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ONE HOST SHIFT LEADS TO ANOTHER? EVIDENCE OF HOST-RACE FORMATION IN A PREDACEOUS GALL-BORING BEETLE

MICKY D. EUBANKS,[1] CATHERINE P. BLAIR,[2,3] AND WARREN G. ABRAHAMSON[2,4]
[1]*Department of Entomology and Plant Pathology, 301 Funchess Hall, Auburn University, Auburn, Alabama 36849*
E-mail: meubanks@acesag.auburn.edu
[2]*Department of Biology, Bucknell University, Lewisburg, Pennsylvania 17837*
[3]*E-mail: cblair@bucknell.edu*
[4]*E-mail: abrahamsn@bucknell.edu*

Abstract.—We show that a predator, the tumbling flower beetle *Mordellistena convicta* (Coleoptera: Mordellidae), has formed host races in response to a host-plant shift and subsequent host-race formation by its prey, the gall-inducing fly *Eurosta solidaginis* (Diptera: Tephritidae). This fly has formed two host races, one that induces stem galls on the ancestral host plant, *Solidago altissima* (Compositae), and another that induces stem galls on the closely related *S. gigantea*. We found that subpopulations of *M. convicta* that attack *E. solidaginis* galls on the different host plants have significantly different emergence times and, although slight, these allochronic differences are consistent across a range of temperatures. More importantly, we found that beetles assortatively mate according to their natal host plants, and female *M. convicta* preferentially attack and/or their offspring have higher survival in galls on natal host plants. Our data suggest that subpopulations of *M. convicta* that attack *E. solidaginis* galls on *S. altissima* and *S. gigantea* have formed host races. This is one of the first studies to demonstrate that a host shift and subsequent host-race formation by an herbivorous insect may have resulted in subsequent diversification by one of its natural enemies.

Key words.—Diversification, ecological speciation, host-plant specialization, host race, *Mordellistena convicta.*

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The striking species-specific affinities for host plants of many herbivorous insects, the richness of herbivorous insect lineages, and the remarkable concordance of many insect and host-plant phylogenies attest to the evolutionary force plants have wielded in the diversification of these animals (Brues 1924; Dethier 1954; Ehrlich and Raven 1964; Futuyma and Moreno 1988; Mitter et al. 1988, 1991). There is a growing awareness that herbivorous insects frequently diversify as a result of host shifts and subsequent host-race formation and this process may be one of the major ways in which plants influence the diversification of animals that consume them (Craig et al. 1993; Bush 1994; Crozier and Pamilo 1996; Wood et al. 1999). According to this scenario, the first step involves mutations for changes in host preferences and for adaptation to new hosts. Assortative mating among individuals adapted to use different host plants is subsequently selected for, eventually leading to genetic differences among subpopulations.

It is possible, however, that other animals whose life histories are closely associated with a single resource may also diversify in response to a shift in resource use. For example, this scenario has been proposed to explain the diversification of specialist natural enemies such as parasitoid wasps and flies (Price 1980; Strong et al. 1984; Tauber and Tauber 1989; Godfray 1994). As a consequence, there is the intriguing and virtually unexplored possibility that specialized natural enemies may diversify in parallel with their herbivorous prey after the herbivores complete a host shift. We tested the hypothesis that a natural enemy associated with two distinct host races of an insect herbivore has formed host races. More specifically, we asked if subpopulations of the natural enemy associated with the two host races of the herbivore differed in emergence time (allochronic isolation) and determined whether there were host-associated mating and ovipositional preferences and/or differential larval survival among the subpopulations.

Study System

Eurosta solidaginis (Diptera: Tephritidae) stimulates galls on two closely related species of *Solidago* (Compositae): *S. altissima* and *S. gigantea* (Lichter et al. 1990; Waring et al. 1990). Sympatric *E. solidaginis* subpopulations that utilize *S. altissima* and *S. gigantea* as hosts represent unique host races with strong ecological, behavioral, and genetic differences. *Eurosta solidaginis* from the two host plants show strong genetic and allochronic differences in emergence times (peak emergence is separated by approximately two weeks), display host-associated assortative mating, and strong oviposition preferences for ''natal'' host plants (i.e., the plants from which they were reared; Waring et al. 1990, Craig et al. 1993; How et al. 1993; Abrahamson et al. 1994; Abrahamson and Weis 1997; Itami et al. 1998).

