Gall Flies, Inquilines, and Goldenrods: A Model for Host-race Formation and Sympatric Speciation[1]

WARREN G. ABRAHAMSON,[2] MICKY D. EUBANKS,[3] CATHERINE P. BLAIR, AND
AMY V. WHIPPLE

Department of Biology, Bucknell University, Lewisburg, Pennsylvania 17837

SYNOPSIS.   Host shifts and subsequent host-race formation likely play a more common role in the speciation of herbivorous insects than has generally been recognized. Our studies of the interactions of goldenrod host plants (*Solidago*: Compositae), the gall fly *Eurosta solidaginis* (Diptera: Tephritidae), and the stem- and gall-boring *Mordellistena convicta* (Coleoptera: Mordellidae) provide behavioral, ecological, and genetic evidence of insect host races that may represent incipient species formed via sympatric speciation. *Eurosta solidaginis* has developed genetically differentiated and reproductively isolated host races that are associated with the ancestral host *Solidago altissima* and the derived host *S. gigantea*. Conventional wisdom suggests that shifts even to closely related host plants are limited by host preferences or the inability to utilize a chemically and developmentally distinct host. However, our preliminary work with *Eurosta* from *S. gigantea* implies that host choice and gall induction do not deter a shift to *S. canadensis*. The galling of *Solidago* by *Eurosta* created a new resource that has led to a subsequent host range expansion by the stem-boring beetle. *Mordellistena convicta* from stems and galls are genetically distinct and likely shifted from stems to galls. Beetles from *S. altissima* versus *S. gigantea* galls exhibit assortative mating and higher preference for and/or performance on their natal host. The present-day distributions of the *Eurosta* host races and their behavioral isolating mechanisms do not suggest that geographic isolation was required for their formation; rather these characteristics suggest a sympatric mode of differentiation. Our findings lend credence to recent assertions that sympatric speciation may be an important source of biodiversity.

INTRODUCTION

Understanding the origin of biodiversity is of fundamental importance to evolutionary biology. Despite long study and debate, many details of the speciation process are not well understood, including whether geographic separation is necessary for speciation to occur. For phytophagous insects, many workers (Bush, 1994; Larsson and Ekbom, 1995; Pellmyr and Leebens-Mack, 1998; Feder, 1998) have suggested that a host shift by a specialist herbivore to a closely related or chemically similar host-plant species is a significant, early step in the diversification process. Subsequent reproductive isolation due to host-associated mating may eventually lead to host-race formation and subsequently to speciation. This diversification scenario, however, has been controversial, and until recently limited data have been available to assess the roles of host shifts and host-race formation in the diversification of herbivorous insects.

Recent evidence suggests that host shifts and subsequent host-race formation by herbivorous insects are more common than has previously been recognized (Bush, 1969, 1994; Tauber and Tauber, 1989; Craig *et al.*, 1993; Pratt, 1994; Crozier and Pamilo, 1996; Johnson *et al.*, 1996; Romstock-Volkl, 1997; Sezer and Butlin, 1998; Wood *et al.*, 1999). Host-race formation, as a first step towards sympatric speciation, promotes novel sub-populations that are reproductively isolated from their ancestral population via behavioral barriers (*e.g.,* mate choice, host-plant choice) rather than by

[2] E-mail: abrahmsn@bucknell.edu
[3] Present address of M. D. Eubanks is Department of Entomology and Plant Pathology, Auburn University, AL 36849.

geographic barriers (Feder *et al.*, 1989; Craig *et al.*, 1993, 1997; Crozier and Pamilo, 1996; Kawecki, 1998; Berlocher, 1999). Behavioral barriers can be created when sub-populations of herbivores have strong and specific host-plant preferences and/or positive assortative mating. In some examples (*e.g.,* Craig *et al.*, 1993, 1997, 2001; Itami *et al.*, 1997), strong host-plant association is tightly coupled with effective assortative mating to produce virtually complete reproductive isolation under sympatric conditions. Such coupling of host-plant choice and mate choice is common among herbivorous insects because mating frequently occurs on the host plants. Although not required, such coupling markedly increases the likelihood of host-race formation.

Many of the details of host-race formation have been elegantly documented for the tephritid fly *Rhagoletis pomonella* since Guy Bush first argued the importance of host-race formation in generating biodiversity (*e.g.,* Bush, 1969; McPheron *et al.*, 1988; McPheron and Han, 1997; Feder, 1998; Berlocher, 1998, 1999). Over the past decade, host races have been documented in another tephritid fly, the goldenrod ball gall inducer *Eurosta solidaginis* (Waring *et al.*, 1990; Craig *et al.*, 1993, 1997, 1999, 2000, 2001; Brown *et al.*, 1995, 1996). As a gall inducer, this herbivore has an intimate association with its host plant which, when taken with the insect's mating and oviposition behavior, creates a strong coupling of host-plant choice and mate choice (Craig *et al.*, 1993; Abrahamson *et al.*, 1994; Abrahamson and Weis, 1997). As a consequence, a host shift from the ancestral host-plant *Solidago altissima* to the novel host-plant *S. gigantea* has resulted in the reproductive isolation and differentiation of two host races (Abrahamson *et al.*, 1994; Craig *et al.*, 1994, 2001).

