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1 Can monophagous specialists mediate host plant choices in generalist planthoppers (Hemiptera:
2 Delphacidae)?

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5
6 **Abstract.** 1. A preference experiment was set up with two planthopper species (Hemiptera:
7 Delphacidae) to test the influence of competition on host plant choice.

8 2. The delphacid *Javesella pellucida* was chosen as a generalist, and the rarer *Ribautodelphax imitans*
9 as a monophagous specialist, which feeds on the grass, tall fescue *Schedonorus arundinaceus*.

10 3. In the absence of the specialist, the generalist showed a marked preference for tall fescue. In some
11 experiments however, the introduction of the specialist resulted in a shift of preference to an alternative
12 plant, if the specialist was established prior to the introduction of the generalist.

13 4. This experiment supports the hypothesis that, specialist herbivores can potentially alter the host
14 plant choices of generalists. Which may lead to differing host plant use patterns in insect communities.

15 **Keywords**

16 Insect plant interactions, Auchenorrhyncha, rarity, planthopper, competition

17
18 **Introduction**

19 Interspecific interactions are important because they mediate community composition and have far
20 reaching impacts on the long term stability of complex insect-plant networks, and how they are
21 structured (Frank van Veen *et al.*, 2005; Denno & Kaplan, 2007; Kaplan & Denno, 2007). Studies of
22 direct competition, particularly among phytophagous groups, have largely been focussed on fitness,
23 fecundity rates, growth and survival (reviewed by: Denno *et al.*, 1995; Kaplan & Denno, 2007).
24 Competition however, can affect factors not solely attributed to community and population fitness, such
25 as host plant and microhabitat use, and position on plants (Ferrenberg & Denno, 2003).

26 Within phytophagous insect communities, generalists and specialists coexist (Bernays, 1998),
27 with the majority of species being specialist (Tallamy, 2004). Moreover, most studies of competition
28 between species, specialist or generalist, centre on those directly sharing resources (Denno & Kaplan,
29 2007; Kaplan & Denno, 2007; Ali & Agrawal, 2012); with little work carried out on how competition
30 affects host plant utilisation. The majority of previous work focussed on host displacement, where non-

31 native species have displaced their native counterparts (Kenis *et al.*, 2009) or where there is resulting
32 niche shift or death of an outcompeted species under experimental conditions (Kaplan & Denno, 2007).
33 In order to understand other aspects of the roles that specialists have on generalists, there is a need for
34 more experimental work.

35 Two-species experiments are useful models because they can elucidate, potential community
36 effects, at a level more accurately measured under controlled conditions, rather than more observational
37 field based studies (Kaplan & Denno, 2007). This paper looks at one such system, an interaction
38 between two co-occurring grass feeding planthopper species (Hemiptera: Auchenorrhyncha:
39 Delphacidae), and the influence of one species feeding on the other's preferred host within mesocosms.
40 The species used were a generalist *Javesella pellucida* (Fab.) (Nickel & Remane, 2002) and a specialist,
41 *Ribautodelphax imitans* (Ribaut.) which is only known to feed on tall fescue *Schedonorus arundinaceus*
42 (Schreb.) (den Bieman, 1987; Nickel & Remane, 2002; JNCC, 2010; Dittrich, 2016; Dittrich & Helden,
43 2016). It was hypothesised, that because the specialist was adapted to utilising one grass species
44 efficiently it would drive a host plant shift in the generalist. Thus, testing the paradigm that there is a
45 potential trade-off between using many resources adequately, and being able to move between them
46 and avoid competition, versus being able to use one resource better than all others, thus outcompeting
47 any potential competitors (McPeck, 1996; Noriyuki & Osawa, 2012). We tested this with experiments
48 in which we observed the host choice of the two delphacid species in single and mixed species culture.