Mordellistena convicta (Coleoptera: Mordellidae; referred to as *M. unicolor* in earlier publications; Ford and Jackman 1996) is an omnivore commonly found inside the galls formed by *E. solidaginis* on goldenrod (Ping 1915; Uhler 1951; Abrahamson and Weis 1997). *Mordellistena convicta* feeds on the rich parenchymal tissue of the gall and on *E. solidaginis* larvae and pupae. Females oviposit individual eggs on the surface of young developing galls in early summer. The eggs hatch on the surface and the first-instar larvae begin boring through the epidermis of the gall, rapidly chewing a small tunnel into the parenchymal tissue (Ping 1915). Once inside the gall, the larvae continue to tunnel through the gall, consuming gall tissue. Although *M. convicta* can

complete development while consuming only plant tissue, approximately 70% of the time the last-instar larvae bore into *Eurosta*'s central chamber and consume the fly larva or pupa (Uhler 1951; Abrahamson et al. 1989). As a result, *M. convicta* is an important natural enemy of the fly on both host plants (Uhler 1951; Abrahamson et al. 1989; Brown et al. 1995). Although allozyme analyses confirmed that beetles associated with different host races of the fly on the two plant species are not cryptic species (e.g., MDH^{67} allozyme frequencies were 0.000 for *S. altissima* beetles and 0.014 for *S. gigantea* beetles, $P > 0.05$; and MDH^{100} allozyme frequencies were 0.942 for *S. altissima* beetles and 0.961 for *S. gigantea* beetles, $P > 0.05$), our preliminary behavioral observations and large size differences among beetles reared from galls on different host plants suggested that ecological differences existed among *M. convicta* associated with galls on *S. altissima* and galls on *S. gigantea* (C. P. Blair, W. G. Abrahamson, and J. A. Jackman, unpubl. ms.; Abrahamson et al. 2001).

Materials and Methods

We tested the hypothesis that subpopulations of *M. convicta* that attack the galls of *E. solidaginis* on *S. altissima* and *S. gigantea* have formed host races. Specifically, we conducted experiments to determine whether host-associated differences in emergence times among subpopulations occur (allochronic isolation), conducted a series of laboratory experiments to determine whether host-associated mating occurs among beetles reared from different galls, and determined whether female beetles preferentially attack and/or their offspring have higher survival in galls on their natal host plants.

Allochronic Emergence

To determine whether *M. convicta* emergence times from *S. altissima* and *S. gigantea* galls differ under ambient conditions, we collected overwintering galls of both plant species and monitored beetle emergence (e.g., Craig et al. 1993; Itami et al. 1998). We collected 2409 *S. altissima* galls and 1979 *S. gigantea* galls where these plants grew in sympatry at multiple sites in New Hampshire in January 1997. Galls were stored outdoors under ambient conditions until mid-May at the Bucknell campus. Galls were then segregated by plant species and site, placed into screen cages, and incubated at 23°C in the laboratory (15:9 h light : dark). Cages were monitored daily for beetle emergence until insect emergence ceased (approximately two months).

Previous studies have shown that year-to-year variation in spring temperatures can strongly affect emergence times and increase or decrease the magnitude of allochronic isolation among putative host races (Abrahamson and Weis 1997). To see whether allochronic isolation varied with temperature, we conducted a growth-chamber experiment to test the effects of temperature on beetle emergence times. Approximately 10,000 galls collected in December 1998 from sympatric sites in New Hampshire and Vermont were used in the experiment. Galls were returned to Auburn University, stored at −15 to −20°C for approximately two months, then randomly assigned to one of five growth chambers at 18, 20, 22, 24, or 26°C (80% relative humidity, 15:9 h light : dark). These temperatures were selected to mimic the range of spring temperatures at our field sites when beetles are emerging from galls (Craig et al. 1993; Abrahamson and Weis 1997). Each growth chamber contained two mesh cages, one containing galls collected from *S. altissima* and one containing galls collected from *S. gigantea*. Galls were lightly misted with water and monitored twice daily for insect emergence. The emergence date and host plant of each beetle was recorded. Analysis of variance was used to partition the effects of host plant, temperature, and their interaction on beetle emergence.