Such host shifts to closely related plants often appear to be limited by herbivore host-plant preference or an herbivore's inability to utilize a chemically and developmentally distinct host. However, for *Eurosta* that induce galls on the closely related but infrequently attacked *S. canadensis*, our on-going studies imply that host choice and gall induction do not restrain a range expansion to *S. canadensis* (unpublished data, A.V.W.). Understanding the factors that both promote and restrain host shifts and host-race formation is fundamental to our comprehension of the speciation of herbivorous insects.

Studies of *Rhagoletis* and *Eurosta*, as well as findings with other insects (*e.g.,* Menken, 1981; Abe, 1991; Singer *et al.*, 1993; Guldemond *et al.*, 1994; Sezer and Butlin, 1998; Wood *et al.*, 1999), make clear that host-race formation occurs frequently and that it is an important evolutionary mechanism that creates biodiversity. In this paper, we report on how the formation of galls by the goldenrod gall fly has promoted a host shift and differentiation of the beetle *Mordellistena convicta*. Below, we provide a summary of the ecological, behavioral, and genetic attributes of host-race formation by the gall-inducer *E. solidaginis*, furnish an overview of the pattern of genetic differentiation and reproductive isolation within the beetle, and discuss the implications for sympatric speciation.

Host-race formation criteria

A host race has been defined as ''a population of a species that is partially reproductively isolated from other conspecific populations as a direct consequence of adaptation to a specific host'' (Diehl and Bush, 1984). Jaenike (1981) more narrowly defined host races as being ''restricted solely or primarily because of different host preference.'' Using these definitions, we have proposed criteria or lines of evidence that may exist in order for conspecific, herbivorous insects that consume different host plants to be considered host races (Abrahamson and Weis, 1997):

1. *Sympatry*—Populations must be sympatric (Jaenike, 1981).
2. *Genetic Differences*—If host-race formation has occurred, then gene flow among host-associated populations should be low and genetic differentiation between sympatric, host-associated populations is likely (Feder *et al.*, 1988; McPheron *et al.*, 1988; Waring *et al.*, 1990). Furthermore, host-race formation

gantea'' fly populations (Waring *et al.*, 1990; Brown *et al.*, 1996). The greater heterozygosity of loci in ''altissima'' populations and the patterns of clade formation based on mtDNA sequences of cytochrome oxidase I & II suggest that the host shift occurred from *S. altissima* to *S. gigantea* and that the shift took place in the northeastern USA (Waring *et al.*, 1990; Brown *et al.*, 1996).

Gene flow between the two host races is reduced by a number of mechanisms including emergence time, assortative mating, adult oviposition choice, and reduced hybrid performance (Craig *et al.*, 1993, 1997, 2000, 2001). For example, emergence times of the two host races are allochronic with the emergence of ''gigantea'' flies occurring on average 10–13 days earlier than ''altissima'' flies (Craig *et al.*, 1993; Abrahamson *et al.*, 1994). Furthermore, ''altissima'' and ''gigantea'' flies demonstrate strong assortative mating in the presence of host plants (Craig *et al.*, 1993). Gall flies associate with their natal hosts and mate on these plants, consequently the host plants mediate the meeting of mates. Disruptive selection against hybrids may further reduce gene flow between ''altissima'' and ''gigantea'' flies. Although the host races form hybrids when forced in captivity, the hybrids and their backcross progeny perform more poorly than parental types on all host plants (Craig *et al.*, 1997, 2000, 2001; Itami *et al.*, 1997).

The survivorship of the derived host race attacking *S. gigantea* may be increased by reduced natural enemy attack and diminished competition. Parasitism may be higher in the ancestral ''altissima'' host race than in the ''gigantea'' host race. A survey of goldenrod fields that included sympatric ''altissima'' and ''gigantea'' populations in Vermont and New Hampshire found, on average, that *Eurosta* survivorship was higher on the derived host plant, *S. gigantea*, than on the ancestral host plant, *S. altissima*. This improved survivorship was a consequence of reduced natural enemy attack from the parasitoid wasp *Eurytoma obtusiventris* and from downy woodpeckers (Abrahamson *et al.*, 1994; Brown *et al.*, 1995). *Eurytoma obtusiventris* appears to

use host-plant cues to locate its prey so a shift to a novel host plant may provide reduced enemy space (Brown *et al.*, 1995). Furthermore, larval competition among flies attacking the ancestral host *S. altissima* appears to be more intense than among flies infesting *S. gigantea* because of higher levels of oviposition on *S. altissima* buds (Abrahamson *et al.*, 1994; Hess *et al.*, 1996; Craig *et al.*, 2000).