49 Methods

50 In order to determine the life cycles and abundance of the test specialist *R. imitans* and the test generalist
51 *J. pellucida* bi-monthly randomised suction samples were taken on Coe Fen, Cambridge, UK
52 (52.198885, 0.118247) April – October 2011, consisting of 40 x 10 local subsamples each (full details
53 can be found in Dittrich, 2016; Dittrich & Helden, 2016). Each sub sample consisted of one full power
54 16 second suck with a Vortis™ suction sampler (Arnold, 1994; Brook *et al.*, 2008). The catch was
55 emptied into a canvas sweep net and all adult Auchenorrhyncha (both Cicadellidae and Delphacidae)
56 were removed by pooter for later identification. Throughout 2011 live specimens were also obtained
57 for insect cultures, and the offspring following the F2 generation used in these experiments.

58 A host preference experiment was set up using two grass species, tall fescue *S. arundinaceus*
59 and Yorkshire fog *Holcus lanatus* (L.) within mesocosms. The latter plant was chosen because it was
60 the second most common plant on the study site (after tall fescue), and one to which the generalist had
61 a strong positive response in laboratory trials (Dittrich, 2016). Tall fescue was chosen because of the
62 host plant relationships with the specialist (Dittrich, 2016; Dittrich & Helden, 2016). Approximately 10
63 tall fescue and Yorkshire fog seeds were planted 3cm apart in round clear polyethylene terephthalate
64 900ml [60x150mm] containers with 5 micron mesh affixed to the top held in place with an elastic band,

65 preventing insect escape. Growth was thinned to a pair of plants, one of each species, and the
66 experiments started when plants had three tillers of growth. There were two experimental treatments
67 used; one where the specialist species were allowed to first settle on plants, before the generalist species
68 was added, and one where the generalist species were allowed to establish on plants before the specialist
69 was added.

70 In the first test (generalists established) eight mesocosms were set up; in each 10 generalists
71 were allowed to establish themselves. After one week, 10 specialists were added to those mesocosms
72 containing the generalists. The host plant choice of the generalists were recorded immediately before
73 and 48 hours following this introduction. Planthoppers were observed to move quite readily between
74 their feeding positions through the course of a day, so a period of 48 hours was considered a reasonable
75 interval between recording.

76 For the second test (specialists established), eight mesocosms were set up, each with 10
77 specialists, which were allowed to establish for one week, after which 10 Generalists were then added.
78 The host plant choices were recorded immediately before and 48 hours after introduction of the
79 generalist.

80 A difference in the feeding preference of generalist was tested before and after the addition of
81 the allospecific competitor within the same experimental mesocosm, and between tests where the
82 generalist was added first and where it was added last [at equal density]. All statistics were performed
83 using R (R Development Core Team, 2013). T-tests were used, assuming equal variance, with all effect
84 sizes provided with 95% confidence intervals. An analysis of variance was used to check for differences
85 in tall fescue preference between experiments in the absence of allospecifics between all tests.

86 Results

87 The numbers of adult generalist *J. pellucida* recorded at Coe Fen during 2011 followed an almost
88 identical phenological pattern to the specialist *R. imitans*. However, as expected they were fewer in
89 number (Figure 1).

90 In the absence of specialists, generalists showed an overall choice preference for tall fescue
91 where a mean proportion of 0.66 (95% CI = 0.57, 0.75) of the individuals settled. The preference for
92 tall fescue did not differ from this average, for generalists between experiments when allospecifics were
93 absent ($F_{2,19} = 0.29$, $p = 0.972$). On Yorkshire fog mean proportions of 0.34 (95% CI = 0.25, 0.43) of
94 individuals settled. A significant difference in proportions between host plants of 0.32 (95% CI = 0.26,
95 0.57; $t_{15} = 5.45$, $p < 0.001$; Figure 2a).

96 There was no difference in the proportion of generalists on alternate host plants, after the
97 addition of the specialist to mesocosms where generalists were already established (non-significant

98 mean difference of 0.06, 95% CI = -0.12, 0.54; $t_{15} = 0.60$; $p = 0.559$). However overall preference for
99 tall fescue changed, in experiments where specialists were established on plants prior to their
100 introduction. When generalists were added to experimental arenas with specialists already established,
101 there was a marked change in preference, with a mean proportion of 0.23 (95% CI = 0.09, 0.37)
102 individuals found on tall fescue. A significant reduction in difference in proportions of 0.41 (95% CI =
103 0.35, 0.77; $t_{15} = 13.70$; $p < 0.001$).

