HOST PLANT GENOTYPE INFLUENCES SURVIVAL OF HYBRIDS BETWEEN *EUROSTA SOLIDAGINIS* HOST RACES

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Extrinsic, host-associated environmental factors may influence postmating isolation between herbivorous insect populations and represent a fundamentally ecological cause of speciation. We investigated this issue in experiments on hybrids between the host races of *Eurosta solidaginis*, a fly that induces galls on the goldenrods *Solidago altissima* and *S. gigantea*. To do so, we measured the performance of parental host races and their hybrids on five genotypes of *S. gigantea* and nine genotypes of *S. altissima* to test hypotheses about how variation in plant genotype affects performance (i.e., fitness) and potentially influences gene flow between these host races. We found that rates of gall induction and of survival to adult emergence by hybrid larvae were significantly lower than those of both parental host races on both host species, adding support to the hypothesis that there is partial postmating isolation between the host races. Hybrid flies significantly varied in their performance across plant genotypes of both host species. A significant interaction between the effects of plant genotype and mating treatment (parental vs. hybrid crosses) on larval performance indicated that the relative suitability of particular plant genotypes differed between the parental host races and their hybrids. These patterns illustrate a poor correspondence between optimal parental and hybrid environments, consistent with the hypothesis that these host races are partially isolated due to extrinsic (ecological) factors. Based on these findings, we discuss the possibility that plant genotypes in which hybrid performance is high can facilitate hybridization and gene flow between partially reproductively isolated populations of herbivorous insects, thus affecting the dynamics of ecological speciation.

KEY WORDS: Ecological speciation, *Eurosta solidaginis*, Extrinsic isolation, host race, hybrid zone, intrinsic isolation, *Solidago altissima*, *Solidago gigantea*.

The host races of *Eurosta solidaginis* are hypothesized to be in the process of sympatric speciation (Craig et al. 1993, 1997, 2001), and genetic models of sympatric speciation indicate that it is only possible under sustained divergent selection, such as where intermediate (hybrid) genotypes have reduced fitness compared to more extreme (parental) genotypes (Kawecki 2004). This reduced hybrid fitness can result from divergent selection on parental forms to adapt to different ecological factors. In turn, this divergent selection may, for example, directly yield environment-dependent hybrid inviability (extrinsic isolation) or may indirectly yield either extrinsic isolation or environment-independent genetic incompatibilities (intrinsic isolation) as a byproduct (Coyne and Orr 2004; Kawecki 2004). Intrinsic postzygotic isolation has been defined as occurring when "Hybrids suffer developmental defects causing poor or partial inviability" Coyne and Orr (2004, p. 249). However, because performance cannot be measured in isolation from the environment, it may be more useful to define "intrinsic" isolation as reduced hybrid performance due to a poor match of the hybrid genotype to all environments. Extrinsic post-zygotic isolation is defined as occurring when "Hybrids enjoy normal development

but suffer decreased viability, as they cannot find a suitable eco-logical niche," Coyne and Orr (2004, p. 249). Hybrid performance is thus reduced due to a poor match between the hybrid genotype and specific characteristics of the parental niches. Demonstrating the existence of extrinsic isolation can be achieved by separating the decrease in hybrid fitness that occurs across all environments from the decrease in fitness that occurs due to the mismatch of the hybrid with the parental environment.

In the present study, we measured hybrid and parental host race performance (survival) on a range of plant genotypes to de-termine if there is a decrease in hybrid performance due to poor adaptation to the parental host race niche. Under extrinsic isola-tion, hybrids should have a different combination of genes for host plant adaptation than the parental host races. As a result, hybrids should respond differently to intraspecific host plant genotypic variation than do the parental host races. We thus predict that if extrinsic isolation affects these flies, then parental and hybrid performance on plant genotypes will not be correlated, and hy-brids will have lower overall performance due to a high frequency of mismatches between their genes for host plant adaptation and host plant characters. In this case, this lack of correlation would reflect a Genotype × Environment interaction that differs between parental and hybrid classes.