Barriers to host shifts

The shift of *Eurosta* from *S. altissima* to *S. gigantea* raises the question of what prevents host shifts—that is, why did this shift occur only once and why aren't such host shifts even more common? There have been occasional reports of *E. solidaginis* galls on *S. canadensis*. Our extensive experience with *E. solidaginis* galls in New England (where both *S. altissima* and *S. gigantea* host *Eurosta*) suggests that *Eurosta* galls occur very infrequently on *S. canadensis*. However, we have occasionally encountered fields (*e.g.,* Missisquoi National Wildlife Refuge, Swanton, Vt.) with pockets of galls on *S. canadensis* (personal observations, A.V.W., W.G.A.). Oviposition-choice tests show that the derived ''gigantea'' host race, but not the ''altissima'' host race, will oviposit on *S. canadensis* at fairly high rates even when the respective natal hosts are available (unpublished data, A.V.W.). This finding corresponds to the observation that ''gigantea'' flies are in general considerably more promiscuous in both mating and oviposition (Craig *et al.*, 2001; personal observations, W.G.A., M.D.E., A.V.W.). An experiment to determine whether ''gigantea'' flies could form galls on *S. canadensis* found that galls were induced at a higher rate on *S. canadensis* than on *S. gigantea* (unpublished data, A.V.W.). This latter finding suggests that ''gigantea'' flies may be preadapted to use *S. canadensis*. However, *S. canadensis* has an appreciably earlier growth phenology than either *S. gigantea* or *S. altissima* (Abrahamson and Weis, 1997). Because gall induction requires the availability of actively growing undifferentiated plant tissue (Abrahamson and Weis, 1987), this early phenology may lessen the probability of attack by gall flies and cause the

''window of vulnerability'' to gall forma-
tion to close sooner. If so, gall flies attack-
ing *S. canadensis* may be under selection
for earlier emergence. These ''canadensis''
gall flies may provide an opportunity to
study the early stages of a host shift.

Differentiation of Mordellistena convicta

A native North American species of
Mordellistena, a large genus of stem-boring
beetles, has long been known as an inhab-
itant of the goldenrod ball galls induced by
the larva of *E. solidaginis* on *S. altissima*.
This beetle has been variously identified as
M. unicolor LeConte (*e.g.,* Ping, 1915; Uhl-
er, 1951), *M. nigricans* Melsh. (*e.g.,* Har-
rington, 1895), *M. aspersa* Melsh. (Liljeb-
lad, 1945), *Mordellistena* sp. (*e.g.,* Milne,
1940), and lately as *M. convicta* (Ford and
Jackman, 1996). Adult females lay their
eggs on the surfaces of newly formed galls
and the larvae bore into galls where they
develop by feeding on the parenchymal tis-
sues induced by the gall fly larva (Ping,
1915). Although these beetles can complete
their development on this diet of plant tis-
sue, the beetles typically chew into the cen-
tral chambers of the galls where they con-
sume the fly larvae (Uhler, 1951; Abraham-
son and Weis, 1997). In one 14-yr study,
beetles consumed the fly larvae in an av-
erage of 73.2% of the galls in which beetles
were found (Uhler, 1961).

Mordellistena convicta has also been
reared repeatedly from *Eurosta* galls on *S.
gigantea* (Harrington, 1895; Abrahamson *et
al.*, 1989; Sumerford and Abrahamson,
1995). Furthermore, Cappuccino (1992) re-
ported *M. convicta* from the stems of *S. al-
tissima*. Consequently, we cultured exten-
sive numbers of stems from various gold-
enrod species and have reared *M. convicta*
from the stems of *S. altissima*, *S. gigantea*,
Euthamia graminifolia (identification of
beetles by J. Jackman), *S. rugosa*, and *S.
juncea* (unpublished data, C.P.B.). Ford and
Jackman (1996) also report its presence in
Aster vimineus, *Ambrosia artemisiifolia*,
and *Xanthium strumarium*. These findings
suggest that either *M. convicta* is polypha-
gous and attacks a variety of plant organs
and host-plant species or exists as differ-

entiated sub-populations according to host
organ and/or host-plant species.

These observations suggested the hy-
pothesis that reproductively isolated popu-
lations of *M. convicta* exist in the stems and
galls of *S. altissima* or *S. gigantea*. We test-
ed this hypothesis using the same criteria
for determining the existence of host races
as we employed for *Eurosta* host races.
Specifically, we examined whether the host-
plant and host-organ associated beetle pop-
ulations exist in sympatry, whether there is
evidence of genetic differentiation among
host-plant and plant-organ associated pop-
ulations, whether host-plant and plant-organ
associated populations have different emer-
gence times, whether females prefer to ovi-
posit on natal host plants and plant organs,
whether offspring perform better on natal
host plants and plant organs, and whether
assortative mating occurs according to natal
host plant and plant organ. Our behavioral
studies of these *M. convicta* sub-popula-
tions show that the beetles' mating and ovi-
position behaviors may act to reduce gene
flow among sub-populations and could fa-
cilitate diversification (unpublished data,
M.D.E., C.P.B.).

