

1 **SCIENTIFIC NOTE**

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3 Egg cannibalism by passion vine specialist *Disonycha* Chevrolat beetles

4 (Coleoptera: Chrysomelidae: Galerucinae: Alticini)

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24 **Abstract**

25 Cannibalistic behavior is now recognized to be an important component of nutritional ecology in
26 both carnivorous and herbivorous species, including many beetle families (Englert and Thomas
27 1970; Beaver 1974; Dickinson 1992; Bartlett 1987; Alabi *et al.* 2008). This habit was historically
28 viewed by an incidental outcome of unnaturally crowded laboratory situations with little
29 ecological importance (Fox 1975), but it is increasingly acknowledged that cannibalism
30 represents a potentially advantageous behavior (Richardson *et al.* 2010). Here we report on
31 multiple cases of egg cannibalism, or conspecific oophagy, by adults of two species of passion
32 vine (*Passiflora* Linnaeus: Passifloraceae) specialist flea beetles in the genus *Disonycha*
33 Chevrolat (Coleoptera: Chrysomelidae: Galerucinae: Alticini). This is the first report of egg
34 cannibalism from the Galerucinae, and to our knowledge, only the fourth report of egg
35 cannibalism by adults in the Chrysomelidae; the other three reports are of adult Chrysomelinae
36 species eating conspecific eggs (Dickinson 1992; McCauley 1992; Schrod *et al.* 1996). We
37 conclude this note with several questions raised by our observations, followed by a discussion
38 that may contribute to explanations of this behavior.

39
40 The genus *Disonycha* contains approximately 70 nominal species distributed widely from
41 southern Canada to temperate South America and the Caribbean. Species richness is highest in
42 northern temperate and subtropical latitudes, with the greatest number of species known from
43 Mexico (Furth 2017). Adults are large for alticines (7 – 8 mm length), often with brightly colored
44 and striped elytra. All are herbivorous as larvae and adults, with both life stages commonly
45 inhabiting the same host plant. Three *Disonycha* species are known to specialize exclusively on
46 *Passiflora*: *Disonycha discoida* Fabricius, *D. stenosticha* Schaeffer and *D. quinquelineata*

47 Latreille. This note focuses on *D. stenosticha* and *D. quinquelineata* (Fig. 1). *Disonycha*
48 *stenosticha* is distributed from the Rio Grande Valley of Southern Texas to Tamulipas and
49 Veracruz states in south-central Mexico. Larvae and adults consume *P. suberosa* and *P. biflora*
50 in the field, with unconfirmed reports of larvae consuming *P. fillipes* (Clark *et al.* 2004).
51 *Disonycha quinquelineata* is found from the Mexican states of Guerrero, Veracruz and Yucatan
52 to northwest Colombia. Larvae and adults eat *P. auriculata*, *P. biflora*, and newly flushed foliage
53 of *P. pittieri*; adults will eat fresh *P. ambigua* leaves. Host records from the field have been
54 confirmed by feeding trials in the laboratory, however they probably do not capture all host
55 plants across these species' ranges. Both species oviposit egg masses on the abaxial sides of host
56 leaves, as well as leaves of non-host plants near larval foodplants (Fig. 1).

57 *Disonycha* egg cannibalism has been observed ten times, in both the field (N = 2) and the
58 laboratory (N = 8). *Disonycha quinquelineata* was responsible for six of these events, and *D.*
59 *stenosticha* for the other four. Egg masses have been consumed by both males (*D. stenosticha* N
60 = 2 individuals, *D. quinquelineata* N = 2) and females (*D. stenosticha* N = 2 individuals, *D.*
61 *quinquelineata* N = 4), including two instances where an individual *D. quinquelineata* female
62 consumed her own eggs within one day of oviposition. All adult egg cannibalism incidents
63 occurred within 36 h of oviposition. This is about how much time it takes for the chorion to
64 harden to the point where it is stiff to the touch. Prior to this, the eggs are soft and palatable. In
65 three cases the adult did not eat all the eggs in each mass; 65 – 70 % of the eggs were consumed
66 in each of these instances (Fig. 1). *Disonycha quinquelineata* and *D. stenosticha* neonate larvae
67 will also cannibalize unhatched eggs from the same clutch shortly after eclosing. It is not known
68 if all eggs that are consumed by neonates are viable, or unfertilized trophic eggs oviposited to
69 provision the first larvae to eclose (*e.g.* Perry and Roitberg 2006). It is not within the scope of

