

Bird predation and the host-plant shift by the goldenrod stem galler

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Abstract—Escape from natural enemies may favor the incorporation of a novel host plant into the diet of an herbivorous insect. This scenario has been suggested for the recent host-plant shift by the goldenrod stem galler, *Eurosta solidaginis* Fitch (Diptera: Tephritidae), from the ancestral host *Solidago altissima* L. (Compositae) to the derived host *Solidago gigantea* Ait. In this study, we examined the effects of predation from downy woodpeckers, *Picoides pubescens* L. (Aves: Picidae), and black-capped chickadees, *Parus atricapillus* L. (Aves: Paridae), on these two host races of insects at the western edge of their zone of sympatry. Based on a field census, bird predation was concentrated near the cover of trees where *S. gigantea* tends to occur; few attacks occurred in the open where *S. altissima* is prevalent. We conducted a field experiment to evaluate the preference of these avian predators for galls of the two host races when differences in the microgeographic distribution, size, and height of galls were controlled. In allopatric sites where only *S. gigantea* occurs, attacks by birds were 58% more frequent on *S. gigantea* than on *S. altissima* galls. Similar results were found for sympatric sites, although the difference in attack was only 26% and not significant. We could find no difference in the toughness of galls or the nutritional value of a larva within the gall (in terms of biomass) to explain avian preference for the *S. gigantea* host race; however, we found that from 1999 to 2000, the *S. gigantea* race offered a 27–107% higher reward rate (i.e., the probability that a gall harbored a larva of *E. solidaginis*) than the *S. altissima* race. Our studies suggest that avian predators can assess a gall's content prior to pecking it open, preferring galls that are inhabited by both *E. solidaginis* larvae and the inquilin predator *Mordellistena convicta* Leconte (Coleoptera: Mordellidae). It is possible that birds have either learned through experience or evolved through natural selection to choose the more profitable *S. gigantea* galls. Finally, our results suggest that avian predators act against the maintenance of two distinct host races in the midwestern United States.

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Résumé—Une façon pour un insecte herbivore d'échapper à ses ennemis naturels consiste peut-être à adopter une nouvelle plante hôte. Ce scénario a été envisagé pour expliquer le passage récent de la mouche gallicole de la verge d'or, *Eurosta solidaginis* Fitch (Diptera : Tephritidae) de son hôte ancestral, *Solidago altissima* L. (Compositae), à un hôte dérivé, *Solidago gigantea* Ait. Au cours de cette étude, nous avons examiné les effets de la prédation exercée par les pics mineurs, *Picoides pubescens* L. (Aves : Picidae), et les mésanges à tête noire, *Parus atricapillus* L.

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(Aves : Paridae), sur ces deux races d'insectes à la limite ouest de leur zone de sympatrie. Un recensement sur le terrain a démontré que la prédation se faisait surtout près de la couverture des arbres où a tendance à se trouver *S. gigantea* et peu d'attaques ont eu lieu en milieu ouvert où *S. altissima* prédomine. Nous avons procédé à une expérience en nature pour évaluer les préférences de ces oiseaux prédateurs pour les galles des deux races d'insectes en tenant compte des différences dans leur répartition microgéographique, leur taille et la hauteur de leurs galles. Aux sites allopatriques où ne vit que *S. gigantea*, les attaques des oiseaux étaient de 58 % plus fréquentes sur les galles de *S. gigantea* que sur celles de *S. altissima*. Des résultats semblables ont été obtenus aux sites sympatriques, bien que la différence dans la fréquence des attaques n'ait été que de 26 %, une valeur non significative. Nous n'avons pas trouvé de différences dans la dureté des galles ou dans la valeur nutritive (biomasse) de la larve à l'intérieur de la galle qui puissent expliquer la préférence des oiseaux pour la race *S. gigantea*; cependant, nous avons constaté qu'en 1999–2000, la race *S. gigantea* présentait un taux de réussite (*i.e.* la probabilité de trouver une larve d'*E. solidaginis* dans la galle) de 27 à 107 % plus élevé que celui de la race *S. altissima*. Nos résultats indiquent que les oiseaux prédateurs sont capables d'évaluer le contenu d'une galle avant de l'ouvrir et qu'ils préfèrent celles qui contiennent à la fois des larves d'*E. solidaginis* et leur prédateur inquilin *Mordellistena convicta* Leconte (Coleoptera : Mordellidae). Les oiseaux peuvent avoir acquis par expérience, ou sous l'influence de la sélection naturelle, une préférence pour les galles de *S. gigantea*, plus profitables. Enfin, nos résultats indiquent aussi que les oiseaux prédateurs défavorisent le maintien de deux races hôtes d'insectes dans le Midwest américain.