As described above, ''altissima'' and
''gigantea'' galls occur sympatrically across
the northern tier of the USA and southern
Canada (Abrahamson and Weis, 1997). *Eu-
rosta* galls containing *M. convicta* larvae
frequently occur on interdigitated ramets of
S. altissima and *S. gigantea* in our New
England study sites. Furthermore, *M. con-
victa* larvae occur sympatrically within the
same plant ramet—occurring within the
stem and that stem's gall on both host plants
(personal observations, C.P.B., W.G.A.,
M.D.E.). Clearly these sub-populations
meet the criterion for sympatry.

A survey of allozymes found five vari-
able and consistently scorable enzymes:
AAT (EC 2.6.1.1), AK (EC 2.7.4.3), IDH
(EC 1.1.1.42), MDH (EC 1.1.1.37), and
PGM (EC 5.4.2.2) among the stem- and
gall-boring beetle populations (unpublished
data, C.P.B.). At the MDH locus, there were
significant allele frequency differences be-
tween stem and gall populations (Table 1),
but none of the five loci studied distin-
guished between the sub-populations in the

TABLE 1. *MDH (EC 1.1.1.37) allele frequencies for* Mordellistena convicta *illustrating genetic differences between stem-associated and gall-associated beetles,* χ^2 *(stem vs. gall) = 505.9 (df = 1),* P *< 0.0001, (n) = sample size.*

	Stem host race			Gall host race		
Allele	*S. altissima* New England	*S. altissima* Pennsylvania	*S. gigantea* New England	*S. altissima* New England	*S. altissima* Pennsylvania	*S. gigantea* New England
(n)	6	4	23	95	123	255
MDH[67]	0.500	0.625	0.630	0.000	0.000	0.014
MDH[100]	0.417	0.375	0.326	0.942	0.963	0.961

stems of the two *Solidago* species or between the sub-populations in the two galls. The genetic difference between stem and gall beetles suggests that *M. convicta* has shifted at least once, and given that *M. convicta* is a stem-boring species, and that stem-boring is common in *Mordellistena* (Ford and Jackman, 1996) gall-boring seems to be the derived trait and thus the shift occurred from stem to gall.

There is a possibility for reduced gene flow between the stem and gall beetle subpopulations because *M. convicta* emerging from *S. altissima* stems in Pennsylvania appeared an average of 2 wk earlier than did beetles emerging from *S. altissima* galls (unpublished data, C.P.B.). Furthermore, the phenology of gall beetle populations also differed: beetles from New England emerged from *S. gigantea* galls on average 1.1 days earlier than from *S. altissima* galls. However, these results should be viewed cautiously even though they were statistically significant. Such allochronic emergence may not be biologically important because adult *M. convicta* can survive for three months (Weis and Abrahamson, 1985; Jackman and Nelson, 1995). *Mordellistena* adults frequent the flowers of numerous plants to feed on pollen. Long adult life and the possibility that males and females of different sub-populations meet while feeding create the prospect for gene flow among sub-populations.

Likely more important to the reproductive isolation of beetle sub-populations was our finding that *M. convicta* from galls assortatively mate according to their natal host plant (Fig. 1; unpublished data, M.D.E.). We conducted a mate-choice experiment by providing focal beetles with a choice of two potential mates: one beetle from their natal host plant and one reared from galls on the alternate host plant. Each beetle was marked with a tiny dot of model paint (Testors®) applied with a bristle from a fine paintbrush (colors: white, red, and yellow, randomized for each trial). We placed marked beetles into a 15-cm diameter petri dish under standard florescent lighting at room temperature. We monitored the behavior of all beetles for 2 hr and recorded the host-plant origin of beetles that copulated with the focal animal. We conducted 38 trials with focal beetles reared from *S. altissima* galls and 62 trials with focal beetles reared from *S. gigantea*. When offered a choice of mates from the galls of their natal host plant or the alternate host plant, ''altissima'' beetles were much more likely to mate with another ''altissima'' beetle than with a ''gigantea'' beetle and vice versa.

