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## *Datana drexelii* (Lepidoptera: Notododontidae) occurrence and larval survival on highbush blueberry cultivars

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11 ***Datana drexelii* (Lepidoptera: Notododontidae) occurrence and larval survival on highbush**  
12 **blueberry cultivars**

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19           **Abstract**

20           Plant genotype influences plant suitability to herbivores; domesticated plants selected for  
21 properties such as high fruit yield may be particularly vulnerable to herbivory. Cultivated strains  
22 of highbush blueberry, *Vaccinium corymbosum* L. can be high-quality hosts for larvae of the  
23 gregariously-feeding notodontid *Datana drexelii* (Hy. Edwards). We conducted an experiment  
24 assessing *D. drexelii* larval survival and pupal weight when fed foliage from five blueberry  
25 cultivars: ‘Bluecrop’, ‘Bluetta’, ‘Blueray’, ‘Lateblue’, and ‘Jersey’. We complemented this  
26 experimental work with repeated bush-level surveys of a managed blueberry patch for naturally  
27 occurring *D. drexelii* larval clusters. Larval survival and pupal weight were significantly higher  
28 on ‘Lateblue’ foliage than from the ‘Bluecrop’, ‘Bluetta’, and ‘Jersey’ cultivars. The blueberry  
29 patch surveys found more *D. drexelii* larval clusters on ‘Bluehaven’, ‘Collins’, and ‘Darrow’  
30 bushes than on the cultivars ‘Earliblue’ and ‘Jersey’. The low *D. drexelii* occurrence and  
31 performance on the ‘Jersey’ cultivar suggests that this variety may be appropriate for areas where  
32 this pest is common; conversely, their high occurrence on ‘Bluehaven’ ‘Collins’, and ‘Darrow’  
33 suggests that these cultivars may be particularly vulnerable. Cultivar-level variation in herbivore  
34 vulnerability highlights how understanding plant-pest interactions can help manage agricultural  
35 species.

36           **Keywords**

37           Herbivory, preference, performance, defoliator

## 38 Introduction

39 Herbivore fitness is influenced by host plant phenotype. Although wild plants experience  
40 strong selection for herbivore tolerance and/or resistance, domesticated plants are subjected to  
41 different pressures. Selection for high fruit yield in domesticated plants, for example, can reduce  
42 plant defense against herbivores (Sanchez-Hernandez et al. 2006, Turcotte et al. 2014,  
43 Hernandez-Cumplido et al. 2018). Larvae of *Lymantria dispar* L. (Lepidoptera: Erebiidae) grow  
44 more quickly and have lower mortality when reared on domesticated versus wild-type *Vaccinium*  
45 *corymbosum* L. (Hernandez-Cumplido et al. 2018). Wild-type tomatoes (*Solanum lycopersicum*  
46 L.) produce more phenolic compounds than domesticated ones (Sanchez-Hernandez et al. 2006),  
47 and growth rate of the moth *Manduca sexta* L. (Lepidoptera: Sphingidae) is negatively correlated  
48 with such phenolics (Stamp and Yang 1996, Yang and Stamp 1996).

49 *Vaccinium corymbosum* (hereafter ‘blueberry’) is a deciduous ericaceous plant native to  
50 North America grown commercially for its fruits. As with other agricultural plants, blueberry has  
51 multiple cultivars that have been selected for yield, flavor, or pest/disease resistance (Lobos and  
52 Hancock 2015, Clift et al. 2017, Rodriguez-Saona et al. 2019). Cultivar-related differences in  
53 herbivore growth and mortality have been recorded in lepidopteran species such as *Streblote*  
54 *panda* (Hübner, 1820) (Lepidoptera: Lasiocampidae) (Calvo and Molina 2010), and tephritid  
55 flies such as *Bactrocera dorsalis* (Hendel), *Ceratitis capitata* (Wiedemann, 1824) (Follett et al.  
56 2011) and *Rhagoletis mendax* (Curran) (Liburd et al. 1998).