Mating Experiments

No-choice experiment

We paired beetles from the same and different host-plant species in small (60-ml), plastic containers and observed them for two hours to quantify the mating propensity of beetles. *Mordellistena convicta* beetles cannot be sexed without an examination of their internal genitalia, so we could not reliably identify the sex of live beetles before the start of the experiment. We overcame this obstacle by constantly observing paired beetles and scoring a beetle interaction as a copulation when one beetle mounted the other beetle, unsheathed an aedeagus (beetle now designated a male) and inserted the aedeagus into the other beetle (second beetle now designated a female). When no copulation was observed, we sacrificed the beetles at the end of the experiment and examined their genitalia to determine sex. Same sex combinations were not included in the dataset. We monitored 70 opposite-sex pairs of beetles reared from *S. altissima* galls, 86 pairs reared from *S. gigantea* galls, and 58 mixed pairs (one beetle reared from *S. altissima* and one beetle reared from *S. gigantea*). Each beetle was marked with a tiny dot of model paint (Testers Corporation, Rockford, IL) applied with a bristle from a fine paintbrush (white, red, and yellow; randomized for each trial). Mating frequencies were compared with *G* tests.

Both host races present

Mating trials were also conducted in which a beetle was provided with a choice of two potential mates: one beetle from its natal host plant and one reared from a gall on the alternative goldenrod species. Each beetle was marked with a tiny dot of model paint as above. We placed marked beetles into a 15-cm diameter petri dish and monitored the behavior of the beetles for two hours. We 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*. We used *G* tests to determine whether focal beetles preferred to mate with beetles reared from galls from the natal or alternative host plant.

Oviposition Preference/Survival Experiments

No-choice experiment

We wanted to conduct experiments to test for female oviposition preferences among galls on the two host plants and

test for differences in larval survival among different goldenrod species. Several components of the biology of *M. convicta*, however, made execution of these experiments difficult. First, evidence of oviposition by the beetles is nearly impossible to find on the surface of galls and hence scoring oviposition preference is extremely difficult. Second, adult *M. convicta* are pollen feeders and are long lived. As a result, beetles appear less motivated to oviposit under laboratory and greenhouse conditions. Thus, we conducted no-choice and choice tests that included components of both oviposition preference and survival. In the no-choice tests, we caged four beetles from the same goldenrod species onto a three- to four-week-old, rapidly growing gall on a potted goldenrod plant. Beetles were caged with developing galls on either their natal host plant or the alternative species of goldenrod. Beetles were left in the cages for five days to allow mating and oviposition to occur. Cages were constructed of 350-ml clear plastic cups with a hole cut into the top to allow the goldenrod stem to pass through. Foam inserts were used to form the bottom of the cage (mouth of the cup) and cotton was used to prevent insects from escaping around the goldenrod stem at the top of the cage. After five days, the cages were carefully removed and beetles were collected. Beetles were sacrificed and sexed to ensure that at least one male and one female were present in the cage. The plants were reared in the greenhouse until the stems senesced in late fall. The galls were harvested in December and stored individually at −15 to −20°C for approximately 10 weeks. Galls were incubated in small mesh bags at 20°C (80% relative humidity, 15:9 h light : dark), and misted daily with water. Insect emergence was monitored twice a day. We used a *G* test to compare the number of beetles that emerged from the different host-race/host-plant combinations.

Choice experiment

In the choice experiment, we placed six beetles from the same host plant into a 1 m × 0.5 m × 1 m mesh cage that contained six potted goldenrod plants. Three of the plants were *S. altissima* and three were *S. gigantea* and plants were randomly arranged within the cages. All goldenrod plants had a three- to four-week-old, rapidly developing gall. After five days the cages were carefully removed and beetles were collected. Beetles were sacrificed and sexed to ensure that at least one male and one female were present in the cage, plants were reared until senescence, galls were harvested and stored at −15 to −20°C, then incubated individually in small mesh bags at 20°C (80% relative humidity, 15:9 h light : dark) for 60 days. We used a *G* test to compare the number of beetles that emerged from the different host-race/host-plant combinations.