Furthermore, adult beetles differentially oviposit and/or their offspring survive better in their natal host-plant species. For example, in both no-choice and choice tests, we found that offspring emerged more frequently from galls of their parents' natal host plant than from galls of the alternate host plant. In no-choice tests, beetles reared from *S. gigantea* galls or *S. altissima* galls were caged with galled ramets of either *S. gigantea* or *S. altissima*. Beetles reared from *S. gigantea* galls produced offspring that emerged only from galls on *S. gigantea* and beetles reared from *S. altissima* galls produced offspring that emerged only from *S. altissima* galls. Likewise, when beetles were given a choice and caged with both *S. gigantea* and *S. altissima* galled ramets, *S. gigantea* beetles produced offspring that emerged at higher rates from *S. gigantea* galls and *S. altissima* beetles produced off-
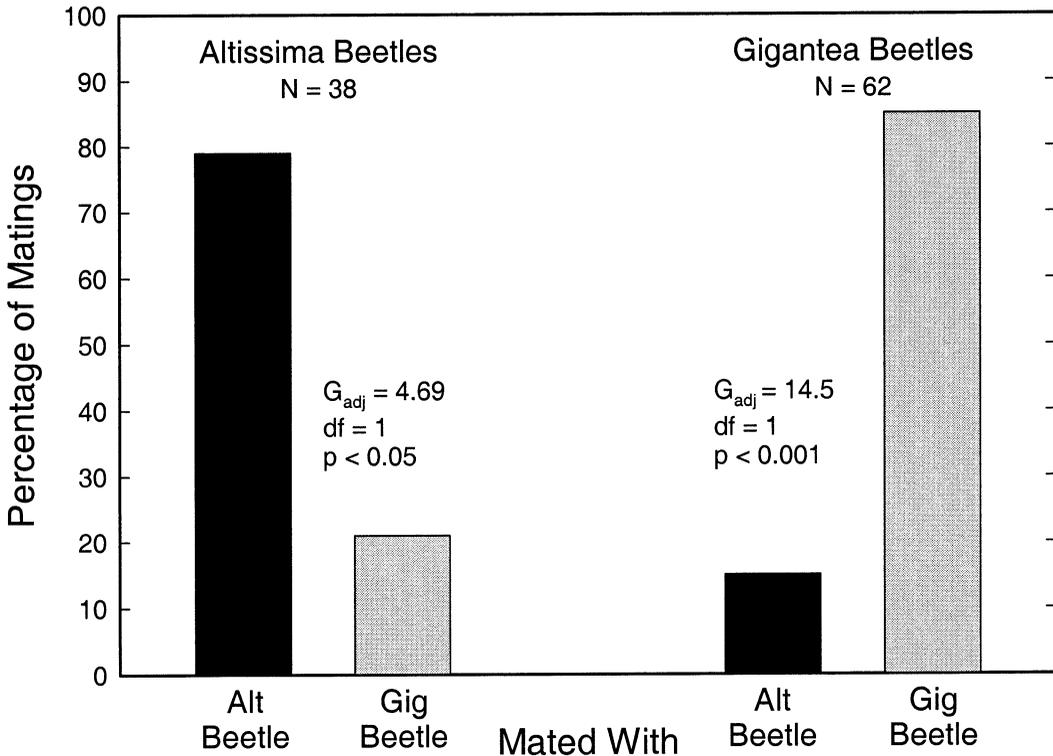
Gall Beetles Exhibit Assortative Mating

FIG. 1. The percentage of matings between adult beetles emerged from New England *S. altissima* galls and *S. gigantea* galls. Beetles were allowed to mate freely with other beetles reared from galls of their natal host plant or from galls of the alternate host plant. Matings were performed in 15-cm petri dishes in the laboratory under standard florescent room lighting and at room temperature (unpublished data, M.D.E.).

spring that emerged at higher rates from *S. altissima* galls (unpublished data, M.D.E.).

Finally, there is evidence that the host shift from stems to galls may be maintained by enemy-reduced attack on the derived gall-dwelling beetle populations. We identified a high level of mortality to stem beetles due to the attack of the chalcid parasitoid *Tetrastichus ainsliei* Gahan (Eulophidae). However, this parasitoid was completely absent from all sampled gall beetle populations (unpublished data, C.P.B.).

Implications for sympatric speciation

We argue that host shifts and subsequent host-race formation such as described here are important, early steps leading to diversification and speciation in herbivorous insects. However, host-race formation via host shifts has been well documented in a limited number of examples. The addition of yet another example from *Mordellistena* suggests that the biodiversity of herbivorous insects may in part be due to sympatric processes.

Our ecological, behavioral, and genetic studies of the *Eurosta* gall inducer and *Mordellistena* stem- and gall-boring beetle illustrate the existence of host and organ races, and offer insights into the conditions necessary for their formation. Colonization of *Eurosta*'s galls by *Mordellistena* stem beetles has facilitated the differentiation of stem- and gall beetle sub-populations. It is conceivable that the gall fly's host shift from *S. altissima* to *S. gigantea* created a new resource for the beetle that will provide the opportunity for the differentiation of beetle sub-populations within the galls of different *Solidago* species. Further research

is needed to establish how closely linked the beetle differentiation is to the fly shift, specifically whether there was a gall-to-gall shift rather than simultaneous colonization and if so, the direction of the shift. Our results lend further credence to recent assertions that sympatric speciation via host-race formation may be an important source of biodiversity (Bush, 1994; Berlocher, 1998, 1999).