[Traduit par la Rédaction]

Introduction

The rapid and extensive diversification of insects is widely considered to be a population-genetic consequence of ecological specialization (Mayr 1976; Price *et al.* 1980; Futuyma and Moreno 1988). For phytophagous insects, the incorporation of a novel host plant into the diet (*i.e.*, a host shift) can represent an important route by which diversification and speciation occur (Bush 1975; Futuyma and Moreno 1988; Jaenike 1990; Thompson 1996). A significant hurdle in the evolution of a shift and subsequent specialization on a novel host plant is that the herbivore must simultaneously acquire a behavioural preference and physiological adaptations for its new host. Predators, parasitoids, or parasites may play an important role in overcoming this hurdle. If natural enemies selectively forage for herbivorous prey on the ancestral host plant, the reduced mortality associated with the novel host may compensate for the lower performance and poor physiological adaptation expected on that host (enemy-free space hypothesis; Gilbert and Singer 1975; Price *et al.* 1980; Jeffries and Lawton 1984). Natural enemies may reinforce the continued use of the novel host plant, leading to the formation of distinct host races (*sensu* Diel and Bush 1984) and eventually sibling species.

Studying the role of natural enemies in the formation and maintenance of host races is an empirical challenge given the temporal scale at which these processes operate; however, good candidates for study are those species that have recently undergone hosts shifts and are incompletely differentiated on the novel and ancestral hosts (Brown *et al.* 1995). For these species, interactions with natural enemies are more likely to be reflective of conditions at the inception of the host shift. To date, there have been only a few studies to explore host shifts *via* enemy-free space (Brown *et al.* 1995; Feder 1995; Sumerford and Abrahamson 1995; Keese 1997; Gratton and Welter 1999; Hufbauer and Via 1999; Rossi *et al.* 1999).

The goldenrod stem galler, *Eurosta solidaginis* Fitch (Diptera: Tephritidae), is one such species that appears to recently have undergone a host shift and now exists as two

distinct host races: one on *Solidago altissima* L. (Compositae) and the other on *S. gigantea* Ait. (evidence summarized in Abrahamson *et al.* 1994; Abrahamson and Weis 1997). Furthermore, it has been inferred from allozyme and mitochondrial DNA analyses that *S. altissima* is the ancestral host and that at least one host shift occurred, probably in New England (Waring *et al.* 1990; Brown *et al.* 1996; Itami *et al.* 1998; PT Smith, K Krager, JT Cronin, and S Kambhampati, unpublished data). At the putative site of the *E. solidaginis* host shift, Brown *et al.* (1995) surveyed sources of mortality in 25 host-race populations and found support for the enemy-free space hypothesis. Mortality was significantly higher on the ancestral than on the derived host plant, and this was brought about primarily by differential larval parasitism by *Eurytoma obtusiventris* Gahan (Hymenoptera: Eurytomidae). Predation by birds [black-capped chickadees, *Parus atricapillus* L. (Aves: Paridae), and downy woodpeckers, *Picoides pubescens* L. (Aves: Picidae)], which can be substantial during the winter (*e.g.*, Milne 1940; Schlichter 1978; Confer and Paicos 1985; Abrahamson *et al.* 1989), was statistically indistinguishable between the two host races (but generally greater for *S. altissima* than *S. gigantea*).

From Brown *et al.*'s (1995) study, it could not be ascertained whether avian predators had a foraging preference for one of the host races. Within sympatric field sites, *S. gigantea* and *S. altissima* exhibit significant microgeographic differences in their distributions (Abrahamson and Weis 1997). The former plant species is more often found on moist clay-loam soils, whereas the latter species is found on better-drained sandy-loam soils. In the Great Plains region of North Dakota and Minnesota, the open prairie tends to be relatively dry (favorable for *S. altissima*) and areas adjacent to tree lines tend to be more moist (favorable for *S. gigantea*) (JT Cronin, personal observation). Because chickadees and woodpeckers prefer to forage near cover (Schlichter 1978; Confer and Paicos 1985; Abrahamson *et al.* 1989), it seems likely that these possible distributional differences in the Great Plains would translate into differential mortality between host races. No information was provided by Brown *et al.* (1995) regarding the distribution of host races or their relation to vegetative cover. Equivalent avian predation rates could have been due to an indifference by predators to *E. solidaginis* host races, or it could have resulted from some combination of microgeographic and host-race preferences that canceled each other out. For example, if avian predators tend to forage near trees where *S. gigantea* is most prevalent, but have an inherent preference for *S. altissima* galls, the proportion of galls preyed upon may be similar between the two goldenrod species. To better understand the role of avian predators in the host shift by *E. solidaginis*, experimental manipulations that account for microgeographic differences in host-race distributions are necessary.

In this study, we first confirmed that microgeographic differences exist in the distribution of *E. solidaginis* galls on *S. gigantea* and *S. altissima* and that avian mortality varies with proximity to woodland cover. In addition, we conducted field experiments in sites allopatric and sympatric for *E. solidaginis* host races to examine host-race preference by avian predators. By controlling for gall location, height above ground, and size, we excluded all but plant- and race-specific differences among galls. We also evaluated the predator's ability to discriminate among gall contents, and how the frequency of occurrence of *E. solidaginis* larvae within a gall, nutritional value *E. solidaginis* larvae, and gall toughness might influence predation by birds. Finally, we addressed the role of avian predators in the initiation and maintenance of the derived host race.