Alternatively, intrinsic isolation could entirely explain any re-duced fitness exhibited by hybrids of the *E. solidaginis* host races. If only intrinsic isolation exists, then the hybrids will not differ genetically from the parental host races with respect to genes that determine the relative degree of adaptation to parental hosts, and they will not differ from the parental populations in their relative responses to host plant genetic variation. That is, even though hy-brids may have lower viability than parental host races, the relative success of a hybrid on a given plant genotype will be predicted by that of parental host race. In this case, there would be no G × E interaction and variation in performance across host genotypes would simply reflect host quality per se. The null hypothesis of our study is that hybrid performance and parental host race perfor-mance will be correlated on host plant genotypes and that hybrid performance will be lower on all host plant genotypes because hy-brids are intrinsically poorly adapted to the overall environment.

Although the primary focus of this study is on the exami-nation of evidence on postmating isolation between *Eurosta* host races, our use of host plant genotypes as test environments al-lowed us to gain insights on a rarely studied issue. Specifically, they allow us to consider the potential role of intraspecific varia-tion in host plant quality or acceptability on opportunities for gene flow between host-associated insect populations. The frequency and geographic pattern of hybridization between partially repro-ductively isolated populations determines the rate and pattern of gene flow between them and a great deal of attention has been focused on the geography of gene flow through the study of hy-brid zones (Barton and Hewitt 1985; Harrison 1993; Coyne and Orr 2004). We propose that for gene flow between host races of herbivorous insects, host plant variation plays an analogous role to that of geography in hybrid zone studies. Indeed, the heteroge-neous distributions of plant genotypes suitable for hybrid survival can present a situation akin to a mosaic hybrid zone of habitat patches presenting divergent adaptive challenges. This analogy may be particularly appropriate for *E. solidaginis* because host plant genotype has been shown to have an important influence on larval survival of the parental host races on the host plants of both of them (Craig et al. 1999, 2000; Cronin et al. 2001). Indeed, although intraspecific host plant variation has been shown to very commonly cause variation in phytophagous insect performance (Karban 1992; Craig and Itami 2007), its role in determining hy-brid survival-–and thus influencing gene flow between partially reproductively isolated populations-–has not been explored.

THE HOST RACES OF *EUROSTA SOLIDAGINIS*

Uhler (1951) described the life history of *E. solidaginis*, and Abra-hamson and Weis (1997) provided an extensive review of the ecol-ogy and evolution of this species. *Eurosta solidaginis* is univol-tine and at our study site adults emerged in mid-to-late May. After mating, females inject an egg into the unexpanded leaves of a host plant's terminal bud. After hatching, the larva burrows sev-eral millimeters into the bud before settling just below the apical meristem. Larval feeding is necessary to induce and maintain gall formation. *Eurosta solidaginis* larvae complete development and diapause in the gall.

Eurosta solidaginis (Diptera: Tephritidae) has formed host races that induce galls on two species of goldenrod, *Solidago altissima* and *S. gigantea* (Waring et al. 1990; Craig et al. 1993, 1997, 2001; Brown et al. 1996; Itami et al. 1998; Stireman et al. 2005). We refer to flies reared from *S. gigantea* as gigantea flies, and those from *S. altissima* as altissima flies. Multiple factors contribute to the reproductive isolation between these host races. First, the emergence times of the host races differ, contributing to temporal isolation (Craig et al. 1993; Itami et al. 1998). Second, each host race mates on its own host species, resulting in habitat isolation (Craig et al. 1993). Third, reduced performance of F1 and backcross hybrids between the host races demonstrates a degree of postmating isolation (Craig et al. 1997).

We tested three predictions about variation in the perfor-mance of parental *E. solidaginis* host races and their hybrids across multiple host plant genotypes of *S. altissima* and *S. gigantea*. First, we predicted that mean hybrid performance would be lower than mean parental host race performance across all genotypes, corroborating past evidence of postmating isolation (Craig et al. 1997). Second, we predicted that hybrid performance would vary among host plant genotypes. Third, we predicted that the relative performance of parental host races and hybrids across different

host plant genotypes would differ rather than be strongly correlated. This pattern would indicate that hybrids perform best in different environments (host genotypes) than their parnetal host race, consistent with environment-dependent extrinsic isolation. We additionally discuss the potential implications of our findings on host-genotype-specific hybrid fitness on gene flow between these host races.