Our behavioral work with *Eurosta* implies that the coupling of mate choice and host-plant choice may make it easier for host races to form via their combined effect on the reduction of gene flow among host-associated populations. For this gall inducer, genetic differentiation likely is maintained by disruptive selection for host-plant use because the F1 and F2 hybrids, as well as backcross progeny, exhibit reduced performance relative to the pure host-race offspring (Craig *et al.*, 1997, 2001). The results from our *Mordellistena* studies imply that diversification can occur if assortative mating and oviposition preference and/or offspring survival promote reproductive isolation. Finally, for both *Eurosta* and *Mordellistena*, the reduction of mortality to the derived host-associated populations due to partial escape from a natural enemy may maintain, if not promote, the derived population. The critical consequence for both *Eurosta* and *Mordellistena* is that behavior, rather than geography, limits gene flow and hence may enable the genetic differentiation of sub-populations. The behavioral, ecological, and genetic attributes of these sub-populations are currently such that geographic isolation may not be a prerequisite to their formation (Abrahamson and Weis, 1997). Consequently, there is no need to invoke allopatric conditions to explain the patterns of variation seen in both the gall inducer and its inquiline beetle. The results detailed above suggest a sympatric mode of differentiation suggesting that these sub-populations have originated in sympatry.

The concept of sympatric speciation by host-race formation remains contentious because of the restrictive conditions that many workers have suggested are required, based on models using assumptions that may not be true (Tauber and Tauber, 1989). These restrictions make it improbable that sympatric speciation could ever occur (Futuyma, 1983; Futuyma and Peterson, 1985; but see Johnson *et al.*, 1996; Kawecki, 1998 for arguments that loosen these restrictions). However, findings with *Rhagoletis* (*e.g.,* Feder and Filchak, 1999), as well as those summarized above for *Eurosta* and *Mordellistena* suggest that some of these restrictions can be relaxed. We can never be certain that present-day ecological and genetic conditions match past circumstances or that present population-level situations can be extended to explain larger-scale, phylogenetic patterns (Rausher, 1988). Furthermore, because speciation is a historical process, studies like ours can only suggest the most parsimonious explanation of how speciation has proceeded (Wood and Keese, 1990). Hence, we will never know all the details of the genetic differentiation of sub-populations of *Eurosta* and *Mordellistena*. Nonetheless, studies like those reported here provide important insights into the process of herbivorous insect speciation.

CONCLUSION

Conventional wisdom is that new species arise when geographic barriers divide an existing species into two or more isolated populations. When mountains, oceans, or other barriers prevent the exchange of genes between the isolated populations, each evolves along an independent path. If geographic isolation lasts long enough, the populations may diverge to a point that interbreeding is no longer possible—one species divides into several. With an herbivore such as *Eurosta*, barriers to gene exchange arise not out of geography, but out of behavior. When mating occurs only on the host, a sub-population consistently choosing one host will not mate with that choosing the other. For *Mordellistena*, assortative mating according to natal host plant coupled with preferential oviposition by females and/or differential offspring survival on their natal host plant appear to contribute to its formation of sub-populations (unpublished data, M.D.E.). Our results support the suggestion that differentiation and subsequent speciation may occur in the absence of geographic separation (Johnson *et*

al., 1996). Many have argued that the conditions for sympatric speciation are too restrictive for it to be important. Our work on *Eurosta* and *Mordellistena* indicates that mating and oviposition behaviors can provide a barrier to gene exchange. Given that over 25% of all species are herbivorous insects (Strong *et al.*, 1984), sympatric speciation may be an important source of the earth's biodiversity.

REFERENCES

Abe, Y. 1991. Host race formation in the gall wasp *Andricus mukaigawae*. Entomol. Exp. Appl. 58: 15–20.

Abrahamson, W. G. and A. E. Weis. 1987. Nutritional ecology of arthropod gall makers. *In* F. Slansky, Jr. and J. G. Rodriguez (eds.), *Nutritional ecology of insects, mites, spiders, and related invertebrates,* pp. 235–258. John Wiley & Sons, Inc., New York.

Abrahamson, W. G. and A. E. Weis. 1997. *Evolutionary ecology across three trophic levels: Goldenrods, gallmakers, and natural enemies.* Princeton University Press, Princeton, New Jersey.

Abrahamson, W. G., J. M. Brown, S. K. Roth, D. V. Sumerford, J. D. Horner, M. D. Hess, S. T. How, T. P. Craig, R. A. Packer, and J. K. Itami. 1994. Gallmaker speciation: An assessment of the roles of host-plant characters and phenology, gallmaker competition, and natural enemies. *In* P. Price, W. Mattson, and Y. Baranchikov (eds.), *Gall-forming insects*, pp. 208–222. USDA Forest Service, North

Central Experiment Station—General Technical Report NC-174.