Methods

Study system

Along the border between the United States and Canada, from the Atlantic coast

to the Midwest, galls from the *S. altissima* and *S. gigantea* host races can be found in sympatry (Lichter *et al.* 1990; Waring *et al.* 1990; Brown *et al.* 1995; Itami *et al.* 1998; Cronin and Abrahamson 2001). *Eurosta solidaginis* is univoltine. Adults emerge from the previous year's galls in late spring, mate, and oviposit on the terminal buds of goldenrods. Larvae induce the formation of spherical galls that are visible 3 weeks later. At summer's end, the larva prepares an exit tunnel that extends from the central chamber to the epidermis of the gall. Third-instar larvae overwinter within galls that are still attached to senescent goldenrod stems, pupate, and emerge through the exit tunnel the following spring. Uhler (1951) and Abrahamson and Weis (1997) provide further details on the biology and life history of *E. solidaginis*.

Eurosta solidaginis larvae within mature galls are an important food source for downy woodpeckers and black-capped chickadees throughout the winter months (Milne 1940; Schlichter 1978; Confer and Paicos 1985). Attacks by these two species can be easily distinguished as chickadees tear large irregular holes, whereas woodpeckers make narrow conical holes (Confer and Paicos 1985; Abrahamson and Weis 1997). Percentage of galls attacked by birds is variable among sites and years, ranging from 2.3 to 80.5% (Uhler 1951, 1961; Cane and Kurczewski 1976; Moeller and Thorgerson 1978; Schlichter 1978; Confer and Paicos 1985; Weis and Abrahamson 1985; Walton 1988; Weis *et al.* 1992). Currently, no information exists on avian preference for the different host races.

Microgeographic distribution of galls and predation

We conducted a field survey in late-winter 2001 to determine whether differences existed in the spatial distributions of *S. gigantea* and *S. altissima* galls and gall attack rates by chickadees and woodpeckers. Five sites were chosen from within the Felton Prairie Wildlife Management Area (20 km northeast of Moorhead, Minnesota; 47°03'00''N, 96°26'79''W) that were 0.3–10 km apart, sympatric for the two host races, and had a well-defined shelter belt or stand of mature hardwood trees. We walked a transect at two distances from the tree line, 0–5 and >10 m, and recorded the host race of each gall and whether it was preyed upon by woodpeckers or chickadees. We recorded data for, at most, 1 gall per step along the transect and a total of 100 galls from each distance (in two transects, fewer galls were available). The proportion of galls that were *S. gigantea* near (0–5 m) and away (>10 m) from the tree line was compared using a paired *t* test (transects paired within a site). Similarly, a paired *t* test was used to assess differences in predation rates at the two distances.

Host-race preference by birds

We conducted winter field experiments to determine whether woodpeckers and chickadees have a preference for *S. gigantea* or *S. altissima* galls when differences in distribution, height, and size of galls are eliminated. Experiments were conducted at two sites in western Minnesota, one in which *S. gigantea* occurs in allopatry (Chicog Wildlife Management Area, 17 km southeast of Crookston, Minnesota; 47°35'83''N, 96°23'20''W) and the other in which both host races occur in sympatry (Felton Prairie). The experiments in Chicog and Felton Prairie were conducted from 18 January to 11 April 2000 and from 15 January to 8 March 2001, respectively.

An experimental replicate consisted of field-collected galls (with 10 cm of stem below the gall) from each host race that were placed together at a site and exposed to attack by avian predators. An equal number of galls from each host race were used, 25 at Chicog and 20 at Felton. Each gall was inserted by its stem into the end of a thin bamboo stake. The stakes were similar in appearance and color to winter-worn senescent

goldenrod stems, and previous field studies indicated that avian predation rates were indistinguishable between galls on natural and these artificial stems (JT Cronin, unpublished data). In this study, bamboo stakes with galls were placed in two rows that were parallel to, and at a distance of 3 m from, the tree line. The host race of galls alternated between stakes, and each stake and row was separated by 1 m. The height of each gall was set initially at 45 cm above the snow. Finally, galls were matched for size (maximum diameter perpendicular to the stem) to within 1 mm. Among replicates, galls varied in size, but all were large and suitable for bird attacks (range 22–30 mm; Abrahamson *et al.* 1989). A total of six replicates were established at Chicog and seven at Felton Prairie, and the distance between replicates was 0.3–1.6 km.

Galls were checked weekly for evidence of bird attacks and the replicate was terminated when bird predation was between 40 and 60%. We inspected the galls in the laboratory and categorized each as either unattacked, chickadee attacked, or woodpecker attacked. We excluded galls that had bird damage that was too slight (*e.g.*, scoring) to ascertain the perpetrator. Differences in avian predation between the two host races were evaluated with a paired *t* test, where the proportion of bird-attacked galls of *S. gigantea* and *S. altissima* within a replicate represented the pair. Separate tests were performed for the allopatric and sympatric sites.