Methods and Materials

PLANT GENOTYPE INFLUENCE ON PARENTAL HOST RACE AND HYBRID SURVIVAL

Performance is any proxy measure of fitness, including offspring survival, growth or reproduction (Singer 1986; Thompson 1988; Craig et al. 1989). We used two performance measures to evaluate the influence of plant genotype on *E. solidaginis*: survival to the stage of gall formation and survival until adult emergence. Gall formation is induced by larval feeding and thus indicates larval survival to that stage. Gall formation additionally predicts whether offspring will survive to emergence (Craig et al. 1997).

We measured *E. solidaginis* performance on *S. altissima* and *S. gigantea* genotypes in an experiment at Cedar Creek Natural History Area, Bethel, Minnesota, USA. *Solidago* test plants were obtained from Carlos Avery Wildlife Area, Wyoming, Minnesota, 20 km from Cedar Creek. All test plants representing a single genotype were originally obtained from rhizomes that were physically connected. These rhizomes were cut into equal size sections and propagated in 3.8-L pots for a year, and then transferred to 18.9-L pots and grown for three years, prior to use in this experiment. Generally, a single rhizome will yield a single stem (ramet) that may produce multiple new rhizomes and associated stems each year. Thus, after three years a single genetic individual consists of multiple stems per pot. Each stem generally has a single terminal bud, which is the oviposition site of *E. solidaginis*.

Ten 5 × 8 m cages were used in the experiment. Each cage housed 85 potted plants. These comprised numbered host genotypes (number of replicates) as follows: *Solidago altissima* = 1 (9), 2 (6), 3 (6), 4 (7), 5 (10), 7 (4), 8 (4), 9 (3), and 10 (4); and *Solidago gigantea* = 2 (5), 3 (8), 4 (7), 5 (9), and 6 (3). Pots were randomly assigned positions within the cages with respect to host species and genotype.

Test flies were reared from galls collected within a 50-km radius of the experimental site. Galls were over-wintered in outdoor cages and then placed in screen cages prior to adult emergence. Adult flies were collected each morning before mating occurred. These virgins were then mated before being released into the test cages on 29 May 1995.

We measured survival from egg to adult emergence for both parentals and hybrids in cages assigned to "parental host race larvae" and "hybrid larvae" treatments. The parental host race cages received five gigantea females that had mated with gigantea

males, and five altissima females that had mated with altissima males. All these females thus oviposited eggs with a pure parental host race genotype. The F1 hybrid cages received five altissima females that had mated with gigantea males and five gigantea females that had mated with altissima males. These females thus oviposited eggs with a hybrid genotype. Five cages were assigned to each treatment.

Insertion of the ovipositor leaves a visible wound, an "ovipuncture" that can be used to identify cases of oviposition. An egg is not inserted with every ovipuncture, but Craig et al. (1997) found a highly significant correlation between the number of ovipunctures and the number of eggs oviposited for the populations used in this study (altissima flies, $y = 0.056 + 0.196x$, $r^2 = 60.2\%$, $P < 0.0001$, gigantea flies, $y = 0.519 + 1.76 \log x$, $r^2 = 28.8\%$, $P < 0.0001$). Ovipunctures were counted between 3 June and 5 June 1995. Three cages had very few ovipunctures so a second set of five mated females was released in these cages on 4 June 1995; ovipunctures in these cages were recounted on 9 June 1995. Cages were removed on 21 June 1995, more than a week after the cessation of oviposition by wild *E. solidaginis*. Galls were collected in October 1995, placed in individual rearing bags, and over-wintered outdoors. Flies emerging from these galls were collected in May and June 1996.