70 this contribution to report on *Disonycha* larval cannibalism, however it is important to the
71 context of this observation to note that this also occurs.

72 Cannibalistic juvenile behavior is relatively common among generally non-carnivorous
73 insect orders (78% percent of 178 studies reviewed by Richardson *et al.* 2010). However, adult
74 consumption of conspecific eggs is less common, less frequently observed, or underreported.
75 Adult egg cannibalism has been noted in the Blattodea, Hemiptera, Hymenoptera, Orthoptera,
76 and Coleoptera. Beetle families where adult consumption of conspecific eggs has been observed
77 include: Zopheridae (Kubik *unpublished data*), Tenebrionidae, Coccinellidae, Cucujidae,
78 Dermestidae, Scolytidae, Silphidae, and Chrysomelidae (*see references within Richardson et al.*
79 2010). Two subspecies of adult milkweed leaf beetles, *Labidomera c. clivicollis* Kirby and *L. c.*
80 *rogersii* LeConte, will consume conspecific egg masses (Dickinson 1992). Conspecific egg
81 cannibalism has also been observed in the Colorado potato beetle, *Leptinotarsa decemlineata*
82 Say (Schrod *et al.* 1996), and the false Colorado potato beetle, *L. juncta* Germar (McCauley
83 1992). Cases of egg cannibalism by larvae are more commonly reported for chrysomelid beetles
84 (*e.g.* Eberhard 1981; Windsor *et al.* 2013). Chrysomelid larvae are also known to eat unfertilized
85 trophic eggs. However, this is not egg cannibalism *sensu stricto*, in that these unviable eggs are
86 intentionally laid for purposes other than producing offspring directly. For example, gravid *L.*
87 *decemlineata* mothers experiencing predation risk from stinkbugs lay unfertilized trophic eggs to
88 supplement the nutrition of their offspring (Tigreros *et al.* 2017). Upon hatching, neonate larvae
89 consume the trophic eggs, giving them extra nutrition to grow quickly while avoiding exposure
90 to stink bugs, and other natural enemies, while foraging on leaves. Egg viability was not assessed
91 in all previous reports of chrysomelid larvae consuming conspecific eggs. Thus, prevalence of

92 true egg cannibalism by larvae versus offspring resource provisioning with trophic eggs remains
93 unclear.

94 It is important to disentangle the social and ecological contexts under which beetle
95 cannibalism occurs (Trumbo and Valletta 2007; Wood *et al.* 2014). Egg cannibalism is generally
96 attributed to density-dependent factors, such as crowding situations in which high larval
97 abundances lead to rapid consumption of food resources that result in starvation of the whole
98 group. In a review of insect cannibalism, Richardson and colleagues (2010) attributed
99 consumption of beetle conspecifics to density-dependent factors in 70% of studies reporting
100 cannibalism. However, density-dependent resource scarcity alone does not account for the
101 frequency of egg cannibalism by *Disonycha* adults. Cannibalized egg masses were consumed in
102 locations with abundant host plant material in both the laboratory and the field, in all cases. Two
103 instances of a *D. quinquelineata* adult consuming eggs in the field occurred at the La Selva
104 Biological Reserve in Costa Rica (10°25'53" N / 84°00'17" W) in a large *Passiflora* garden (~
105 15 x 15 m) with copious foodplant for adults to eat. In the laboratory at The University of Texas
106 at Austin, egg masses were consumed in large (0.53 m³), medium (0.07 m³), and small (0.03 m³)
107 mesh pop-up cages replete with fresh *Passiflora* shoots or potted host plants with abundant new
108 growth. Cannibalism occurred in cages where egg masses were present on nearby foodplants (N
109 = 4), as well as in cages without eggs (N = 4). Egg consumption occurred in cages with different
110 densities and adult sex ratios. Specifically, cannibalism occurred in cages housing multiple adults
111 of both sexes (N = 4), cages with a single mated pair (N = 2), and cages with only the female that
112 oviposited the eggs (N = 2). This is evidence for the hypothesis that relative lifestage abundance
113 is not linked to egg cannibalism. The influence of larval presence on adult egg cannibalism
114 cannot be inferred because eggs, adults, and larvae were never housed together in the same cage.