Factors influencing host-race preference

We explored several possible reasons why chickadees and woodpeckers may exhibit a host-race preference. Differential predation of host races may be due to differences in the expected reward rate of galls (*i.e.*, the probability that a gall contains a *E. solidaginis* larva), occurrence of other gall inhabitants, nutritional value of *E. solidaginis* larvae, or toughness of galls between the two races.

We determined whether there were differences between host races in terms of gall inhabitants [*E. solidaginis*, the inquiline and facultative predator *Mordellistina convicta* Leconte (Coleoptera: Mordellidae), the solitary endoparasitoid *Eurytoma gigantea* Walsh (Hymenoptera: Eurytomidae), or empty], and whether these gall inhabitants influenced avian predation rates. Studies have suggested that birds may avoid empty galls or those inhabited by species other than *E. solidaginis* (Schlichter 1978; Confer and Paicos 1985). We dissected all the galls that were used in the Felton Prairie experiment and identified the contents. For unattacked galls, the inhabitants could be directly observed and easily identified. For attacked galls, in which the inhabitants were removed, we used the traces left behind to identify them (Uhler 1951). Galls that contained a healthy *E. solidaginis* larva were identified by the presence of an emergence tunnel. Galls that contained an *Eurytoma* parasitoid had larger central chambers, darker frass, and no emergence tunnel. Living *M. convicta* larvae were often found in attacked galls and their presence was also indicated by distinct tunnels through the gall tissue.

For the galls used in the Felton Prairie (sympatric) experiment, we tested for differences between the two host races in the proportion of each gall inhabitant using paired *t* tests. Separate tests were used for each inhabitant type (empty, *E. solidaginis* only, *M. convicta* only, both *E. solidaginis* and *M. convicta*). Because only large galls were used, *E. gigantea* parasitoids were rare (<2%). To correct for an inflated Type-I error rate associated with these four nonindependent tests, we used a sequential Bonferroni correction based on the Dunn-Šidák method (Box 9.9, Sokal and Rohlf 1995). The critical level for rejection of each null hypothesis was $\alpha' = 1 - (1 - \alpha)^{1/k}$, where $\alpha = 0.05$ (experimentwise error rate) and $k =$ number of tests (this number decreases by one with each rejection of the null hypothesis). According to Holm (1979) and Rice (1989) the power of this sequential test is much improved over standard Bonferroni procedures. To test whether gall inhabitants influenced bird predation, we

first computed the proportion of galls in each of the four inhabitant categories and host race that were attacked by birds. We tested for differences in proportional attacks by avian predators between all six possible pairs of gall inhabitants (*S. gigantea* and *S. altissima* galls were treated separately), using separate paired *t* tests. As before, we used the sequential Bonferroni method in evaluating the significance of these six nonindependent tests from each host plant.

Additional data on the frequency of gall inhabitants in the two host races were gathered from galls collected in sympatry from The University of North Dakota's Oakville Prairie Station (16 km west of Grand Forks, North Dakota; 47°56'00"N, 96°19'24"W); the source of galls for the preceding experiment. In November 1999, and again in 2000, a large collection of *S. gigantea* and *S. altissima* galls was made. The galls were dissected and the contents identified. Because this is an open prairie with few trees, there were no bird-attacked galls. The 1999 and 2000 collections represent unbiased estimates of the gall contents for the Chicog and Felton Prairie experimental galls, respectively. Differences between host races in the frequency of galls occupied by *E. solidaginis* larvae were evaluated with a χ^2 test (separate test for each year).

In addition to quantifying the reward rate for each host race, we also determined whether the nutritional value of the *E. solidaginis* larvae (in terms of larval biomass) differed between the two races. Thirty-six winter-collected galls that contained larval *E. solidaginis* were used from each race. We measured the maximum diameter of each gall, then removed the larva and dried it for 48 h at 50°C. Larval dry biomass was obtained using a Sartorius electrobalance. Differences in biomass between the two races were assessed with a one-way ANCOVA, where gall size was the covariate.

To examine the possible influence of gall toughness on host-race preference by birds we quantified the toughness of *S. gigantea* and *S. altissima* galls with a penetrometer that was described by Feeny (1970) and modified for galls (see Craig *et al.* 1990). We measured the force (kilograms of water added at 0.08 L/s) required to insert a pointed steel rod (6.2-mm diameter) 4 mm into a gall. The galls were collected in late-winter 2001 and kept frozen at -3.3°C to maintain galls in their natural winter condition. Galls were removed from the freezer one at a time immediately before testing. For each gall, toughness was measured at three evenly spaced points and an average was computed. The galls were subsequently dissected and the inhabitants identified. The effect of host race, gall inhabitant, and gall size (covariate) on gall toughness was assessed with a two-way ANCOVA.