Cages contained females of both host races and both host plants, but we assumed that females oviposited almost exclusively on their natal host plants, as has been demonstrated in earlier studies Craig et al. (1993, 2001). Oviposition of hybrid eggs on the nonnatal host plant of the female would have no impact on our interpretation of the results. Oviposition by the pure parental host races into the nonnatal host species would result in very low gall induction and survival (Craig et al. 1997), leading to a conservative interpretation of our results because it would decrease our chances of finding a significant difference in performance between the hybrids and the parental host races.

EVALUATING POTENTIAL CONFOUNDING FACTORS

We also considered two explanations for possible differences in *E. solidaginis* performance among plant genotypes other than our presumed cause: differential genotype-specific larval survival. First, we evaluated the possibility that our estimate of adult emergence rates reflected variation in the number of eggs laid per ovipuncture across host genotypes. To do so, we released five mated females for 24 h in cages with 15 stems of 19 *S. altissima* genotypes in a randomized design. We then collected buds and counted the number of ovipunctures and eggs in each bud. This experiment was conducted at Bucknell University, Lewisburg, Pennsylvania, USA (see Craig et al. 2000). Second, we evaluated the possibility that our estimates reflected differences in levels of larval exploitation competition (Hess et al. 1996; Craig et al. 1999). We did so by determining whether rates of oviposition and

emergence were negatively correlated across genotypes. Such a relationship would indicate reduced larval survival at elevated larval densities.

STATISTICAL ANALYSIS

The number of *E. solidaginis* galls formed and the number of *E. solidaginis* that survived to adult emergence were analyzed using a mixed ANOVA with treatment as a fixed effect, plant genotype as a random effect, and cage as a random effect nested within treatment. The number of stems ovipunctured was used as a covariate. We used the general linear model program in the Minitab® statistical package that is suitable for unbalanced designs.

To analyze the differential oviposition experiment we used ANOVA with plant genotype as a random variable, and plant height and number of ovipunctures as covariates. To analyze the larval competition experiment we regressed the mean number of ovipunctures per stem on the arcsine-square-root transformed percent of emergences per ovipuncture, across genotypes.

Results
PLANT GENOTYPE INFLUENCES ON PARENTAL HOST RACE AND HYBRID SURVIVAL

Mating Treatment and the Mating Treatment × Plant Genotype interaction both had a significant effect on survival until emergence on *S. altissima*, although this interaction was not significant with respect to survival to gall formation. Notably, survival to emergence was relatively high for the parental host race but relatively low for the hybrids on genotypes 7 and 8. The altissima host race larvae had higher survival than the hybrid larvae from ovipuncture to gall formation, and from ovipuncture to emergence on *S. altissima* (Fig. 1, Table 1). *Solidago altissima* plant genotype did not significantly influence either estimate of performance despite exhibiting considerable variation in means. However, the Plant Genotype × Stems Ovipunctured interaction was significant (Table 1, Fig. 1) and analysis of individual genotypes indicated that survival increased with the number of ovipunctures whereas on other genotypes it did not. Thus this interaction term indicates that there was a strong impact of plant genotype on larval performance. Plant genotypes showed large differences in the relative survival of parental host races and hybrids.

On *S. gigantea*, Plant Genotype, Mating Treatment and the Mating Treatment × Plant Genotype interaction all had significant effects on both estimates of larval performance (Table 1, Fig. 1). Parental host race larvae significantly outperformed hybrid larvae for both estimates (Table 1, Fig. 1). Notably, on *S. gigantea* 2, 3, and 4 parental survival was relatively high and hybrid survival was relatively low.

