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Reduced *Compsilura concinnata* parasitism of New England saturniid larvae

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1 Running head: Silkmoth parasitism by *Compsilura*

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4 Reduced *Compsilura concinnata* parasitism of New England saturniid larvae

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24 **Abstract**

25 1. In the northeastern United States, the non-native generalist parasitoid *Compsilura*
26 *concinata*, introduced in the early 20th century to control forest pests, has been linked to the
27 decline of giant silk moths (Lepidoptera: Saturniidae).

28 2. Field research conducted in New England in the late 1990s on two saturniid species,
29 *Hyalophora cecropia* and *Callosamia promethea*, found *C. concinnata* parasitized 81% and 68%,
30 respectively, when larvae were reared outdoors and replaced weekly. These parasitism rates,
31 extrapolated over the larval period, would prevent any larvae from reaching pupation.

32 3. In 2017 and 2018, we repeated this field experiment using these same two saturniid
33 species for the same duration, and at the same site, location, and time of year. In 2017, *C.*
34 *concinata* parasitized only 19% of *H. cecropia* larvae and 1% of *C. promethea* larvae; in 2018,
35 parasitism rates were 3% and 0%, respectively.

36 **Key Words**

37 saturniid, parasitoid, invasive species, community ecology

38 **Introduction**

39 Populations of silk moths (Lepidoptera: Saturniidae) in the northeastern United States
40 have declined precipitously over the past half-century (Boettner et al. 2000, Wagner 2012,
41 Goldstein et al. 2015). All saturniids have been affected, and the regal moth (*Citheronia regalis*)
42 has been extirpated from the New England mainland, the imperial moth (*Eacles imperialis*) is a
43 Massachusetts Division of Fish and Wildlife Threatened Species, and the barrens buck moth
44 (*Hemileuca lucina*) is a Species of Special Concern in Massachusetts (Wagner 2012, Goldstein et
45 al. 2015). Several anthropogenic causes for this decline have been hypothesized: these include
46 habitat loss, human development (including electric lighting), and control efforts for gypsy moth

47 (*Lymantria dispar*) and other forest pests (Fitzgerald 1995, Wagner 2012). The latter threat
48 reflects the fact that since saturniids and gypsy moth larvae overlap in host usage, pesticide use
49 on deciduous trees should affect both groups. Because most pesticide use was localized and
50 heavier in the 1940's and 1950's, however, silk moths should have recovered in the past 70 years.
51 The increasing abundance of deer and birds in the wake of increased human development is
52 another potential cause of decline, since deer browse plants containing moth eggs and larvae and
53 birds prey heavily upon larvae and pupae (Wagner 2012). While each factor is likely important,
54 they cannot explain why saturniids outside of New England appear largely unaffected.

55 Researchers have suggested that the parasitoid *Compsilura concinnata* (Meigen 1824)
56 (Diptera: Tachinidae; hereafter *Compsilura*) might help explain saturniid declines (Boettner et al.
57 2000, Kellogg et al. 2003, Wagner 2012, Goldstein et al. 2015). This multivoltine tachinid was
58 first introduced to New England in 1906 (and repeatedly over the next 80 years) for control of *L.*
59 *dispar* and 12 other pests (reviewed in Elkinton et al. 2006). *Compsilura* established quickly in
60 North America, where it can attack and kill over 180 native insect species (Arnaud 1978).
61 *Compsilura* was even used against one native saturniid moth, the range caterpillar *Hemileuca*
62 *oliviae*, but without any apparent success (Boettner et al. 2000). Stamp and Bowers (1990)
63 documented high *Compsilura*-induced mortality on the saturniid *Hemileuca lucina*, although a
64 study of the closely related *H. maia* found lower parasitism rates (Selfridge et al. 2007). Between
65 1995-1998, Boettner et al. (2000) assessed the impact of *Compsilura* on the saturniids
66 *Hyalophora cecropia* and *Callosamia promethea*. They found 60-80% of larvae were parasitized
67 over a three-instar period, a rate high enough (if extrapolated over the larval period) to kill the
68 entire experimental larval cohort (n=965). Their results suggested that *Compsilura* may have
69 played a major role in saturniid decline and disappearance in the Northeast. In the Appalachian

70 region of Virginia, saturniids remain common (Kellogg et al. 2003) despite the presence of
71 *Compsilura*. *Actias luna* larvae deployed in the region were frequently (16-60% of cases)
72 hyperparasitised by trigonalid wasps after *Compsilura* parasitism, a degree of top-down control
73 that may dampen the suppression of moth populations (Kellogg et al., 2003). More recently,
74 surveys failed to detect *Compsilura* on New England islands with high saturniid densities
75 (Goldstein et al. 2015). While the fly's effect on saturniids is now accepted (Wagner and Van
76 Driesche 2010), how *Compsilura* populations are affected by fluctuations in the densities of *L.*
77 *dispar* or other hosts (Hajek et al. 2015) is unknown.