RESULTS

Allochronic Emergence

Under ambient conditions, beetles emerged from *S. gigantea* galls, on average, 1.1 days before beetles from *S. altissima* galls (13.3 ± 0.14 days for beetles emerging from *S. gigantea* galls vs. 14.4 ± 0.4 days for beetles emerging from *S. altissima* galls, $P < 0.05$). In our incubation study, beetles consistently emerged from *S. gigantea* galls before beetles from *S. altissima* galls, regardless of the incubation temperature (Table 1). The relative difference in emergence time of beetles from the two galls was, however, affected by temperature: the difference in emergence decreased as incubation temperature increased (plant species × temperature interaction, $F_{4,821} = 10.91$, $P < 0.01$).

TABLE 1. Mean number of incubation days until emergence (± 1 SE) of beetles reared from *Solidago altissima* and *S. gigantea* galls.

Temperature (°C)	*S. altissima*	*S. gigantea*
18	83.04 (0.74)	73.81 (0.55)
20	44.73 (0.68)	42.29 (0.54)
22	40.79 (0.66)	37.2 (0.49)
24	35.78 (0.58)	32.94 (0.50)
26	28.48 (0.59)	26.67 (0.59)

Mating Experiments

In no-choice experiments, pairs of beetles reared from different host plants were significantly less likely to mate than pairs of beetles reared from the same host plant. Of the beetle pairs reared from *S. altissima galls*, 31.4% mated, and 44.2% of the beetle pairs reared from *S. gigantea* galls mated, but only 17.2% of the mixed pairs mated ($G_{adj} = 11.5$, df = 2, $P < 0.005$). When marked beetles were given a choice of mates, they preferred to mate with beetles reared from the same host plant. Of the focal beetles reared from *S. altissima* galls, 78.6% mated with other beetles from *S. altissima galls* and only 21.4% mated with beetles reared from *S. gigantea* galls ($G_{adj} = 4.69$, df = 1, $P < 0.05$). Focal beetles reared from *S. gigantea* galls showed the opposite pattern: 85.2% of these beetles mated with other beetles reared from *S. gigantea* and only 14.8% mated with beetles from *S. altissima* galls ($G_{adj} = 14.5$, df = 1, $P < 0.001$).

Oviposition Preference/Survival Experiments

The results of our no-choice oviposition preference/survival experiments suggested that there were strong, host-plant-related differences in oviposition and/or survival. When we caged beetles reared from *S. altissima* galls onto either *S. altissima* galls or *S. gigantea* galls, we only recovered progeny in *S. altissima* galls. Of the emerging beetles that we collected from caged *S. altissima* galls, 100% were the progeny of beetles reared from *S. altissima* galls ($G_{adj} = 6.57$, df = 1, $P < 0.025$). Likewise, 100% of the beetles that we reared from *S. gigantea* galls were the progeny of beetles reared from *S. gigantea* galls ($G_{adj} = 9.5$, df = 1, $P < 0.005$). The results of the choice test were similar. Of beetles reared from *S. altissima* galls, 84% attacked galls on *S. altissima* stems ($G_{adj} = 11.2$, df = 2, $P < 0.025$), and 82% of the beetles reared from *S. gigantea* galls attacked galls on *S. gigantea* stems ($G_{adj} = 10.5$, df = 2, $P < 0.025$).

DISCUSSION

This study provides ecological evidence that two subpopulations of a beetle associated with different host races of an insect herbivore are themselves host races. *Mordellistena con-*

victa beetles reared from *E. solidaginis* galls on two goldenrod species emerged at different times across a range of temperatures, assortatively mated according to natal host plant, and either had strong oviposition preferences, strong host-plant-related survival differences, or a combination of the two. Our study system is unique in that a host shift and subsequent host-race formation by one herbivorous insect may have contributed to the host shift and host-race formation of a second, unrelated species.

Our study system may also be unique because factors that are typically important in promoting or maintaining reproductive isolation during host-race formation in other insects may not be as important for this beetle. Allochronic or host-associated differences in emergence time are important sources of reproductive isolation among the host races of *R. pomonella* and *E. solidaginis* (Bush 1969; Craig et al. 1993). Host races of the apple maggot fly differ in peak emergence by as much as 30 days (Bush 1969) and host races of the ball gall inducer emerge up to two weeks apart (Craig et al. 1993). Adults of these fly species are also relatively short-lived in the field ($\approx$20 days for *R. pomonella* and seven to 10 days for *E. solidaginis*) and spend most of their adult life on their host plant (Bush 1969; Abrahamson et al. 1994). In contrast, we found that subpopulations of *M. convicta* that attack *E. solidaginis* galls on *S. altissima* and *S. gigantea* emerged, on average, only one day apart. These beetles are long lived as adults ($>$30 days and perhaps as long as 90 days [M. Eubanks, C. Blair, and W. Abrahamson, pers. obs.; Jackman and Nelson 1995]), are highly mobile and spend a large amount of their adult lives foraging for pollen on flowers of non-*Solidago* plants. Long adult life and the possibility that males and females of different subpopulations meet while feeding on non-*Solidago* plants create the prospect for gene flow among subpopulations. As a result, we think it is unlikely that an emergence difference of only one or two days would contribute meaningfully to reproductive isolation among host-associated subpopulations of this beetle.