115 Density-independent factors such as poor host plant nutritional quality (O'Rourke and
116 Hutchinson 2004), and developmental asynchrony within populations (Nakamura and Ohgushi
117 1981) can also influence herbivorous insect cannibalistic behavior. Investigation of the relative
118 influence of environmental and demographic variables on frequency of egg cannibalism by
119 *Passiflora* specialist *Disonycha* flea beetles is open for study.

120 Newly oviposited eggs may represent a concentrated nutritional supplement to beetles
121 that may not be receiving sufficient protein from host plant material alone. *Disonycha*
122 *stenosticha* and *D. quinquelineata* eggs have higher protein concentration per unit mass than new
123 leaves of the principal host plants that they feed on in the field (Fig. 2). This stoichiometric
124 discrepancy is true of individual eggs, and the entire egg mass relative to foodplant material.
125 Protein concentration comparisons were made between *D. quinquelineata* eggs and *P. biflora* (t-
126 test; N = 8; $P < 0.005$), *D. stenosticha* eggs and *P. suberosa* (t-test; N = 5; $P < 0.001$). These data
127 support the hypothesis that consumption of one's own eggs may arise from a need to re-
128 assimilate protein stores necessary for maximizing performance, and by extension their fitness.
129 One possibility is that consuming egg masses with a disproportionate protein concentration
130 relative to host leaves would improve a *Disonycha* beetle's current chances of surviving so that
131 reproductive effort can be maximized in the future. Such a situation has been described with
132 cannibalistic *Coleomegilla maculata lengi* De Geer larvae (Coleoptera: Coccinellidae) that
133 displayed strong preference for eating conspecific eggs over aphid prey (Gagné *et al.* 2002);
134 preference for egg consumption correlated with superior performance leading the authors to infer
135 that *C. m. lengi* eggs had higher nutritional quality than equivalent quantities of aphids.

136 *Disonycha stenosticha* and *D. quinquelineata* adults frequently live for six to nine months
137 in the laboratory (we assume at least half this long in the field), and females can oviposit

138 multiple egg masses over this period. These long-lived adults have multiple opportunities to pass
139 on their genes. However, different selection pressures create costs on gamete production and
140 resource investment that differ for males and females (Blum and Blum 2012). Males are
141 expected to mate with as many females as possible. If a male has mated with multiple females,
142 cannibalism of a given egg mass represents a low risk of consuming his own offspring.
143 Cannibalism of egg masses oviposited by other females would be advantageous to the relative
144 fitness of a female that is still sourcing her offspring into the population. Consuming her own
145 eggs does not appear beneficial because she would be decreasing her relative fitness in that
146 population. However, there exist external constraints on female reproductive investment and
147 survival that were not accounted for here (*e.g.* living to produce future clutches of healthy
148 offspring) that prevent us from making strong inferences about what would be selectively
149 advantageous to a beetle that eats her own eggs.