57 Members of the notodontid genus *Datana* (Walker, 1855) are defoliating pests of  
58 agricultural, silvicultural, and horticultural crops (Cutler and Harris 1979, Harris 1983). *Datana*  
59 *drexelii* (Hy. Edwards) (hereafter ‘*Datana*’) is a native defoliating pest of ericaceous plants in  
60 the genera *Vaccinium* L. and *Gaylussacia* (Kunth). Females lay clusters of up to 200 eggs on

61 suitable host plants; their gregarious nature, combined with the fact that larvae can reach six cm  
62 in length, make it an especially destructive pest (Wagner 2005). While this insect does not  
63 directly attack fruit, its defoliation of blueberry bushes reduces the following year's flowering  
64 and subsequent fruit crop (Lyrene 1992, Williamson and Miller 2000). We reared *Datana* larvae  
65 on different blueberry cultivars and measured their survival to pupation and pupal weight. In  
66 addition, we repeatedly surveyed a patch planted with multiple blueberry cultivars for naturally-  
67 occurring clusters of *Datana* larvae. Together, the data reveal substantial differences in *Datana*  
68 preference for and occurrence on different blueberry cultivars.

## 69 **Materials and Methods**

70 Performance Assay: In June 2019, we mated adults from a lab colony of *Datana drexelii*,  
71 reared on wild-type *V. corymbosum*, in an outdoor emergence cage at the University of Rhode  
72 Island's East Farm research facility (Kingston, RI). We collected their eggs and assigned five  
73 each to 946 mL polypropylene cups (Pactiv LLC, Lake Forest, IL). Each cup was randomly  
74 assigned to one of five blueberry cultivars: 'Bluecrop', 'Blueray', 'Bluetta', 'Jersey', or  
75 'Lateblue'. There were 22-23 replicate cups per cultivar. Eggs in a given cup generally hatched  
76 on the same day; in three cups one day, and in one cup two days, elapsed between the emergence  
77 of the first and last hatchling. Host foliage from the appropriate cultivar was added to the cup  
78 immediately following emergence of the first hatchling. Larvae received four-leaf sections of  
79 foliage from current year's growth (as indicated by soft, green bark); no other leaf position  
80 standardization was done. Prior to adding foliage to each container, each piece was dipped in a  
81 2% bleach (=0.1% NaOCl) solution and allowed to air dry; this measure was taken to decrease  
82 the threat posed by pathogenic fungi and bacteria (Trivedy et al. 2011). Foliage was replaced  
83 every three days or as needed to ensure a constant food supply.

84 Four days after the last hatchling in a given cup eclosed, we weighed all hatchlings  
85 together and counted the number of larvae and unhatched eggs. The total number of hatched  
86 larvae was our starting number of larvae for a cup, regardless of how many eggs hatched. We  
87 used this data to calculate post-hatching survival. Larvae were subsequently counted and  
88 weighed together each week; we recorded the date each larva entered the prepupal phase.  
89 Prepupae were left in cups until all larvae in a cup reached such a state or died. When all  
90 prepupae had either died or become pupae, each pupa was sexed, weighed and then held in a 6L  
91 polypropylene bin (Sterilite Corp, Townsend, MA) of moist coconut coir for overwintering.

92 Occurrence Assay: In summer 2019, we conducted a six-week *Datana* survey of an East  
93 Farm blueberry patch enclosed in bird-proof netting that did not exclude insects. The patch  
94 consisted of 240 bushes arranged in eight rows of 30 bushes. The cultivars represented (numbers  
95 of bushes in parentheses) were ‘Bluecrop’ (25), ‘Bluegold’ (5), ‘Bluehaven’ (15), ‘Bluejay’ (15),  
96 ‘Blueray’ (15), ‘Bluetta’ (15), ‘Chandler’ (5) ‘Collins’ (20), ‘Darrow’ (20), ‘Earliblue’ (30),  
97 ‘Herbert’ (15), ‘Jersey’ (15), ‘Lateblue’ (15), ‘Northland’ (15), and ‘Reka’ (15). Cultivars were  
98 arranged in five-bush groups within a given row.

99 Between July 16<sup>th</sup> and August 26<sup>th</sup>, we conducted 15 total censuses (with as many as nine  
100 days and as few as one day between censuses) for *Datana* larval clusters. We walked on both  
101 sides of each bush and scanned for larval clusters. We spent a minimum of thirty seconds per  
102 bush and longer if necessary and recorded the number of larval clusters on each bush before  
103 removing them from the bush. Following the final census, we measured the height and maximum  
104 width of each bush.