It is much more likely that assortative mating among beetles maintains host races in this species. We found strong evidence of assortative mating among putative host races of *M. convicta*. Host-plant-associated assortative mating is an important mechanism that reduces gene flow among host races of *R. pomonella* and *E. solidaginis* (Bush 1966, 1969; Craig et al. 1993; Abrahamson et al. 1994). In both cases, however, males stake out territories on the host plant while awaiting the arrival of the female and virtually all courtship and copulation occurs on the host plant. Although recent studies suggest that assortative-mating mechanisms in addition to host-associated mating may operate in these systems (e.g., Craig et al. 2001), it is believed the coupling of host-plant choice and mating location is vital to the formation of host races in both of these fly species. That does not appear to be the case for *M. convicta* because as adults they spend a great deal of time foraging for pollen on non-*Solidago* plants (goldenrod is not flowering when they are active as adults) and we found evidence of strong assortative mating in the absence of host plants. Instead, we believe that host-associated differences in adult body size, chemical cues associated with natal host plants, or some combination generates assortative mating between the two putative host races (e.g., Eber et al. 1999).

Our results also suggest that *M. convicta* females preferentially oviposit on galls of their natal host plant, their offspring have higher survival in galls on natal host plants, or some combination of the two is occurring. In both choice and no-choice experiments, we were much more likely to recover offspring from galls of the natal host plant than galls of the alternative host plant. This could be due to strong ovipositional preferences by females, differential survival of larvae once they hatch from eggs, or both.

Although we believe our results are intriguing, there are several shortcomings to our approach. Because it is almost impossible to place *M. convicta* offspring on or in galls on different goldenrod plants, we could not separate genetic versus environmental components of allochronic emergence, mate choice, oviposition choice, and larval survival. For example, allochronic emergence could be due to different diets rather than genetic differences. Similarly, host-plant chemistry may play a role in mate choice if individuals preferentially mate with beetles that have similar plant-derived chemistry. Nevertheless, even if the processes that we observed are completely environmentally determined, they are consistent enough to result in the restriction of gene flow among host races.

To our knowledge, this is one of the first studies suggesting that specialist natural enemies may diversify in parallel with the specialized herbivores that they attack. In contrast, Cronin and Abrahamson (2001) found no evidence that a parasitoid wasp, *Eurytoma gigantea* (Hymenoptera: Eurytomidae), that attacks *E. solidaginis* galls on both host plants has formed host races in response to the formation of *E. solidaginis* host races. Wasps reared from galls on *S. altissima* and *S. gigantea* showed no allochronic emergence, no assortative mating, and female *E. gigantea* did not prefer to oviposit on galls on their natal host plants. These two natural enemies have apparently responded differently to the host shift and host-race formation of *E. solidaginis*. This difference is likely a consequence of the feeding and oviposition behaviors of the two species. *Mordellistena convicta* is an omnivore that consumes a great deal of plant tissue as well as *Eurosta* larvae. Host-plant chemistry, therefore, is likely to play a large role in both the performance of *M. convicta* larvae and the oviposition choice of adult females. *Eurytoma gigantea* is exclusively carnivorous and the host plant seems to play a much smaller role in the development of wasp larvae. As a consequence, the fly larva/host plant species combination may not create divergent selective pressures for the wasp (Cronin and Abrahamson 2001). Thus, the life history of the natural enemy may promote or retard parallel diversification with herbivorous hosts. If parallel diversification by natural enemies is common, this could be a potentially important and overlooked source of biodiversity. We encourage workers who study host-race formation and sympatric speciation to expand their studies to include the response of associated organisms.

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