EVALUATING POTENTIAL CONFOUNDING FACTORS

The number of eggs oviposited was significantly related to the
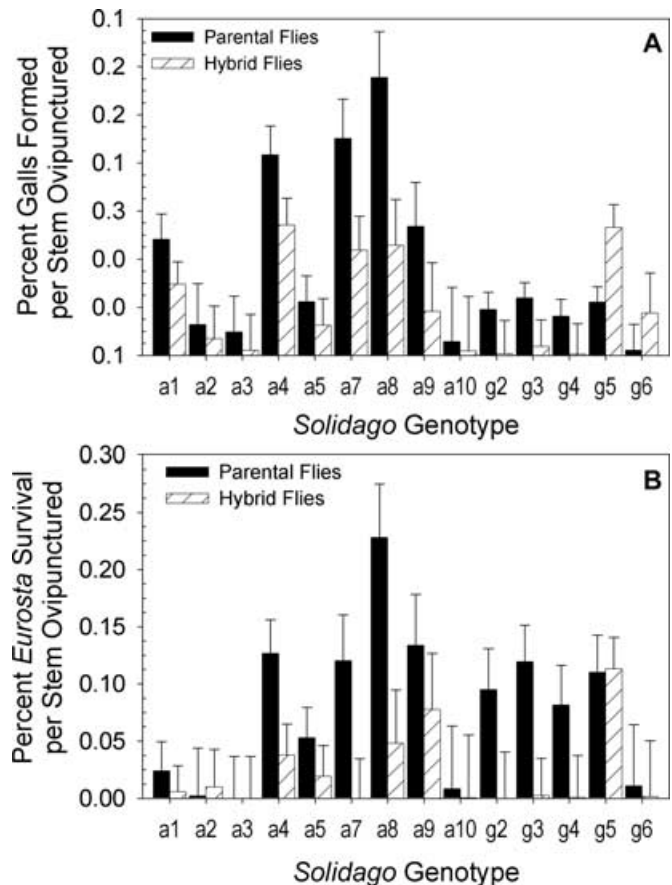
Figure 1. The proportion (+SE) of ovipunctured stems that (A) formed galls in the parental host race and hybrid treatments and (B) that produced adult flies in the parental host race and hybrid treatments. *Solidago altissima* genotypes begin with an "a," and *S. gigantea* genotypes begin with a "g."

number of ovipunctures, but was not significantly influenced by Plant Genotype, Height, or interactions among factors (Table 2). The lack of a significant Plant Genotype × Ovipunctures interaction indicated that the number of eggs per ovipuncture did not differ among plant genotypes and thus did not confound our interpretations. We similarly found no significant relationship between ovipuncture number and larval survival across genotypes, and thus no evidence that larval competition influenced our results.

Discussion

Our experimental results supported all three of our predictions about the impact of plant genotype on parental host race and hybrid survival. First, mean hybrid survival was lower than that of the parental host races, demonstrating that there is postmating isolation between the host races of *E. solidaginis*, as has been previously reported (Craig et al. 1997). Second, we found significant differences among plant genotypes in hybrid survival rates, indicating that hybrid viability is environment dependent. Third,

Table 1. ANOVA to determine the effects of mating treatment, plant genotype, and cage on the survival of the *Eurosta solidaginis* on *Solidago altissima* and *S. gigantea* from ovipuncture to gall formation and from ovipuncture until emergence.

Source	Stems ovipunctured to gall formation			Stems ovipunctured to emergence		
	df	F	P	df	F	P
Solidago altissima						
Mating treatment	1,441	9.10	0.003	1, 441	15.42	0.001
Plant genotype	8,441	0.84	ns	8,441	0.19	ns
Stems ovipunctured	1,441	25.41	0.0001	8,441	12.83	0.0001
Cage (treatment)	8,441	1.67	ns	8, 441	0.66	ns
Mating treatment × plant genotype	8,441	1.26	ns	8, 441	2.09	0.035
Stems ovipunctured × plant genotype	8,441	4.09	0.0001	8,441	2.95	0.003
Solidago gigantea						
Mating treatment	1,272	15.95	0.0001	1,272	6.15	0.027
Plant genotype	4,272	4.37	0.002	4,272	2.48	0.040
Stems ovipunctured	1,272	66.30	0.0001	1,272	8.40	0.004
Cage (treatment)	8,272	0.76	ns	8,272	0.61	ns
Mating treatment × plant genotype	4,272	3.70	0.006	4,272	2.52	0.042

significant differences in the relative survival rates of parental host races versus hybrids were observed among and within genotypes. This poor correlation of parental and hybrid performance on plant genotypes is consistent with the hypothesis that the combination of genes for host plant adaptation in hybrids differed from those of the parental host races as predicted by the extrinsic isolation hypothesis.