105 Statistical Analysis: For the performance assay, mean pupal weight and percent survival  
106 (average per cup) to pupation were analyzed using analysis of covariance (ANCOVA), with

107 ‘cultivar’ as the main effect and ‘hatch date’ and, because we were concerned about sex-  
108 mediated performance differences, ‘number of female pupae per cup’ as covariates. We excluded  
109 15 cups in which only a single larva hatched, leaving a total of 98 cups (=replicates). When the  
110 ANCOVA revealed a significant main effect, we used Tukey’s HSD tests ( $\alpha=0.05$ ) to  
111 differentiate between treatment. We also conducted an overall linear correlation analysis between  
112 weight and survival across all cultivars.

113 For the occurrence assay, we summed the total number of larval clusters counted per  
114 bush over the fifteen censuses. Prior to analysis, we removed data from two cultivars, ‘Bluegold’  
115 and ‘Chandler’, only represented by a single five-bush cluster within the patch; all other cultivars  
116 were each represented by between three and six five-bush clusters. During our surveys, we  
117 noticed that small (~0.5 m in height) recently-planted bushes had virtually no larval clusters  
118 regardless of their cultivar. We addressed this bias by excluding bushes below the 10<sup>th</sup> percentile  
119 in height (0.7 m) from the analysis; this excluded 27 bushes from five cultivars but only two of  
120 108 larval clusters. We used GLMM (poisson distribution with log-link function) to analyze the  
121 203-bush data set. The model was generated with the main effect ‘cultivar’ and the blocking  
122 variables ‘row’ and ‘column’ as random effects; ‘bush height’ was included as a covariate. The  
123 GLMM was initially run using both blocking variables; the non-significant blocking variable  
124 ‘row’ was then removed and the resulting GLMM re-run. When the GLMM revealed a  
125 significant main effect of ‘cultivar’, we used likelihood-ratio  $\chi$ -square tests ( $\alpha=0.05$ ; controlled  
126 for type 1 errors due to multiple comparisons) to differentiate between treatments.

127 All analyses were performed using JMP 9.0.0 (SAS 2010).

## 128 **Results**

129 Performance Assay: Larvae reared on ‘Lateblue’ pupated at nearly three times the weight  
130 of larvae reared on ‘Blueray’, ‘Bluetta’, and ‘Jersey’ (0.375 g versus 0.127 g, respectively;  $F_{4,91}$   
131 = 3.18,  $P = 0.017$ ; Fig. 1A). Survival to pupation was also higher on ‘Lateblue’ than on  
132 ‘Bluecrop’, ‘Bluetta’, and ‘Jersey’ (16.9% versus 5.1%;  $F_{4,91} = 3.62$ ,  $P = 0.009$ ; Fig. 1B). Hatch  
133 date affected survival, with later-hatching larvae having higher mortality ( $F_{1,91} = 7.84$ ,  $P =$   
134 0.006). The number of female pupae per cup was correlated with both weight at and survival to  
135 pupation (both  $P < 0.001$ ). There was a significant cultivar-level correlation between mean pupal  
136 weight and mean survival to pupation ( $R^2 = 0.84$ ,  $F_{1,3} = 15.6$ ,  $P = 0.029$ ).

137 Occurrence Assay: We found a total of 108 *Datana* larval clusters over the six-week  
138 course of the survey. The distribution of larval clusters over time was as follows: 14 on July 16<sup>th</sup>,  
139 ten on July 18<sup>th</sup>, 35 on July 22<sup>nd</sup>, one on July 23<sup>rd</sup>, five on July 25<sup>th</sup>, three on July 26<sup>th</sup>, one on  
140 July 29<sup>th</sup>, two on July 30<sup>th</sup>, two on July 31<sup>st</sup>, 11 on Aug. 1<sup>st</sup>, 12 on Aug. 2<sup>nd</sup>, one on Aug. 6<sup>th</sup>, two  
141 on Aug. 11<sup>th</sup>, eight on Aug. 20<sup>th</sup>, and one on Aug. 26<sup>th</sup>. Cultivars differed in *Datana* colonization  
142 (L-R  $\chi^2 = 28.01$  with 12 df,  $p = 0.006$ ; Fig. 2), with ‘Bluehaven’, ‘Collins’, and ‘Darrow’ having  
143 more *Datana* clusters (1.00/bush, 0.75/bush, and 0.85/bush, respectively) than either ‘Jersey’ or  
144 ‘Earliblue’ (0.13 and 0.07 per bush, respectively). Neither bush height (L-R  $\chi^2 = 0.52$  with 1 df,  $p$   
145 = 0.47) nor column (L-R  $\chi^2 = 39.3$  with 29 df,  $p = 0.096$ ) affected *Datana* colonization.