Results

Microgeographic distribution of galls and predation

Among the five sympatric sites in Felton Prairie, we found significant differences in the microgeographic distributions of the two *E. solidaginis* host races. The *S. gigantea* race accounted for 94.7% of the galls near the tree line but only 24.4% of the galls out in the open ($t_4 = 4.44$, $P = 0.011$). As expected for avian predators, predation was higher along tree lines (38.8%) than in adjacent open fields (1.4%; $t_4 = 9.59$, $P = 0.001$). Consequently, the percentage of galls attacked was higher for the *S. gigantea* than the *S. altissima* race (32.7 versus 2.2%, respectively; $t_4 = 5.98$, $P = 0.004$). This trend was consistent for both chickadees and woodpeckers: chickadees attacked 25.4% of *S. gigantea* galls and 1.9% of *S. altissima* galls, whereas woodpeckers attacked 7.3% of *S. gigantea* galls and 0.3% of *S. altissima* galls.

Host-race preference by birds

Chickadees accounted for 69.8% of bird attacks at the allopatric site, with woodpeckers attacking the remaining 30.2%. Proportions of galls attacked were more equitable between the two bird species at the sympatric site (46.3% chickadees, 49.4% woodpeckers, and 4.2% unknown). At the allopatric site, 60.6% of the *S. gigantea* and 38.3% of the *S. altissima* experimental galls were attacked ($t_5 = 4.81$, $P = 0.005$). At the sympatric site, a similar result was found, i.e., 61.9% of *S. gigantea* and 49.1% of *S. altissima* galls were attacked ($t_7 = 1.78$, $P = 0.121$). Because attacks by one avian predator preclude attacks by the other, it was not possible to statistically compare the separate responses of chickadees and woodpeckers to the two host races. We do note that both species had higher attack rates on *S. gigantea*, suggesting that they responded similarly to host races.

Factors influencing host-race preference

In the sympatric experiment, the frequency of galls containing only *E. solidaginis* larvae did not differ between *S. gigantea* (42.1%) and *S. altissima* (22.4%) ($\alpha' = 0.0125$, $t_6 = 2.75$, $P = 0.033$). Low statistical power (0.29) was likely responsible for our inability to detect this almost twofold difference between host plant species. The frequencies of the remaining gall-inhabitant types were also indistinguishable between the two host races (separate paired t tests, mean differences <7.5%, $P > 0.08$). Similar results were found over 2 years at Oakville Prairie, the source of galls for our experiments; however, *S. gigantea* galls were more likely to harbor *E. solidaginis* larvae than *S. altissima* galls in both 1999 (21.9 versus 10.6%; $\chi^2_1 = 18.95$, $P < 0.001$) and 2000 (36.9 versus 29.0%; $\chi^2_1 = 8.36$, $P < 0.004$).

For galls from the sympatric experiment, comparisons of predation rates between all possible pairs of gall inhabitants (examined separately for each host race because of differences in overall attack rates) revealed few significant differences (Fig. 1). Galls inhabited by *E. solidaginis* larvae had 6% (*S. gigantea* galls) and 24% (*S. altissima* galls) higher attack rates by avian predators than empty galls; however, these differences were not significant (Fig. 1). For *S. altissima* galls, the ability to detect a significant difference between empty and *E. solidaginis* inhabited galls may have been hampered by relatively low statistical power (0.53). Interestingly, *S. altissima* galls containing both an *E. solidaginis* and a *M. convicta* larva were preyed upon at significantly higher rates than galls with other inhabitants (Fig. 1). Finally, we could find no evidence that woodpeckers selectively attacked galls containing an exit tunnel (a possible indication that a healthy *E. solidaginis* larva was present; Moeller and Thogerson 1978; Confer and Paicos 1985). Of the galls that were attacked by woodpeckers, only 59.3% of the *S. gigantea* galls and 42.6% of the *S. altissima* galls had exit tunnels (neither of these percentages differed significantly from 50%; $\chi^2_1 = 1.85$, $P = 0.174$ for *S. gigantea*; $\chi^2_1 = 1.04$, $P = 0.307$ for *S. altissima*). If a tunnel was present, however, woodpeckers were likely to use them to access the central chamber: 68.8% for *S. gigantea* galls ($\chi^2_1 = 6.75$, $P = 0.009$) and 71.4% for *S. altissima* galls ($\chi^2_1 = 5.14$, $P = 0.023$). Because of the large holes torn into galls by chickadees, it was not always possible for us to ascertain whether an exit tunnel was present. Therefore, we could not assess whether exit tunnels were used by chickadees in selecting galls.