78 We report the results of surveys conducted in 2017 and 2018 that repeated work
79 described in Boettner et al (2000). To investigate whether parasitism rate of saturniids by
80 *Compsilura* have changed over the past 20 years, we deployed *C. promethea* and *H. cecropia*
81 larvae in conditions replicating those of the previous study, then assayed parasitism rates. We
82 found that parasitism was substantially lower on *H. cecropia* larvae than in the previous study
83 and virtually nonexistent on *C. promethea* larvae. Our results, although only a two-year snapshot,
84 suggest that the ecological importance of this parasitoid has changed.

85 **Methods**

86 Eggs of both *H. cecropia* and *C. promethea* were obtained by pairing unrelated captive
87 individuals from New England (RI and CT) populations collected the prior year. Eggs were
88 incubated in 240mL polypropylene cups (Pactiv, Lake Forest, Illinois). As per Boettner et al.
89 (2000), the emerging *H. cecropia* and *C. promethea* larvae were reared on *Prunus serotina* and
90 *Sassafras albidum*, respectively. Larvae were reared outdoors on live hosts within one-meter-
91 long agribon (Berry Plastics, Evansville, Indiana) bags to exclude predators and parasitoids. Pilot

92 experiments found these bags effective at predator/parasitoid exclusion, and larvae reared
93 outdoors within them experienced minimal mortality (A. Baranowski, *unpublished data*).

94 Once larvae had reached the 3rd-5th instar, they were deployed on naturally growing
95 understory *P. serotina* and *S. albidum* saplings, respectively, along transects in Cadwell
96 Memorial Forest (Pelham, Massachusetts). Both this site, and the location of the transects within
97 it, were the same as reported in Boettner et al. (2000). As per the prior studies, three larvae (3rd-
98 5th instar) were placed on each plant, which were spaced 1-3 m apart and marked with flagging
99 tape; different transects were used for the two saturniid species. The 'stocking density' of three
100 larvae/plant follows Boettner et al. (2000), who found no evidence for density-dependent
101 parasitism. We also conducted our surveys at the same time of the year that the previous study
102 did; Boettner et al. deployed *C. promethea* larvae on July 22-24 1995, while *H. cecropia* larvae
103 were deployed on June 19-24 and July 2 1997.

104 The survey began on 2 July when we deployed 89 *C. promethea* larvae. We retrieved
105 these larvae on 8 July; if all three larvae were not found, we searched the surrounding vegetation
106 for five minutes. Following retrieval, we deployed an additional 104 *C. promethea* larvae. We
107 retrieved these larvae on 15 July. That same day, we deployed 72 *H. cecropia* larvae; these were
108 retrieved on 22 July. The final survey took place when we deployed 102 *C. promethea* larvae on
109 12 August (retrieved 19 August).

110 Retrieved larvae were reared individually in the lab in 473mL polystyrene cups (Pactiv,
111 Lake Forest, Illinois) on fresh leaves from the appropriate host; wilted leaves were replaced with
112 fresh foliage. Rearing cups were covered with cheesecloth held in place with a rubber band, and
113 cups were placed on a bench over a moist section of absorbent liner to maintain humidity. Indoor
114 rearing temperatures were 21-28° C during both years. Host sprigs were kept fresh by means of

115 moist floral foam (Smithers-Oasis brand, Kent, OH). During 2018 rearing, cut host branches
116 were briefly immersed in a 1% bleach solution and shaken dry before placement into rearing
117 cups; this was done to reduce the spread of larval pathogens. Larvae were inspected and waste
118 removed from cups daily, and their status (live/dead/pupated) recorded. Dead larvae were held
119 individually for ten days to check for parasitoid emergence, then frozen for dissection to
120 determine if they contained larval parasitoids. Cocoons were inspected for parasitoid emergence,
121 then held outdoors in a mesh cage until moth emergence the following spring. Parasitoids were
122 identified to species whenever possible.

123 In 2018, we repeated the above procedures for both moth species. We deployed *H.*
124 *cecropia* and *C. promethea* larvae on 28 June, 5 July, 12 July, and 20 July; they were collected on
125 5 July, 12 July, 20 July, and 27 July, respectively. Numbers of *H. cecropia* larvae deployed per
126 day were 63, 87, 71, and 16, respectively. Numbers of *C. promethea* larvae deployed per day
127 were 89, 104, and 102 (we did not deploy this species on 20 July), respectively.