Intrinsic postmating isolation may also exist between the host races, and hybrid performance on individual plant genotypes may be the result of the interaction between intrinsic and extrinsic isolation. For example, the low hybrid survival on *S. altissima* genotype 8 could reflect a combination of lack of genes needed to perform well on that genotype (extrinsic factors) and a generally unfit genotype that would perform poorly in any environment (intrinsic factors). Separating the effects of intrinsic and extrinsic postmating isolation is difficult as it requires determining how much of the fitness reduction in hybrids is due to the mismatch of their genes with the characteristics of specific environments (e.g., the parental niche), and how much is due to poor overall adaptation to

Table 2. The effects of plant genotype, plant height, and number of ovipunctures on number of eggs oviposited.

Source	df	Adjusted MS	F	P
Plant genotype	15	0.6914	0.82	ns
Ovipunctures	1	5.4080	6.38	0.013
Height	1	0.0329	0.04	ns
Plant genotype × Height	15	1.0637	1.26	ns
Ovipunctures × Height	1	0.0496	0.06	ns
Plant Genotype × Ovipunctures	15	1.0788	1.27	ns
Error	121	0.8474		
Total	169			

any environment at all. Previously, distinguishing these contributions has been attempted by comparing parental and hybrid performance in field versus laboratory environments (Rice and Hostert 1993; Hatfield and Schluter 1999; Schluter 2000). This approach is based on the notion that to the degree that extrinsic factors are to blame, hybrid inviability exhibited under natural conditions (in which environment-specific fitness effects are encountered) should diminish under the constant environmental conditions of the laboratory. Rundle and Whitlock (2001), however, argued that the same result would be observed even if hybrids were strongly affected by intrinsic factors promoting inviability. This is because such low vigor hybrids might nonetheless perform better in the laboratory due to the "benign" nature of such environments, in which the intrinsic weaknesses of the hybrids are not manifested. Therefore, laboratory environments may fail to help discriminate between the two isolating factors because they remove both the specific parental niche characteristics that produce extrinsic isolation, and the many other miscellaneous environmental challenges that produce intrinsic isolation.

One means of demonstrating a contribution of extrinsic isolation to reduced hybrid performance would require isolating and measuring the effects of the specific ecological factors that exert divergent selection on hybridizing populations. For example, if it were known that divergent selection on two host-specific herbivore populations was entirely a consequence of the different suites of allelochemicals in their respective host species, then a decrease in hybrid performance in response to those compounds could be fairly confidently, if partly, attributed to chemistry-specific extrinsic isolation. A clear delineation of what is meant by intrinsic and extrinsic isolation will allow the development of additional experimental approaches to differentiate between these two components of reproductive isolation and lead to progress in understanding the speciation process.

A novel result of this study, with important implications for speciation biology, is the documented variation in hybrid survival among plant genotypes. Certain plant genotypes serve as better conduits for gene flow between *E. solidaginis* host races than do others. This suggests that the level of gene flow between any given pair of local host race populations—and thus the likelihood that these populations will ultimately fuse versus speciate—will depend on the local composition of host plant genotypes. Some plant genotypes may act as a bridge permitting gene flow between the host races, whereas others may act as a roadblock strongly impeding gene flow and facilitating speciation. The frequency of such host-genotype-based bridges and roadblocks may differ among geographic areas and this may help explain geographic variation in the degree to which populations are reproductively and genetically differentiated. Given abundant evidence that intraspecific host plant variation impacts herbivore performance (Karban 1992; Craig and Itami 2007) it seems highly plausible that it may also commonly affect hybrid performance. In doing so, host plant genetic variation may play a role in speciation of unrecognized importance.

Conclusions

We have shown that intraspecific host plant variation is important in determining hybrid performance in partially reproductively isolated herbivore populations. Our results suggest that *E. solidaginis* may be partly reproductively isolated due to extrinsic postmating isolation. They further illustrate the possibly great potential of genetic variation in host plants to mediate the dynamics of host-associated speciation.