The nutritional quality of *E. solidaginis* larvae, in terms of their biomass, increased significantly with increasing gall size ($F_{1,66} = 31.83$, $P < 0.001$; Fig. 2). When gall size was controlled for, we could find no difference in biomass between larvae from *S. gigantea* and *S. altissima* galls ($F_{1,66} = 0.30$, $P = 0.584$). Gall toughness also did not vary with host race ($F_{1,75} = 1.75$, $P = 0.190$), gall inhabitant (*E. solidaginis* only,

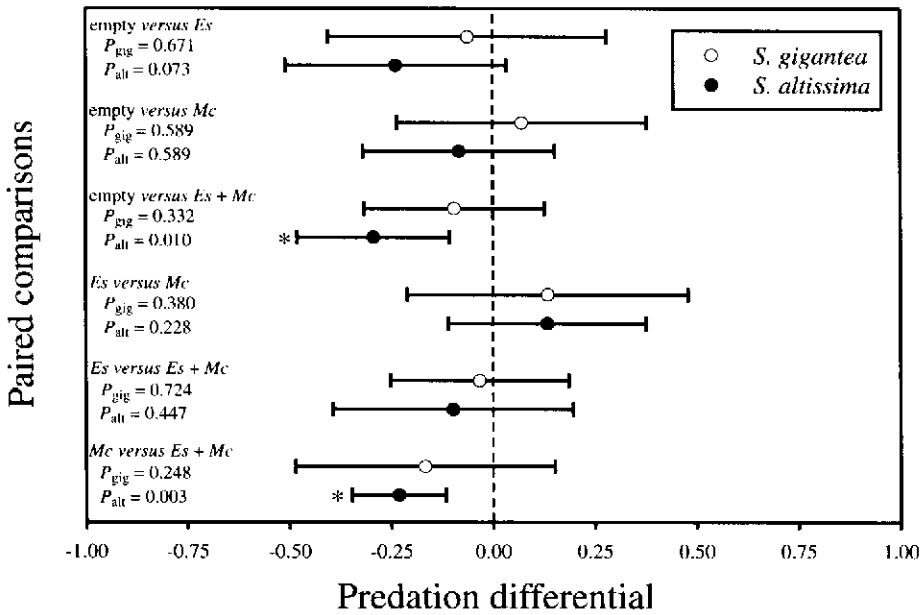


FIGURE 1. Differences in predation between galls with one of four inhabitants: empty, *Eurosta solidaginis* larva only (*Es*), *Mordellistena convicta* larva only (*Mc*), and both larvae together (*Es + Mc*). The predation differential is the mean difference in proportion of galls attacked of the first minus second inhabitant ($\pm 95\%$ confidence intervals). *P* values are reported for each test, and the two *E. solidaginis* host races (*alt*, *Solidago altissima*; *gig*, *S. gigantea*) were evaluated separately. An asterisk denotes a significant difference between two inhabitant types based on sequential Bonferroni corrections (overall Type-I error rate for the six tests per host race was set at $\alpha = 0.05$).

M. convicta only, or *E. solidaginis* and *M. convicta*; $F_{2,75} = 0.58$, $P = 0.564$), or gall size ($F_{1,75} = 0.35$, $P = 0.554$) (Fig. 3).

Discussion

In the Great Plains, where we conducted our research, *S. gigantea* is found primarily in association with the edge of wet, poorly drained areas inhabited by trees, whereas *S. altissima* grows in drier open fields away from tree cover. Similar moisture-related differences in the distribution of the two goldenrod species were noted in Abrahamson and Weis (1997). In our census of five sympatric sites, we found that natural levels of predation on *S. gigantea* galls were 14 times higher than on *S. altissima* galls. Several factors could explain the differential predation of *E. solidaginis* host races. First, black-capped chickadees and downy woodpeckers are known to concentrate their foraging efforts near cover (see also Schlichter 1978; Confer and Paicos 1985; Abrahamson *et al.* 1989), and consequently may have preyed almost exclusively on *S. gigantea* galls. Second, avian predators prefer larger galls (Confer and Paicos 1985; Abrahamson *et al.* 1989; Lichter *et al.* 1990), which, on average, are the *S. gigantea* galls (Lichter *et al.* 1990; Abrahamson *et al.* 1994; Brown *et al.* 1995; Sumerford and Abrahamson 1995). Third, birds more frequently attack galls on taller stems (Cane and Kurczewski 1976) and *S. gigantea* galls may have stood higher above the snow line than *S. altissima* galls. Fourth, all else being equal, chickadees and woodpeckers may simply prefer the *S. gigantea* host race as a food source.