150 Egg cannibalism by conspecifics may contribute to the difficulty finding high density
151 populations of *Disonycha* in the field. With the exception of semi-artificial habitats such as
152 native plant nurseries in South Texas and passion vine gardens in Costa Rica, we have not
153 observed *Disonycha* beetles aggregating at host plant patches in high numbers. Larval *Disonycha*
154 consume a greater amount of plant material per unit time than adults and the *Passiflora* that host
155 these species are usually not abundant in the habitats where they occur. *Passiflora* primarily
156 occur in spatially and temporally ephemeral gaps, and edge habitats where competition for space
157 and light is intense. This creates a situation where populations that are not self-regulated and/or
158 diminished in size by interspecific competition and mortality from natural enemies could easily
159 defoliate host plant patches resulting in resource scarcity, potentially resulting in local starvation.

160 Egg cannibalism may serve as a population level mechanism to dampen the number of
161 individuals competing for these scarce resources.

162 It is possible that *Disonycha* adults are only consuming unfertilized eggs. We considered
163 this caveat for three reasons: 1) adults did not always consume every egg in a mass; 2) *D.*
164 *quinquelineata* egg mass dissections (N = 10) showed a range of egg viability ranging from 0 to
165 95%; and 3) no *D. stenosticha* or *D. quinquelineata* egg masses in which any larvae eclosed have
166 had 100% hatching success. Despite this caution, we reason that specific consumption of
167 unfertilized eggs is not likely to be the case. Fertilized and unfertilized eggs appeared to be
168 randomly distributed in a given egg mass, and adults proceeded to eat eggs indiscriminately from
169 the periphery of the egg mass to a specific point where consumption ceased during events in
170 which less than 100% of eggs were consumed. Thus, egg cannibalism is occurring unless
171 *Diconycha* beetles have the capacity to discriminate between viable and unviable eggs (*e.g.*
172 homogenous egg dispersal in bruchid beetles; Messina *et al.* 1987), or they are only consuming
173 masses that contain unviable eggs.

174 The observations reported here suggest that egg cannibalism by *D. stenosticha* and *D.*
175 *quinquelineata* adults is meaningful for the fitness of these species. These are the main questions
176 that these observations compelled us to ask: 1.) Does genetic relatedness between eggs and
177 adults affect an individual's propensity to cannibalize eggs? 2.) Is egg cannibalism density-
178 dependent? 3.) Are trade-offs in propensity to eat eggs different over the course of an adult's
179 life? 4.) Are adults only consuming unfertilized eggs? 5.) Is egg cannibalism an important
180 determinant of *Disonycha* population structure within the greater *Passiflora* specialized
181 herbivorous insect community? The observations presented here provide a foundation for turning
182 these questions into testable hypotheses. Specifically, we hypothesize that genetic relatedness

183 does not predict propensity to cannibalize eggs as we have observed females eating their own
184 egg masses as well as those of other individuals. Egg cannibalism occurs regardless of egg mass
185 density in a given area but occurs more frequently at higher egg mass densities. Eggs provide
186 adults with more protein than equivalent amounts of host leaves and this disparity drives age-
187 specific variation in cannibalism rates. These beetles are long-lived, and with such longevity
188 comes the eventuality of protein limitation for an individual to generate new gametes and
189 maintain cell division and repair processes (*e.g.* Dunlap-Pianka et al. 1977). Thus, we predict
190 older adults that have used up protein stores from the immature stage will cannibalize eggs more
191 often than younger adults. Adults eat eggs regardless of whether they are viable. Discrimination
192 between viable and unviable eggs is unlikely given that viable eggs are oviposited among
193 unfertilized eggs in a given mass. However, the ability to differentiate between viable and
194 unfertilized eggs via chemosensory pathways could provide for such discriminatory ability. Such
195 pathways have been reported on in the Chrysomelidae (Mitchel 1994; van Loon 1996; Fernandez
196 and Hilker 2007). Many proximate factors contribute to variation in population density and host
197 usage by *Disonycha* and other members of the *Passiflora* specialist insect community (Smiley
198 1982; Gilbert 1991; Engler and Gilbert 2007). Egg cannibalism may contribute to this
199 heterogeneity by maintaining the relatively uniform spatial distribution of *D. stenosticha* and *D.*
200 *quinquelineata* individuals that we have observed in nature.

