlane *et al*. 1995). They kill their hosts within 10–12 days of

38 oviposition. Hosts are induced to burrow into the ground and the fly pupates inside the dead host

39 (Schmid-Hempel 2001).

40   In old fields at the University of Toronto at Mississauga in August 1996, one of us

41 (W.B.) first found *Stylogaster neglecta* larvae (identified by Jeff Skevington, Canadian National

42 Collection of Arthropods, Arachnids, and Nematodes, Ottawa, Ontario, Canada) emerging from

43 juvenile *Oecanthus nigricornis* Walker (Orthoptera: Gryllidae) (blackhorned tree crickets),

44 pupating and then eclosing. The larvae emerged and pupated between late August and mid

45 September, with adults eclosing from late November to early January (L.F.B., unpublished data).

46 *Oecanthus nigricornis* are found across eastern North America, hatching around mid June and

47 reaching maturity in August. Eggs are laid in August and September and hatch the following

48 June (Fulton 1915; Vickery and Kevan 1985). *Oecanthus* are parasitised by several

49 hymenopteran egg parasitoids (Smith 1930a, 1930b; Udine and Pinckney 1940) and some

50 helminths (Denner 1968; Sonin 1990). However, there are currently no known dipteran

51 parasitoids of the genus, despite other Orthoptera (including gryllids) commonly being

52 parasitised by Sarcophagidae (Diptera) and Tachinidae (Diptera). This includes the well-known

53 genus *Ormia* Robineau-Desvoidy, which is attracted to songs of male gryllid hosts (Rees 1973;

54 Cade 1975; Lehmann 2003). Our observations are the first case to our knowledge of *Oecanthus*

55 juveniles or adults as hosts for a dipteran parasitoid and the first report of a host for *S. neglecta.*

56   We collected further *O. nigricornis* samples at University of Toronto at Mississauga

57 (Ontario, Canada) in the summer of 2017 and 2018 and identified emerging adults as *S. neglecta*

58 using Burt *et al*. (2015). In 2017, *O. nigricornis* were collected from natural populations at

59   discrete time intervals to determine when in the season conopid parasitism occurs. In 2018, *O.*

60   *nigricornis* were sampled from several sites to determine population level variation in parasitism.

61

62   **Methods**

63   **Natural history of *Stylogaster neglecta***

64   In 2017 we sampled *O. nigricornis* approximately every two weeks from 28 June until 13

65   September (Fig. 1, Table 1–2) from old fields at the University of Toronto, Mississauga Campus

66   (43.55°N, 79.66°W) (total = 131 *O. nigricornis*). The start date was chosen as the first day in

67   which were successfully able to sample *O. nigricornis* from the site. The end date was chosen as

68   the first sample in which we no longer found any *S. neglecta* larva emerging from the sampled

69   *O. nigricornis*. We reared *O. nigricornis* individually in open-ended plastic cylinders, 8 cm in

70   diameter and 7.5 cm long, with metal mesh covering the ends, at 25 ºC and 70% humidity.

71   *Oecanthus nigricornis* were fed pollen and dry dog food and containers were sprayed with water

72   every second day. We recorded the date on which *O. nigricornis* were caught, when they died,

73   and whether a parasitoid emerged. *S. neglecta* pupae found in the containers were removed and

74   placed in a petri dish on filter paper and sprayed with water daily. Chi-squared tests were used to

75   determine if there were significant differences in the proportion of *O. nigricornis* parasitised on

76   different sampling dates. Confidence intervals were calculated using the Clopper-Pearson

77   method. Cases of multiple conopid parasitism of a single host were also recorded.

78   To examine whether *S. neglecta* was actively laying eggs the entire summer or during a

79   shorter period of time, an analysis of variance was performed to determine if the length of time

80   between when we collected the host and parasitoid emergence differed between collection dates.

81   If *S. neglecta* oviposits on hosts throughout the summer, then larvae in the sampled *O.*

82   *nigricornis* should be at different stages of development and there will be no correlation between

83   date of sampling and length of time from host capture until parasitoid emergence. If however, *S.*

84   *neglecta* females oviposited roughly concurrently, then we expect *O. nigricornis* sampled on the

85   same date would have parasitoids that emerge after similar lengths of time, and that the length of

86   time between when the host *O. nigricornis* was sampled and the parasitoid emerging will be

87   longer earlier in the summer and shorten as the season progresses. Specimens were deposited at

88   the Royal Ontario Museum (Toronto, Ontario, Canada).