Abrahamson, W. G., K. D. McCrea, and S. S. Anderson. 1989. Host preference and recognition by the goldenrod ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae) Am. Midl. Nat. 121:322–330.

Averill, A. L. and R. J. Prokopy. 1987. Intraspecific competition in the tephritid fruit fly *Rhagoletis pomonella*. Ecology 68:878–886.

Berlocher, S. H. 1998. Origins: A brief history of research on speciation. *In* D. J. Howard and S. H. Berlocher (eds.), *Endless forms: Species and speciation,* pp. 3–15. Oxford University Press, Oxford.

Berlocher, S. H. 1999. Host race or species? Allozyme characterization or the 'flowering dogwood fly', a member of the *Rhagoletis pomonella* complex. Heredity 83:652–662.

Brown, J. M., W. G. Abrahamson, R. A. Packer, and P. A. Way. 1995. The role of natural-enemy escape in a gallmaker host-plant shift. Oecologia 104:52–60.

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

Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). Evolution 23:237–251.

Bush, G. L. 1975. Modes of animal speciation. Ann. Rev. Ecol. System 6:339–357.

Bush, G. L. 1994. Sympatric speciation in animals: New wine in old bottles. Tree 9:285–288.

Cappuccino, N. 1992. The nature of population stability in *Eurosta solidaginis*, a nonoutbreaking herbivore of goldenrod. Ecology 73:1792–1801.

Craig, T. P., W. G. Abrahamson, J. K. Itami, and J. D. Horner. 1999. Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. Oikos 86:119–128.

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.

Craig, T. P., J. D. Horner, and J. K. Itami. 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.

Craig, T. P., J. K. Itami, J. D. Horner, and W. G. Abrahamson. 1994. Host shifts and speciation in gall-forming insects. *In* P. Price, W. Mattson and Y. Baranchikov (eds.), *Gall-forming insects,* pp. 194–207. USDA Forest Service, North Central Experimental Station—General Technical Report NC-174.

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. 25:1–12.

Crozier, R. H. and P. Pamilo. 1996. One into two will go. Nature 383:574–575.

Diehl, S. R. and G. L. Bush. 1984. An evolutionary and applied perspective to insect biotypes. Ann. Rev. Entomol. 29:471–504.

Diehl, S. R. and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. *In* D. Otte and J. A. Endler (eds.), *Speciation and its consequences,* pp. 345–365. Sinauer Associates, Sunderland, Massachusetts.

Feder, J. L. 1995. The effects of parasitoids on sympatric host races of *Rhagoletis pomonella* (Diptera: Tephritidae). Ecology 76:801–803.

Feder, J. L. 1998. The apple maggot fly, *Rhagoletis pomonella*: Flies in the face of conventional wisdom about speciation? *In* D. J. Howard and S. H. Berlocher (eds.), *Endless forms: Species and speciation*, pp. 130–144. Oxford University Press, Oxford.

Feder, J. L. and K. E. Filchak. 1999. It's about time: The evidence for host plant-mediated selection in the apple maggot fly, *Rhagoletis pomonella*, and its implications for fitness trade-offs in phytophagous insects. Entomol. Exp. Appl. 91:211–225.

Feder, J. L., C. A. Chilcote, and G. L. Bush. 1988. Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis pomonella*. Nature 336:61–64.

Feder, J. L., C. A. Chilcote, and G. L. Bush. 1989. Are the apple maggot, *Rhagoletis pomonella*, and blueberry maggot, *R. mendax*, distinct species? Implications for sympatric speciation. Entomol. Exp. Appl. 51:113–123.

Feder, J. L., K. Reynolds, W. Go, and E. C. Wang. 1995. Intra- and interspecific competition and host race formation in the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae). Oecologia 101:416–425.

Ford, E. J. and J. A. Jackman. 1996. New larval host plant associations of tumbling flower beetles (Coleoptera: Mordellidae) in North America. The Coleopterists Bulletin 50:361–368.

Futuyma, D. J. 1983. Selective factors in the evolution of host choice by phytophagous insects. *In* S. Ahmad (ed.), *Herbivorous insects: Host-seeking behavior and mechanisms,* pp. 227–233. Academic Press, New York.

Futuyma, D. J. and S. C. Peterson. 1985. Genetic variation in the use of resources by insects. Ann. Rev. Entomol. 30:217–238.

Guldemond, J. A., A. F. G. Dixon, and W. T. Tigges. 1994. Mate recognition in *Cryptomyzus* aphids: Copulation and insemination. Entomol. Exp. Appl. 73:67–75.

Harrington, W. H. 1895. Occupants of the galls of *Eurosta solidaginis*, Fitch. Can. Entomol. 27:197–198.

Hess, M. D., W. G. Abrahamson, and J. M. Brown. 1996. Intraspecific competition in the goldenrod ball-gallmaker (*Eurosta solidaginis*); larval mor-

tality, adult fitness, ovipositional and host-plant response. Am. Midl. Nat. 136:121–133.