LITERATURE CITED

Abrahamson, W. G., and A. E. Weis. 1997. Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies. Princeton Univ. Press, Princeton, NJ.

Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. Annu. Rev. Ecol. Syst. 16:113–148.

Brown, J. M., W. G. Abrahamson, and P. A. Way. 1996. Mitochondrial DNA phylogeography of host races of the goldenrod ball gall-maker, *Eurosta solidaginis* (Diptera: Tephritidae). Evolution 50:777–786.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer, Sunderland, MA.

Craig, T. P., and J. K. Itami. 2008. The resource constraints hypothesis and the evolution of preference and performance relationships. in K. Tilmon ed. The evolution of plant-insect interactions. Univ. of California Press, Berkeley, CA.

Craig, T. P., J. D. Horner, and J. K. Itami. 1997. Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. Evolution 51:1552–1560.

———. 2001. Genetics, experience and host-plant preference in *Eurosta solidaginis*: implications for host shifts and speciation. Evolution 55:773–782.

Craig, T. P., J. K. Itami, W. G. Abrahamson, and J. D. Horner. 1993. Behavioral evidence for host–race formation in *Eurosta solidaginis*. Evolution 47:1696–1710.

———. 1999. Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. Oikos 86:119–128.

Craig, T. P., J. K. Itami, and P. W. Price. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology 70:1691–1699.

Craig, T. P., J. K, Itami, C. Shantz, W. G. Abrahamson, J. D. Horner, and J. V. Craig. 2000. The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. Ecol. Entomol. 25:7–18.

Cronin, J. T., W. G. Abrahamson, and T. P. Craig. 2001. Temporal variation in herbivore host-plant preference and performance: constraints on host-plant adaptation. Oikos 93:312–320.

Harrison, R. G. 1993. Hybrid zones and the evolutionary process. Oxford Univ. Press, Oxford, U.K.

Hatfield, T., and D. Schulter. 1999. Ecological speciation in sticklebacks: environment–dependent hybrid fitness. Evolution 53:866–873.

Hess, M. D., W. G. Abrahamson, and J. M. Brown. 1996. Intraspecific competition in the goldenrod ball-gallmaker (*Eurosta solidaginis*): larval mortality, adult fitness, ovipositional and host-plant response. Am. Midl. Nat. 136:121–133.

Itami, J. K., T. P. Craig, and J. D. Horner. 1998. Factors affecting gene flow between the host races of *Eurosta solidaginis*. Pp. 375–404 in S. Mopper, and S. Y. Strauss, eds. Genetic structure and local adaptation in natural insect populations: effects of ecology, life history, and behavior. Chapman and Hall, New York.

Kawecki, T. J. 2004. Genetic theories of sympatric speciation. Pp 36–52 in U. Dieckmann, M. Doebeli, J. A. J. Metz, and D. Tautz, eds. Adaptive speciation. Cambridge Univ. Press, Cambridge, U.K.

Karban R. 1992. Plant variation: its effects on populations of herbivorous insects. Pp. 195–215 in R. S. Fritz, and E. L. Simms, eds. Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. Univ. of Chicago Press, Chicago.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: what have we learned in 40 years. Evolution 47:1637–1653.

Rundle, H. D., and M. C. Whitlock. 2001. A genetic interpretation of ecologically dependent isolation. Evolution 55:198–201.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, New York.

Singer, M. C. 1986. The definition and measurement of oviposition preference in plant feeding insects. Pp. 66–94 in J. Miller, and T. A. Miller, eds. Insect–plant relations. Springer, New York.

Stireman, J. O. III, J. D. Nason, and S. B. Heard. 2005. Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. Evolution 59:2573–2587.

Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47:3–14

Uhler, L. D. 1951. Biology and ecology of the goldenrod gall fly, *Eurosta solidaginis* (Fitch). Mem. Cornell Univ. Agric. Exp. Stn., 0300.

Waring, G. L., W. G. Abrahamson, and D. J. Howard. 1990. Genetic differentiation among host-associated populations of the gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). Evolution 44:1648–1655.

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