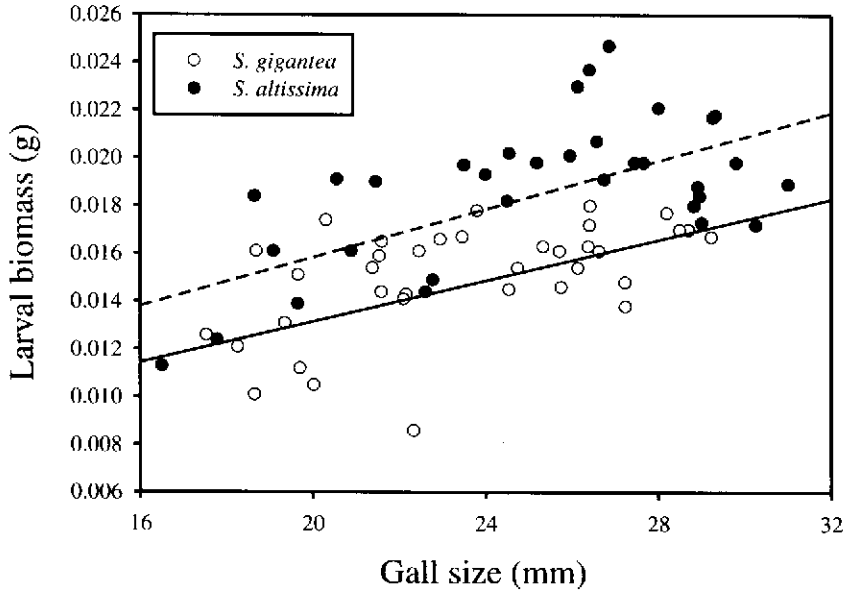


FIGURE 2. Biomass of larval *Eurosta solidaginis* in relation to gall size for the *Solidago gigantea* and *Solidago altissima* host races. Least-squares regression lines are provided for each host race (solid for *S. gigantea* and broken for *S. altissima*). Two outliers (Studentized residuals > 3.0) were omitted.

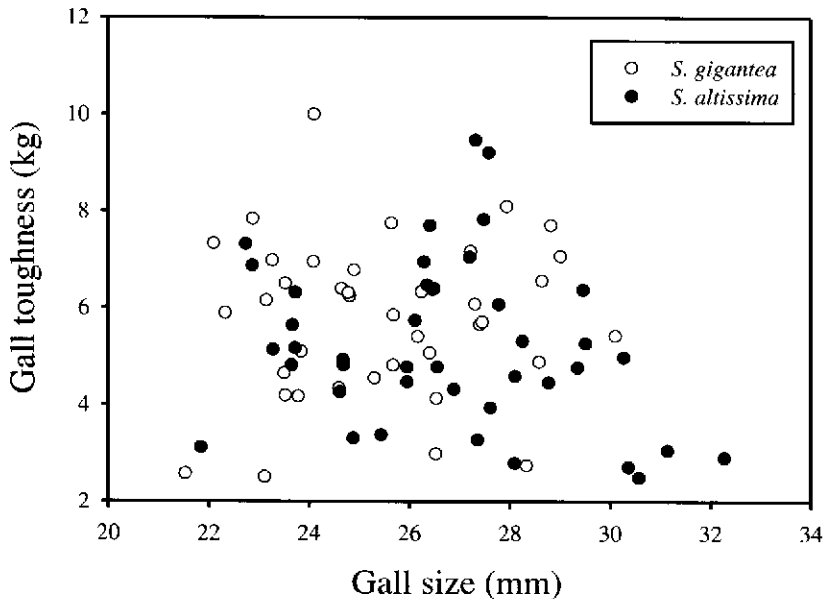


FIGURE 3. The relationship between gall toughness (the mass of water, kg, required to push a pointed steel rod 4 mm into a gall) and the size of *Solidago gigantea* and *Solidago altissima* galls.

Our experimental study allowed us to address this last unexplored possibility for the higher predation rates on *S. gigantea* than on *S. altissima* galls. In our placement of galls out in the field, we controlled for differences in microgeographic distributions,

gall sizes, and gall heights. It was our intent to minimize all differences among galls except for the host race of origin. We found that avian attacks were 58 and 26% more frequent on *S. gigantea* than on *S. altissima* galls in the allopatric and sympatric sites, respectively; although only for the allopatric site was this difference statistically significant. Both chickadees and woodpeckers had elevated attacks on *S. gigantea* galls, but we could not test this statistically. The strong response to *S. gigantea* in the allopatric site, relative to the sympatric site, may be indicative of an habituated or evolved response by the birds to the prey species with which they are normally exposed (Alcock 1997).

We conclude that at least under certain field conditions, avian predators can discriminate between host races and exhibit a preference for *S. gigantea*. Higher predation rates in our census data, therefore, could have been due in part to prey preference. Microgeographic effects primarily, and gall-size differences secondarily, were also likely to contribute to the 14-fold difference in predation in those field sites. In the field survey by Brown *et al.* (1995), the cause for the higher (but not statistically significant) predation on *S. altissima* than on *S. gigantea* galls cannot be understood without some information on the distribution, size, and height of galls of the *E. solidaginis* host races in the New England area.

We examined several possible factors that might explain the higher preference for *S. gigantea* than *S. altissima* galls. One possibility is that *S. gigantea* galls are likely to yield greater rewards, in terms of their nutritive value or probability that an *E. solidaginis* is present in the gall (*i.e.*, the reward rate). For a given gall size, the two host races are of equal biomass, and therefore probably of equal caloric value. In contrast, we found that for galls collected from Oakville Prairie in 1999 and 2000 and used in the allopatric and sympatric experiments, *S. gigantea* galls were significantly more likely to have an *E. solidaginis* larva in them than *S. altissima* galls (2.1 time more in 1999 and 1.3 times more in 2000). Brown *et al.* (1995) also found higher frequencies of *E. solidaginis* larvae in *S. gigantea* galls. Thus, *S. gigantea* galls may be generally more profitable to avian predators. The higher predation rates of *S. gigantea* relative to *S. altissima* galls corresponded fairly closely with the difference in *E. solidaginis* frequencies in the two experimental studies. *Solidago gigantea*, relative to *S. altissima* galls, were 2.1 times more likely to contain an *E. solidaginis* larva and 1.6 times more likely to be preyed upon by birds in the allopatric site, and 1.3 times more likely to contain an *E. solidaginis* larva and be preyed upon by birds in the sympatric site. Avian preference for the *S. gigantea* galls may therefore be the result of an evolved response (natural selection favoring the choice of galls with the higher reward rate) and (or) a learned response (experience directing the birds to the gall type that has the higher reward rate) to the more profitable host race. Long-term studies are needed to determine whether this difference in reward rate is temporally invariant.