201 Cannibalism can be a significant driver of an organism's life history, ecology, and fitness.
202 Unfortunately, this behavior is underreported, and studied empirically even less frequently.
203 There is reason to think that adult insects functionally characterized as herbivores cannibalize
204 conspecific eggs more often than what the current literature currently describes. This is a rich

205 area for study, and we encourage researchers with knowledge of their study organisms to report
206 on this behavior when the opportunity is presented.

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208

209 **Acknowledgments**

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211 specialized flea beetles and supporting us to investigate diverse aspects of the system.

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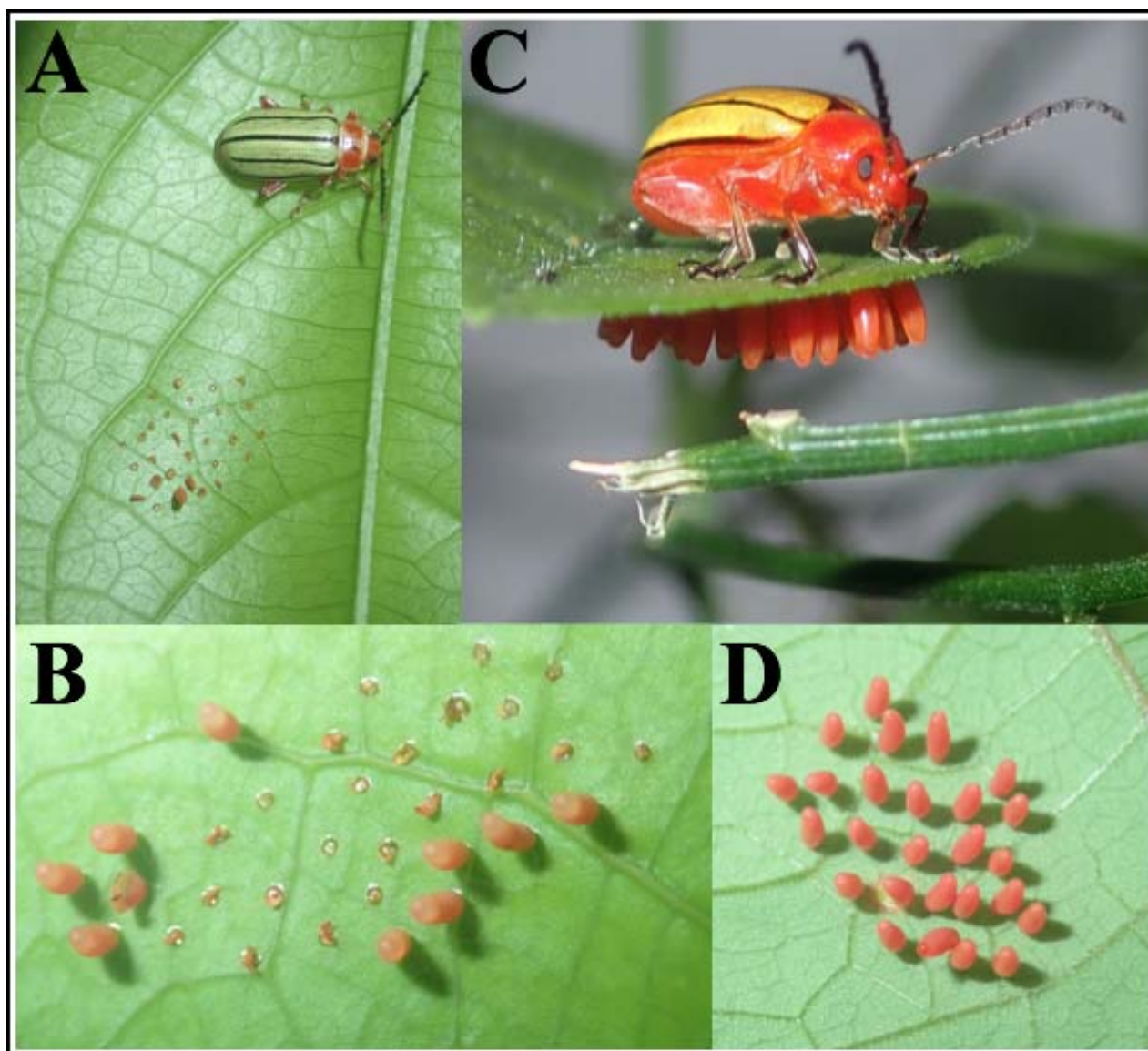
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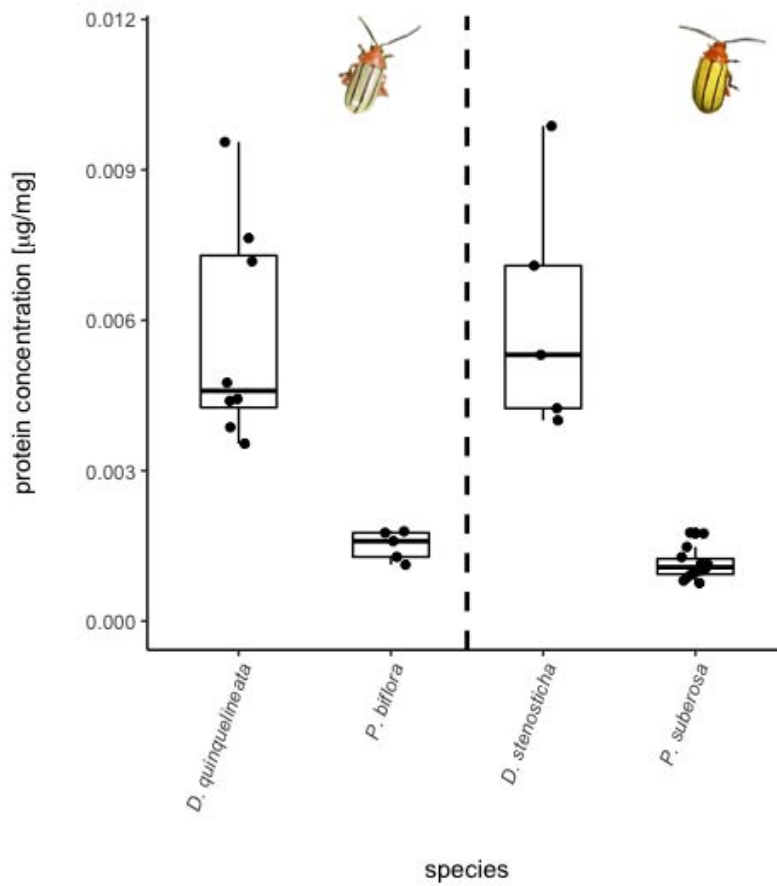
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342 **Figures**



343
344 **Figure 1.** Passion vine specialist *Disonycha* egg cannibalism habits. A) Male *Disonycha*
345 *quinquelineata* that just finished consuming all but one egg in a conspecific egg mass at La Selva
346 Biological Station, Costa Rica; B) *D. quinquelineata* egg mass on *Passiflora ambigua* with 10/32
347 eggs consumed at La Selva; C) *D. stenosticha* female with newly oviposited egg mass on *P.*
348 *suberosa* at National Butterfly Center, Mission, Texas; D) 3 d old *D. stenosticha* egg mass on *P.*
349 *biflora* in research culture at UT Austin.



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351 **Figure 2.** Comparison of *Disonycha quinquelineata* and *D. stenosticha* egg mass and host plant
352 leaf protein concentration. Beetle species are paired with their preferred host plants on each side
353 of the vertical dashed line. These data were analyzed with Welch's t-tests.

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