128 We analyzed data on the number of *Compsilura*-parasitized larvae in 2017 versus 2018,
129 and in both years of our study versus the data reported in Boettner et al. (2000), using likelihood
130 ratio χ^2 tests. All data were analyzed in JMP 9.0.0 (SAS 2010).

131 **Results and Discussion**

132 In 2017, we deployed 72 *H. cecropia* larvae and recovered 31 (Table 1); seven of the 31
133 (22%) survived to pupation. Six dead larvae had been parasitized by *Compsilura* (19.3%); these
134 produced a total of ten *Compsilura* pupae. One prepupal larva was killed by the *H. cecropia*
135 tachinid specialist *Lespesia samiae*; this single cecropia larva produced 22 adult parasitoids.
136 None of the pupated *H. cecropia* had *Compsilura* emerge from them. In 2018, we deployed 198
137 larvae and recovered 32; only one survived to pupation. *Compsilura* killed one prepupal larva

138 (3.1%) and produced a single parasitoid pupa; no other parasitoid species emerged. Parasitism
139 rates were slightly higher in 2017 than in 2018 ($\chi^2_{1 \text{ df}} = 4.59, p=0.032$), but both years of our
140 study differed greatly from the results reported in Boettner et al. (2000) ($\chi^2_{2 \text{ df}} = 98.5, p<0.001$).

141 In 2017, we deployed 295 *C. promethea* larvae and recovered 190 (64.4%) (Table 1);
142 approximately 40% (n=77) of the retrieved larvae pupated. No *Compsilura* emerged from the
143 dead larvae; a single *C. promethea* larvae was parasitized and killed by an unknown
144 ichneumonid. Two *Compsilura* emerged in spring 2018 from *C. promethea* cocoons, having
145 evidently overwintered inside them. This is the first record of how *Compsilura* overwinters we
146 can find in the literature. No other cocoons contained either *Compsilura* pupae or adult flies. A
147 subsequent examination revealed two cocoons that each had one hole in its side, indicative of
148 parasitoid escape. Since no other parasitoids emerged from these cocoons, we suspect the two
149 *Compsilura* each emerged from a unique host larva. In 2018, we deployed 155 larvae and
150 recovered 48. Thirty (55%) of the recovered larvae pupated; no parasitoids emerged from dead
151 larvae. There was no difference in *Compsilura* parasitism rates between 2017 and 2018 ($\chi^2_{1 \text{ df}} =$
152 0.45, $p=0.5$); again, however, there was a highly significant difference between our results and
153 those of the previous study ($\chi^2_{2 \text{ df}} = 223, p<0.001$). We dissected all larvae of both moth species
154 that died prior to pupation to ascertain cause of death and count any immature larval parasitoids.

155 Despite lower rates of *Compsilura* parasitism, the *H. cecropia* larvae we recovered from
156 the field experienced high rates of pathogen-related mortality in both 2017 (55%) and 2018
157 (94%). This also affected *C. promethea* larvae (58% and 45% in 2017 and 2018, respectively).
158 Pathogen-killed larvae went from apparently healthy to dead, with their integument turning a
159 distinctive black color, in a short (1-2 day) period. Pathogen presence was confirmed via
160 dissection and microscopy (G.H. Boettner, *unpublished data*); the dark fluid that we found

161 oozing from the dead larvae is typical of viral epizootics in captive stocks of other saturniid
162 moths (Skowron et al. 2015). While larvae occasionally died in the field sleeves, none exhibited
163 the same symptoms as those dying post-retrieval. The >10-day lag between retrieval and the
164 death of pathogen-killed larvae, in combination with the rapid decline and death of ‘healthy’
165 individuals, further suggests that the mortality resulted from a lab-associated pathogen, the stress
166 of multiple moves (from field cages to survey trees to the lab over a 7-9 day period), or some
167 combination of the two factors.

168 We found no larval parasitoids in the dissected larvae. While this might have resulted
169 from the high rates of pathogen-induced mortality, the time from retrieval to death of pathogen-
170 killed *H. cecropia* larvae was 10.8 ± 1.5 days, versus 6.2 ± 0.9 days for *Compsilura*-killed *H.*
171 *cecropia* larvae. Because *Compsilura* develops quickly within its host, this difference in time
172 suggests that any *Compsilura* larvae present should have grown to sizes detectable by dissection.
173 The fact that *Compsilura* inserts its hatchlings into, and lurks within, the immune system-
174 neglected peritrophic membrane of its host (Caron et al. 2008), also makes it unlikely that
175 immune activity of sick larvae could reduce survival of this parasitoid.

176 While care must be taken when extrapolating from a two-year survey, the decline in
177 *Compsilura* parasitism suggests that important changes in the ecological impact of this tachinid
178 may be occurring. There are many possible explanations for our results; we discuss below
179 several of the more compelling hypotheses for the apparent decline.