104 Generalist feeding preference between conditions where they were established first versus last
105 in the presence of the specialist (at equal density) demonstrated an overall proportional reduction in
106 preference for tall fescue of 0.36 (95% CI = 0.15, 0.58, $t_{15} = 3.7982$, $p = 0.003$, figure 2b).

107 Discussion

108 When established before the generalist, the specialist planthopper *R. imitans* affected the host plant
109 preference of the generalist *J. pellucida*, supporting our hypothesis. However, this pattern was not
110 apparent if the generalist established first, where there was no change in preference. Both species adult
111 phenology is similar, and adults are spatiotemporally sympatric in the field (Dittrich *et al.*, 2013;
112 Dittrich & Helden, 2016), although the egg incubation periods for the specialist *R. imitans*, may be
113 slightly quicker (Raatikainen & others, 1967; Dittrich, 2016). Faster development may lead to earlier
114 establishment on food plants, and in some species is indicative of competitive advantage, or numerical
115 dominance (Krijger *et al.*, 2001; Hunter & Yeorgan, 2014). Specialist species dictating the specific
116 feeding niches of others, based on their own feeding ecology however, may provide a broader
117 explanation as to how generalists and specialists coexist within insect herbivore communities.

118 Host choice mediated by interspecific interactions, are not widely studied. However, it may
119 have much farther-reaching implications for understanding how insect herbivore communities are
120 constructed, and how generalist and specialist interactions help to shape them. Of the two study species
121 *R. imitans* is rare, and *J. pellucida* common, and it stands to reason that where the two coexist the
122 community position of *J. pellucida* may be different to sites where the two species do not coexist.
123 Moreover due to the rarity of *R. imitans*, it is likely that the two species co-occur less frequently than
124 when *J. pellucida* - the very widespread generalist - is found without *R. imitans* (Le Quesne, 1960;
125 Gaston, 1994; Nickel, 2003). If most species in grassland communities are monophagous and rare,
126 particularly in the case of the planthoppers (Delphacidae) (Gaston, 2010; Denno & Perfect, 2012), it is
127 likely that these interactions play a part in shaping how communities of herbivorous insects differ from
128 one location to the next, and between a range of different hosts.

129 The lottery hypothesis proposed by Chesson and Warner (1981) in which temporal
130 environmental fluctuations leads to the coexistence of competing species, is supported here. In our paper
131 the competing specialist is at an advantage if it arrives first. However, in systems where non-equilibrium

132 dynamics are at play, the recruits to vacant space may vary in time, and it is these fluctuations which
133 enable coexistence (Munday, 2004). Similar colonisation competition trade-offs, where disturbances
134 shape community structure may be common, such as in the heavily disturbed grasslands that our study
135 species were found (Levins and Culver, 1971; Beisner *et al.*, 2003; Munday, 2004). Conversely, as
136 grasslands are one of our most human impacted habitats, the interactions that are described within this
137 paper may decrease in their frequency, together with insect biodiversity, as disturbance increases.

138 The importance of monophagous herbivore species within communities is not unstudied (e.g.
139 Harrison *et al.*, 2008; Mouillot *et al.*, 2013). However, the range of roles that these species fill is not
140 fully understood, as highlighted by the finding of our work. It may be the case that rarer insect specialists
141 have an important role in modifying the host plant choices of generalists. The influence of one species
142 on how others utilise feeding location on single hosts is known to some extent (Denno *et al.*, 2003;
143 Ferrenberg & Denno, 2003), and how direct competition affects the fitness of species through direct
144 plant mediated and indirect effects is also well studied (Denno *et al.*, 1995; Kaplan & Denno, 2007).
145 This case of host-mediated choice, however, is unique and warrants further investigation, particularly
146 in field studies and presents an interesting line of enquiry, that may enable a greater understanding of
147 wider community effects.

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