Our data indicate that avian predators can discriminate among galls bearing certain inhabitants. Although we did not detect a statistically significant difference, attack rates on *E. solidaginis* inhabited galls, relative to empty galls, were 6% higher for the *S. gigantea* host race and 24% higher for the *S. altissima* host race. Interestingly, for the *S. altissima* host race significantly higher proportions of galls were attacked when inhabited by both an *E. solidaginis* and a *M. convicta* larva than when empty or inhabited by *M. convicta* alone (similar but nonsignificant trends were found for the *S. gigantea* host race). Perhaps the semiochemical or auditory signal emanating from *S. altissima* galls containing both of these larvae is sufficient to be detected by woodpeckers and chickadees. In contrast to our results, Schlichter (1978) suggested that woodpeckers have the ability to discriminate among gall contents and avoid galls containing *M. convicta*. Woodpeckers attacked three times as many galls with *E. solidaginis* only as galls containing *E. solidaginis* and *M. convicta*. Moreover, Confer and Paicos (1985)

found that woodpeckers were more likely to abandon galls that did not possess an exit tunnel, and therefore contained no *E. solidaginis* larvae. The difference in results between our study and these two studies could be due in part to differences in gall sizes used. For our experiments, we used only large galls, while Schlichter (1978) and Confer and Paicos (1985) made use of the range of gall sizes found in nature. It may be easier for birds to evaluate the contents of small galls and reject those inhabited by *M. convicta*. Moreover, smaller galls are less likely to have exit tunnels because of premature larval death and a preference for small galls by the parasitoid *E. gigantea* (Weis and Abrahamson 1985; Abrahamson *et al.* 1989; Weis *et al.* 1992) than larger galls. Thus, a preference for galls with exit tunnels may really be a preference for large galls; large galls are known to be preferred by woodpeckers and chickadees (Confer and Paicos 1985; Abrahamson *et al.* 1989; Lichter *et al.* 1990). By using only large galls, we would have eliminated a primary factor upon which discrimination among galls is based. If the above arguments are true, then we must qualify our previous statement about the discriminatory abilities of avian predators to indicate that for large galls, birds have little ability to discriminate among gall contents.

Another factor that could influence the profitability of an *E. solidaginis* larva is the amount of effort required for a bird to access the central chamber where a larva resides. Tougher (harder) galls may require more time and energy to open, thus reducing their value to the predator. In this study, we found no consistent difference in toughness of *S. gigantea* and *S. altissima* galls that might explain the difference in predation between them. Furthermore, there was no evidence that other gall inhabitants affected gall toughness. Therefore, we can rule out the possibility that *M. convicta* alters the toughness of the gall by tunneling through the gall tissues or that empty galls can be distinguished by their toughness. Although we found no evidence to suggest that toughness affects *E. solidaginis* predation, Craig *et al.* (1990) found that small galls of the shoot-gall sawfly, *Euura lasiolepis* (Smith) (Hymenoptera: Tenthredinidae), were significantly softer than large galls, making them more vulnerable to parasitoid attack.

To summarize, at the western edge of the sympatric zone for the two *E. solidaginis* host races, the *S. gigantea* race suffered 14 times more predation by downy woodpeckers and black-capped chickadees than the *S. altissima* race. A closer proximity to arboreal cover, larger galls on average, and a higher reward rate all likely contributed to the preference by avian predators for the *S. gigantea* race. These results suggest that birds act against the maintenance of distinct host races in this region of *E. solidaginis*' distribution, and may explain why host races are genetically more closely related in the midwest than in the northeast (Waring *et al.* 1990; Itami *et al.* 1998). If similar processes were in operation at the time of host-race formation, the barrier to the host shift would have been strengthened, not weakened (*i.e.*, enemy-free space promoting the host shift is not supported for avian predators). In New England where evidence of a host shift from *S. altissima* to *S. gigantea* took place (Brown *et al.* 1996), a different pattern was observed; there was a nonsignificant tendency for birds to prefer *S. altissima* over *S. gigantea* galls (Brown *et al.* 1995). These results might suggest that birds contributed to the initiation and (or) maintenance of the host shift in the northeast, but worked against the initiation (if an independent shift took place in this region; PT Smith, K Krager, JT Cronin, and S Kambhampati, unpublished data) and (or) maintenance of a host shift in the midwest.

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