180 One possible explanation for our results involves climatic differences: extreme
181 temperatures can alter or disrupt host-parasitoid interactions (Hance et al. 2007), and changes in
182 precipitation can impact caterpillar abundance (e.g., Karban et al. 2017). An analysis of daily
183 weather data from the periods when caterpillars were deployed in 1995 (22-31 July) and 1997

184 (19-24 June and 2-9 July) revealed that temperatures averaged $22.4^{\circ} \pm 3.1^{\circ}$ (SE) C and weekly
185 rainfall averaged 2.4 ± 1.13 cm (NOAA 2018). During our work in 2017 and 2018, temperatures
186 averaged $23.0^{\circ} \pm 1.5^{\circ}$ (SE) C and weekly rainfall averaged 4.0 ± 1.1 cm (NOAA 2018). Although
187 rainfall values are higher in our study, our means include one extremely wet week (28 June - 4
188 July 2018) in which 8.1 cm of rain fell; excluding this week reduces our weekly rainfall means to
189 3.25 ± 0.86 cm.

190 The reduction in parasitism may also have resulted from increased predation on
191 *Compsilura* itself. Kellogg et al. (2003) found that ~50% of *Compsilura* pupae collected in
192 Virginia were hyperparasitized by trigonalid wasps and hypothesized that this might explain the
193 continued local abundance of silk moths. We assessed hyperparasitism by rearing the 14
194 *Compsilura* pupae we collected: 13 emerged as adults and one died without producing any
195 hyperparasitoids. In addition, no hyperparasitoids emerged from dead saturniid larvae.

196 A third possibility is that *Compsilura*-saturniid interactions are influenced by the
197 interplay between *L. dispar* and its fungal pathogen *Entomophaga maimaiga*. *Compsilura* was
198 introduced to control *L. dispar*, and Culver (1919) found lower *C. promethea* densities at
199 tachinid release sites. *Compsilura* parasitizes early season *L. dispar* caterpillars (Gould et al.
200 1990), and the ensuing generations of parasitoids attack both early and late season saturniids
201 (Wagner and Van Driesche 2010). Starting in the late-1980s, the establishment of *E. maimaiga* in
202 the northeastern U.S. reduced both the frequency and magnitude of *L. dispar* outbreaks (Hajek
203 2007, Hajek et al. 2015). This pathogen also kills *L. dispar* larvae so quickly that co-infecting
204 parasitoids like *Compsilura* are unable to complete their development (Hajek and van Nouhuys
205 2016). *Compsilura* also tends to attack *L. dispar* during early instars, while *Entomophaga* kills
206 later instar larvae. If early-season hosts determine mid and late season *Compsilura* densities, the

207 impact of *E. maimaiga* on *L. dispar* could affect the ability of *Compsilura* to suppress saturniids,
 208 however, there is little evidence to confirm this.

209 In summary, we consistently found lower rates of saturniid parasitism by *Compsilura*
 210 than previously reported (Boettner et al. 2000) from the same location. If *Compsilura* is not
 211 presently the primary driver and sustainer of saturniid decline, then the reasons for it, particularly
 212 in the Northeast region, remain indeterminate. In addition to surveying for parasitoid presence or
 213 absence, future studies should explore interactions between *Compsilura* and other lepidopteran
 214 hosts. Specifically, it seems important to investigate the phenology of both *L. dispar* and its
 215 natural enemies for possible overlap in pathogen and parasitoid activity. The factors responsible
 216 for wild mortality in other life stages of these declining moths, biotic and abiotic, are also
 217 relatively unexplored. While much remains to be done, our results highlight the importance of
 218 longitudinal survey work capable of detecting cryptic but important changes in community
 219 structure.

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 222 earlier drafts of this manuscript.

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282 **Table 1.** Larval retrieval and parasitoid-related mortality for *Hyalophora cecropia* and
 283 *Callosamia promethea* in 2017 and 2018 and as reported in Boettner et al (2000) for the same
 284 location and site in the late 1990s.

285

Saturniid species	Data set	Larvae deployed	Days in field	Larvae retrieved (%)	Parasitoid-related rearing mortality	
					<i>C. concinnata</i>	Other parasitoids
<i>Hyalophora cecropia</i>	Boettner et al. 2000	300	5-7	134 (45%)	81%	2%
	This survey (2017)	72	7	31 (43%)	19%	3%
	This survey (2018)	198	6-7	32 (16%)	3%	0%
<i>Callosamia promethea</i>	Boettner et al. 2000	665	6-8	117 (18%)	68%	21%
	This survey (2017)	295	6-7	190 (65%)	1%	1%
	This survey (2018)	155	6-7	48 (31%)	0%	0%

286

287