89

90   **Site differences in parasitism**

91   In late July 2018, we collected *O. nigricornis* in southern Ontario (Canada) and New

92   York State (United States of America): from the Koffler Scientific Reserve (King City Ontario,

93   44.03°N, 79.53°W), *rare* Charitable Research Reserve (referred to as *rare*) (Cambridge Ontario,

94   43.38°N, 80.39°W), our University of Toronto at Mississauga site previously sampled in 2017,

95   and the Edmund Niles Huyck Preserve and Biological Research Station (referred to as Huyck)

96   (Rensselaerville New York, 42.10°N, 74.10°W). Late July was chosen based on the results from

97   the 2017 study, which indicated that this was the peak of *S. neglecta* oviposition activity. For

98   each site, two to four old fields within a 1-km radius of each other were sampled by sweep

99   netting. *Oecanthus nigricornis* caught ranged from third to fifth instar. *Oecanthus nigricornis*

100 were frozen and then preserved in 70% ethanol before being dissected and their abdomens

101 examined using a Wild M5A dissecting microscope (Wetzlar, Hesse, Germany). They were

102   scored as parasitised if *S. neglecta* eggs or larvae were found (Fig. 2). A chi-squared test was

103   performed to determine if there were significant differences in the proportion of infected *O.*

104   *nigricornis* between sites. Confidence intervals were calculated using the Clopper-Pearson

105   method.

106

107   **Results**

108   **Natural history of *Stylogaster neglecta***

109   Twenty-four (20%) of the 120 University of Toronto at Mississauga *O. nigricornis* were

110   parasitised by *S. neglecta*. There was a significant difference in the proportion of parasitised *O.*

111   *nigricornis* collected on different dates (χ^2 = 37.014, df = 2, *P* < 0.01) with the highest proportion

112   of parasitised individuals found in the 14 August sample (Fig. 3). Parasitoid larvae emerged from

113   the near the anus of *O. nigricornis* and pupated outside the host. Host *O. nigricornis* remained

114   alive for hours to days after emergence and several observations of *O. nigricornis* after parasitoid

115   emergence suggested that they had lost the use of their metathoracic legs. There were several

116   cases of multiple parasitism: four *O. nigricornis* had two *S. neglecta* larvae, and one hosted

117   three. Parasitoids that shared a host appeared to be smaller than parasitoids that did not (personal

118   observation). Of the pupae, only one eclosed (in December 2017). Mean time from a *O.*

119   *nigricornis* being collected to parasitoid emergence was 16.6 days (standard deviation = 9.04;

120   range 3–31 days). No *O. nigricornis* collected before 17 July or after 29 August were parasitised.

121   Consistent with this narrow oviposition period, mean time from host collection to parasitoid

122   emergence was significantly shorter at later sampling dates (*F* = 32.36, *P* < 0.001) (Fig. 4).

123

124   **Site differences in parasitism**

125   Of 674 *O. nigricornis* from all four sites, 149 or 22% (CI = 0.246, 0.324) were

126   parasitised. There were large differences in parasitism between sites (Fig. 5): at Huyck 2% (n =

127   104, CI = 0.0024, 0.069), at Koffler 11% (n = 178, CI = 0.079, 0.189), at *rare* 26% (n = 193, CI

128   = 0.272, 0.434), and at University of Toronto at Mississauga 39% (n =199, CI = 0.539, 0.717) (χ^2

129   = 70.23, P < 0.001). *Oecanthus nigricornis* hosts were mostly third to fifth instars, and of all *O.*

130   *nigricornis* parasitised, only one had reached adulthood.

131

132   **Discussion**

133   We report *S. neglecta* as the first dipteran parasitoid of *O. nigricornis* as the first known

134   host for this parasitoid. Like *S. biannulata*, *S. neglecta* uses a gryllid cricket host in which the

135   larvae develop internally, pupates outside the host, and occasionally exhibits superparasitism

136   (Woodley and Judd 1998). Like the *Bombus* specialists *Physocephal*a and *Sicus*, *S. neglecta* have

137   a narrow time window of a few weeks in which hosts are parasitised (Macfarlane *et al*. 1995;

138   Schmid-Hempel 2001; Otterstatter 2004). Unlike the *Bombus*-hunting conopids, *S. neglecta*

139   pupates outside of the host. *Stylogaster neglecta* also appear to have longer incubation times than

140   the 10–12 days reported for the *Bombus* hunters (Schmid-Hempel 2001). Further work should

141   examine the nature of overwintering strategies in *S. neglecta* and whether it resembles that of

142   other conopids.

143   The time from host capture until parasitoid emergence decreased over the season with

144   longer intervals in July and shorter ones in August. We did not find any parasitised *O.*

145 *nigricornis* in June or September. The shorter intervals in the late summer are because the larvae

146 had already been developing for some time before we collected their hosts. *Stylogaster neglecta*

147 appears to parasitise hosts from late July to early August and is not active throughout the rest of

148 the summer. This is consistent with unpublished adult collection records of this species by Burt

149 and others (unpublished data), which examined records of adult *S. neglecta* in collections across

150 North America. Of the 128 *S. neglecta* caught in southern Ontario, eight were caught in June,

151 114 in July, five in August, and one in September. Such a narrow time of parasitoid adult activity

152 is expected in hosts with discrete generation times (Godfray 1994). Parasitoids that emerge too

153 early may suffer from greater mortality waiting until hosts emerge, while those emerging late

154 may have difficulty either in finding unparasitised hosts, or in subduing larger-sized hosts.