## 146 Discussion

147 *Datana* larval performance in the lab did not overlap with field observations. Despite  
148 high larval performance on ‘Lateblue’, larval occurrence on it was not the highest on this cultivar  
149 in the field survey. High *Datana* densities on ‘Bluehaven’, ‘Collins’, and ‘Darrow’, cultivars not  
150 included in our performance assay, suggest they may be particularly suitable to this pest. In  
151 contrast, both occurrence and performance were significantly lower for ‘Earliblue’ and ‘Jersey’



152 than other tested cultivars (Figs. 1, 2). This implies that ‘Earliblue’ and ‘Jersey’ may have  
153 antixenotic and antibiotic effects on *Datana*.

154 Mortality in the performance assay occurred mostly within a week of hatching, when  
155 larvae were small and inconspicuous. Our high early larval mortality across treatments could  
156 indicate that either cultivated blueberry is unsuitable for this species (comparison to wild-type  
157 blueberry is needed to determine this), or perhaps that the unnaturally low early instar densities  
158 could be reducing the feeding ability, and thus survival, of hatchlings (Dave Wagner, pers.  
159 comm). It is also possible that the quality of the cut blueberry may diminish more quickly than  
160 the foliage is replaced (within 24hrs instead of 3 days), malnourishing larvae. If similarly high  
161 levels of hatchling mortality also occurred in the field survey, we could have missed some  
162 oviposition events when all larvae died prior to reaching a detectable size. Because of this, the  
163 patterns in our field survey data likely reflect some combination of female oviposition preference  
164 and plant resistance to early-instar larval feeding. While most larval clusters contained a similar  
165 number (10-20 individuals) of small 2<sup>nd</sup>-3<sup>rd</sup> instar larvae, we failed to detect some clusters until  
166 they contained 4<sup>th</sup>-5<sup>th</sup> instar larvae. The laboratory-based oviposition choice tests necessary to  
167 isolate the role of female preference may be complicated by this species’ habit of readily  
168 ovipositing on container walls and other artificial objects.

169 Our work could be extended to comparisons of *Datana* interactions with cultivated versus  
170 wild-type blueberry, as well as with other *Vaccinium* species. Selective breeding for pest  
171 resistance (Lobos and Hancock 2015) and the incorporation of several related *Vaccinium* species  
172 into *V. corymbosum* cultivars (Lobos and Hancock 2015) may alter the cultivar’s suitability to  
173 *Datana*. Both ‘Lateblue’ and ‘Jersey’, cultivars on which larvae did the best and worst, are pure  
174 *V. corymbosum*, but ‘Bluecrop’ is 4% *Vaccinium angustifolium* (Aiton, 1789) and ‘Bluetta’ is

175 28% *V. angustifolium*. Some cultivars are only 42% *V. corymbosum* and contain genes from up  
176 to five other species (Lobos and Hancock 2015). Intrageneric variation in herbivore  
177 susceptibility has been described for other *Vaccinium* (Ieri et al. 2013) species as well as for  
178 genera ranging from *Asclepias* L. (Waterbury et al. 2019) to *Quercus* L. (Rieske and Dillaway  
179 2008).

180 In summary, there were blueberry cultivar-related differences in occurrence and  
181 performance of this blueberry defoliator. This information could prove useful for cultivar  
182 selection in areas where this pest becomes a major problem, and highlights how understanding  
183 plant-pest interactions can help reduce the need for costly chemical or mechanical (removal of  
184 individual larval clusters) treatments.