Itami, J. K., T. P. Craig, and J. D. Horner. 1997. Factors affecting gene flow between the host races of *Eurosta solidaginis*. *In* S. Mopper and S. Y. Strauss (eds.), *Genetic structure and local adaptation in natural insect populations: Effects of ecology, life history, and behavior,* pp. 375–407. Chapman & Hall, New York.

Jackman, J. A. and C. R. Nelson. 1995. Diversity and phenology of tumbling flower beetles (Coleoptera: Mordellidae) captured in a Malaise trap. Entomological News 106:97–107.

Jaenike, J. 1981. Criteria for ascertaining the existence of host races. Am. Nat. 117:830–834.

Johnson, P. A., F. C. Hoppensteadt, J. J. Smith, and G. L. Bush. 1996. Conditions for sympatric speciation: A diploid model incorporating habitat fidelity and non-habitat assortative mating. Evol. Ecol. 10:187–205.

Kawecki, T. J. 1998. Red queen meets Santa Rosalia: Arms races and the evolution of host specialization in organisms with parasitic lifestyles. Am. Nat. 152:635–651.

Larsson, S. and B. Ekbom. 1995. Oviposition mistakes in herbivorous insects: Confusion or a step towards a new host plant? Oikos 72:155–160.

Liljeblad, E. 1945. Monograph of the Family Mordellidae (Coleoptera) of North America north of Mexico. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 62.

McPheron, B. A. and H.-Y. Han. 1997. Phylogenetic analysis of North American *Rhagoletis* (Diptera: Tephritidae) and related genera using mitochondrial DNA sequence data. Molec. Phylo. Evol. 7:1–16.

McPheron, B. A., D. C. Smith, and S. H. Berlocher. 1988. Genetic differences between host races of *Rhagoletis pomonella*. Nature 336:64–66.

Menken, S. B. J. 1981. Host races and sympatric speciation in small ermine moths, Yponomeutidae. Entomol. Exp. Appl. 30:280–292.

Milne, L. J. 1940. Autecology of the golden-rod gall fly. Ecology 21:101–105.

Pellmyr, O. and J. Leebons-Mack. 1998. Herbivores and molecular clocks as tools in plant biogeography. Biol. J. Linn. Soc. 63:367–378.

Ping, C. 1915. Some inhabitants of the round gall of goldenrod. J. Entomol. Zool. 7:161–179.

Pratt, G. F. 1994. Evolution of *Euphilotes* (Lepidoptera: Lycaenidae) by seasonal and host shifts. Biol. J. Linn. Soc. 51:387–416.

Rausher, M. D. 1988. Is coevolution dead? Ecology 69:989–901.

Romstock-Volkl, M. 1997. Host race formation in *Tephritis conura*: Determinants from three trophic levels. *In* K. Dettner, G. Bauer, and W. Volkl (eds.), *Vertical food web interactions,* Vol. 130, pp. 23–38. Springer-Verlag, Berlin.

Sezer, M. and R. K. Butlin. 1998. The genetic basis of host plant adaptation in the brown planthopper (*Nilaparvata lugens*). Heredity 80:499–508.

Singer, M. C., C. D. Thomas, and C. Parmesan. 1993.

Rapid human-induced evolution of insect-host associations. Nature 366:681–683.

Strong, D. R., J. H. Lawton, and R. Southwood. 1984. *Insects on plants.* Harvard University Press, Cambridge, Massachusetts.

Sumerford, D. V. and W. G. Abrahamson. 1995. Geographic and host species effects in *Eurosta solidaginis* (Diptera: Tephritidae) mortality. Envir. Entomol. 24:657–662.

Tauber, C. A. and M. J. Tauber. 1989. Sympatric speciation in insects: Perception and perspective. *In* D. Otte and J. A. Endler (eds.), *Speciation and its consequences,* pp. 307–345. Sinauer Associates, Sunderland, Massachusetts.

Uhler, L. D. 1951. Biology and ecology of the goldenrod gall fly, *Eurosta solidaginis* (Fitch). Cornell Exp. Mem. Sta. 300:1–51.

Uhler, L. D. 1961. Mortality of the goldenrod gall fly, *Eurosta solidaginis* in the vicinity of Ithaca, New York. Ecology 42:215–216.

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.

Weis, A. E. and W. G. Abrahamson. 1985. Potential selective pressures by parasitoids on a plant-herbivore interaction. Ecology 66:1261–1269.

Wood, T. K. and M. C. Keese. 1990. Host-plant-induced assortative mating in *Enchenopa* treehoppers. Evolution 44:619–628.

Wood, T. K., K. J. Tilmon, A. B. Shantz, C. K. Harris, and J. Pesek. 1999. The role of host-plant fidelity in initiating insect race formation. Evol. Ecol. Res. 1:317–332.