155 　　　　Assuming that all *S. neglecta* larvae have a similar incubation times, and the longer

156 lengths of time from host capture until parasitoid emergence are roughly equivalent to the

157 incubation time, then it would appear that *S. neglecta* has an incubation period of about 30 days

158 in its host. This estimate is higher than estimates for other conopid genera, such as 10–12 days

159 found in *Physocephala* and *Sicus* (Schmid-Hempel 2001). However, as noted earlier, the mean

160 time from our collecting the host *O. nigricornis* until parasitoid emergence will be shorter than

161 actual mean incubation time given that eggs had been laid before collection. The actual

162 incubation time is likely to be longer than we recorded but less than 44 days, as there were no

163 indications of parasitism two weeks before the earliest sample.

164 　　　　We found significant differences in the proportion of *O. nigricornis* that were parasitised

165 across four different sites in southern Ontario and upstate New York. The proportion of

166 parasitised individuals ranged from 39% in University of Toronto at Mississauga to 2% in the

167 Huyck Preserve. While there were significant differences between sites in terms of parasitism

168   rate, our sampling only took place over a single season so we cannot confirm if these are long

169   term site differences. There appears to be an inter-year difference in parasitism at University of

170   Toronto at Mississauga, with the parasitism rate in late July 2018 being higher than the

171   parasitism rates found in July 2017. However, the parasitism rate in August 2017 was higher

172   than the single 2018 sample. It appears that the rate of parasitism at University of Toronto at

173   Mississauga peaked slightly earlier in 2018 than in 2017. Parasitoid-host relationships often

174   show cyclical population dynamics across multiple years (Hassell and May 1973; Godfray 1994;

175   Godfray *et al*. 1994) which may explain the between-site differences. Long term sampling will

176   be necessary to determine if these differences are consistent from year to year.

177

178   **Acknowledgements**

187

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267

268

269 **Figure 1**. *Stylogaster neglecta* female raised from a pupa after emerging from *Oecanthus*

270 *nigricornis*. Collected as a pupa on 28 August 1996 by Luc Bussière and emerged as an adult 9

271 January 1997.

272 **Figure 2**. Juvenile fourth instar *Oecanthus nigricornis*, parasitised by *Stylogaster neglecta*.

273 Caught at *rare* Charitable Research Reserve.

274 **Figure 3**. Proportion of *Oecanthus nigricornis* collected in the summer of 2017 that were

275 parasitised at the University of Toronto at Mississauga, with exact binomial confidence intervals

276 and sample sizes.

277 **Figure 4**. Time in days between collection of parasitised *Oecanthus nigricornis* (University of

278 Toronto at Mississauga 2017) and when larval *Stylogaster neglecta* emerged for all *O.*

279 *nigricornis*.

280 **Figure 5**. Time in days between collection of parasitised *Oecanthus nigricornis* (University of

281 Toronto at Mississauga 2017) and when larval *Stylogaster neglecta* emerged, averaged for each

282 collection date, with standard deviation.

283 **Figure 6**. Proportion of *Oecanthus nigricornis* parasitised from samples collected across four

284 sites in July 2018. Exact binomial confidence intervals and sample sizes are given. Huyck,

285 Edmund Niles Huyck Preserve and Biological Research Station; KSR, Koffler Scientific

286 Reserve; UTM, University of Toronto at Mississauga; rare, *rare* Charitable Research Reserve.

287

288 **Table 1.** Sex, location, voucher identification number, and collector of samples used in analysis

289 and referenced.

Voucher ID	Species	Location	Date	Collector	Sex
ROME179756	Oecanthus nigricornis	University of Toronto at Mississauga	31 July 2017	Erik Etzler	Male
ROME179757	Oecanthus nigricornis	University of Toronto at Mississauga	28 June 2017	Erik Etzler	Female
ROME179758	Oecanthus nigricornis	University of Toronto at Mississauga	31 July 2017	Erik Etzler	Female
ROME179759	Oecanthus nigricornis	University of Toronto at Mississauga	17 July 2017	Erik Etzler	Male
ROME179768	Stylogaster neglecta	University of Toronto at Mississauga	11 August 2017	Erik Etzler	N/A
ROME179769	Stylogaster neglecta	University of Toronto at Mississauga	December 2017	Erik Etzler	N/A
ROME179770	Stylogaster neglecta	University of Toronto at Mississauga	January 1997	Luc Bussière	Male

ROME179771	Stylogaster neglecta	University of Toronto at Mississauga	28 November 1996	Luc Bussière	Female

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291

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ROME179771	Stylogaster neglecta	University of Toronto at Mississauga	28 November 1996	Luc Bussière	Female

293 **Table 2**. Dates of collections done over the summer of 2017, with number of samples collected

294 and number of parasitised individuals in each collection.

Collection	Date	Number of samples	Number parasitised
1	26 June	21	0
2	17 July	22	4
3	31 July	20	3
4	14 August	25	13
5	29 August	23	4
6	13 September	20	0

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296