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189

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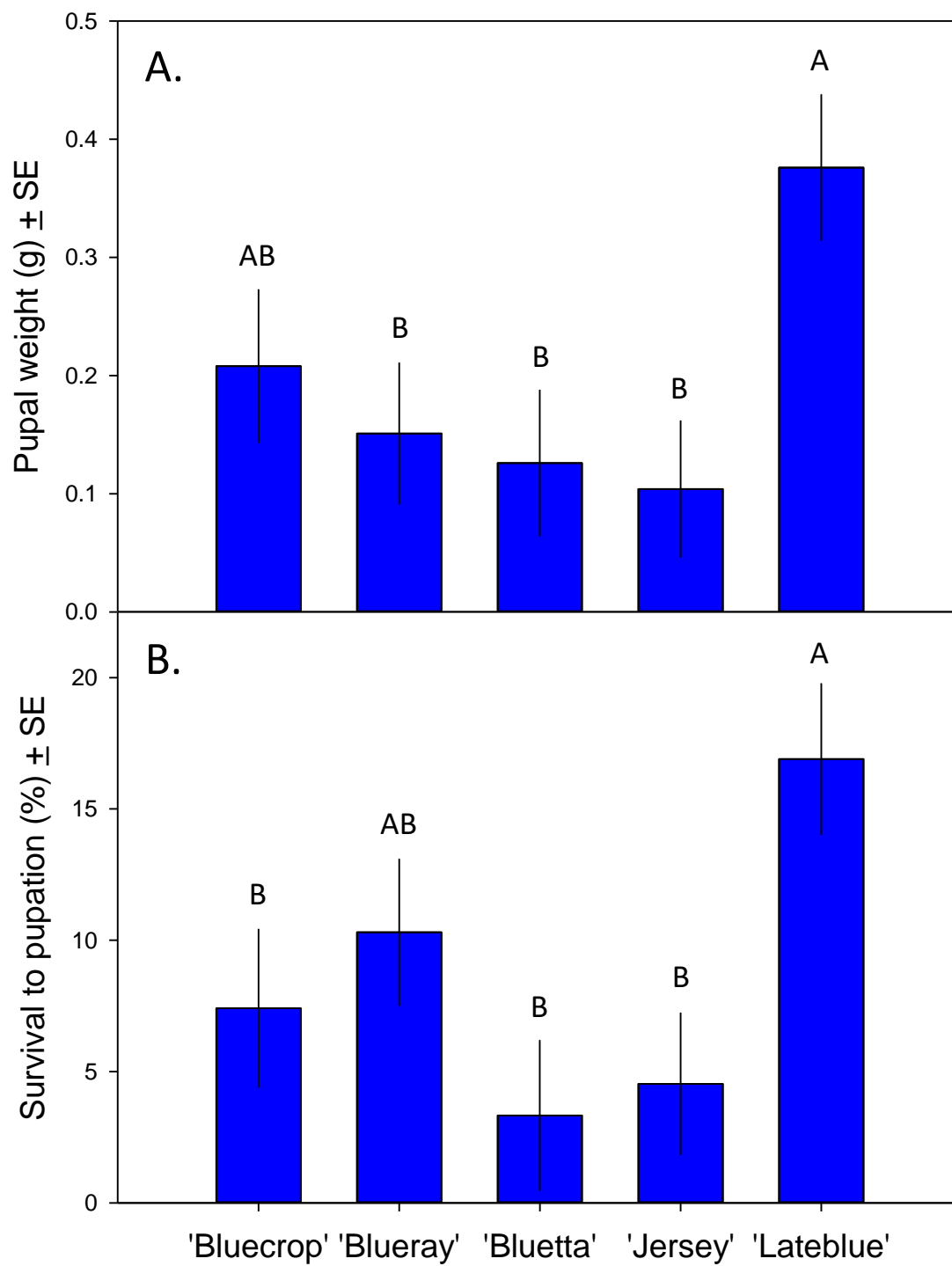
238 **Figure Legends**

239 Figure 1. Mean ( $\pm$  SE) *Datana drexelii* pupal weight (A) and mean ( $\pm$  SE) *D. drexelii*  
240 survival to pupation (B) when reared on five different *Vaccinium corymbosum* cultivars. Bars  
241 with different uppercase letters are significantly different (Tukey's HSD at  $\alpha = 0.05$ ).

242 Figure 2. Mean  $\pm$  (SE) *D. drexelii* larval clusters counted per bush for 13 *V. corymbosum*  
243 cultivars over the course of six weeks and fifteen censuses. Cultivars in dark blue were included  
244 in the performance assay (Fig. 1). Bars with different uppercase letters are significantly different  
245 (Tukey's HSD at  $\alpha = 0.05$ ).

246

Figure 1.



247 Figure 2.

248

249

