

# Do parasitoids diversify in response to host-plant shifts by herbivorous insects?

JAMES T. CRONIN<sup>1</sup> and WARREN G. ABRAHAMSON<sup>2</sup>

<sup>1</sup>Department of Biology, University of North Dakota and <sup>2</sup>Department of Biology, Bucknell University, U.S.A.

**Abstract.** 1. For herbivorous insects, the incorporation of a novel host into the diet, and subsequent formation of distinct host associations (*races*), is thought to be a significant early step in the speciation process. While many studies have addressed this issue, virtually nothing is known about the evolutionary response of natural enemies to herbivore host-race formation.

2. The hypothesis that the parasitoid wasp *Eurytoma gigantea* (Hymenoptera: Eurytomidae) has formed host races in direct response to the host shift and subsequent host-race formation by its host, the gallmaker *Eurosta solidaginis* (Diptera: Tephritidae) was tested. Emergence time, mating preference, and female oviposition preference were determined for parasitoids derived from galls of each *Eurosta* host race.

3. Male and female *E. gigantea* overlap broadly in their emergence times from each *Eurosta* host race, suggesting that there is no phenological barrier to gene flow.

4. In choice experiments, female parasitoids did not mate assortatively: females that emerged from one *Eurosta* host race were equally likely to mate with males from either *Eurosta* host race.

5. Oviposition behaviour experiments revealed that female parasitoids do not prefer to oviposit on their host race of origin and that there is no overall preference for one host race, even though fitness is higher when parasitoids are reared from *Eurosta* galls of the *Solidago gigantea* host race than when reared from *Eurosta* galls of the *Solidago altissima* host race.

6. These results suggest that *E. gigantea* has not diverged in parallel with its host in response to the herbivore host-plant shift. Further studies are needed before the ubiquity of this diversification mechanism can be evaluated fully.

**Key words.** Emergence phenology, *Eurosta solidaginis*, *Eurytoma gigantea*, gall insect, goldenrod, host–parasitoid evolution, host-race formation, mate preference, oviposition preference, plant–herbivore–parasitoid interaction, *Solidago* spp.

## Introduction

Of the extraordinary diversity found within the Insecta (60% of the world's biota; Stork, 1988), herbivores ( $\approx 46\%$ ; Strong *et al.*, 1984) and parasitoids ( $\approx 20\text{--}25\%$ ; Godfray, 1994) comprise the majority of species. The rapid and extensive diversification of these taxa is generally considered to be a population-genetic consequence of ecological specialisation

(Mayr, 1976; Price, 1980; Futuyma & Moreno, 1988; Mitter *et al.*, 1991). Evidence of such specialisation can be found in the stenophagous host ranges of many herbivores and parasitoids and the concordances of herbivore and host-plant phylogenies (e.g. Futuyma & Moreno, 1988; Mitter *et al.*, 1991; Kelley & Farrell, 1998).

For herbivorous insects, the incorporation of a novel host plant into the diet can represent an important route by which diversification and speciation occur (Bush, 1975; Futuyma & Moreno, 1988; Jaenike, 1990; Thompson, 1996). Diet expansions by species that were initially monophagous or narrowly oligophagous throughout their ranges are widespread (e.g.

Correspondence: J. T. Cronin, Department of Biology, University of North Dakota, Grand Forks, ND 58202, U.S.A. E-mail: james\_cronin@und.nodak.edu

Thomas *et al.*, 1987; Carroll & Boyd, 1992; Bush, 1994), and provided that gene flow between the ancestral and novel hosts is reduced sufficiently, separate host-plant races (*sensu* Diehl & Bush, 1984; see also Jaenike, 1981), and eventually sibling species, may evolve.

The accepted paradigm in the diversification of parasitoids follows the same logic offered for phytophagous insects: diversification is linked to a shift from an ancestral to a novel host (Strong *et al.*, 1984; Tauber & Tauber, 1989; Godfray, 1994). Diversification of parasitoids may also be attributable to a host-plant shift by the parasitoid's herbivorous host especially if the parasitoid's fitness is influenced by the host plant of the herbivore. Parasitoid success in attacking hosts ( $\approx$  fitness) can be influenced both directly and indirectly by the herbivore's host plant (e.g. Price *et al.*, 1980; Vinson, 1981; Price, 1986; Barbosa, 1988; Hare, 1992). Various tritrophic mechanisms may explain parasitoid host shifts including a preference for mates that derive from the same host race or a preference by females to forage or oviposit on the plants from which they emerged. Few studies have evaluated whether host-race formation in herbivores may trigger parallel diversification in their parasitoids.

The work reported here was designed to explore whether a eurytomid parasitoid of a stem-galling herbivore that has recently incorporated a new host into its diet and formed two distinct host races has exhibited parallel diversification. Studies were conducted to determine whether parasitoids derived from each host race differed in emergence phenology or exhibited any mating or oviposition preferences for the host race from which they emerged. Size or fecundity differences between parasitoids associated with each host race were also examined. Finally, the role that this parasitoid may have played in promoting the host shift by the stem galler and whether its own evolution was influenced by the host shift are discussed.

## Study organisms

*Eurosta solidaginis* is a univoltine tephritid fly that attacks and induces gall formation on two very closely related species of *Solidago* (Compositae): *S. altissima* and *S. gigantea* (Lichter *et al.*, 1990; Waring *et al.*, 1990). Both plants overlap broadly in their distributions and are found throughout the eastern and central United States, however *S. gigantea*'s range also extends to the north-western United States and British Columbia. Galls from both species are commonly found in sympatry along the northern tier of the United States and southern Canada from New England into the Midwest (Lichter *et al.*, 1990; Waring *et al.*, 1990; Brown *et al.*, 1995; Sumerford & Abrahamson, 1995).

In late spring, *Eurosta* emerge from the previous year's galls, mate, then females oviposit into the terminal buds of goldenrods. Within a few days, the larvae hatch, bore into the stem, and induce the development of a spheroid gall. These galls become visible within about a month and reach full size in mid summer. The flies overwinter as third-instar larvae within the gall of a senescent goldenrod stem, then pupate and eclose the following spring. Further details on the life history

and biology of *E. solidaginis* are presented by Abrahamson and Weis (1997).

Several lines of evidence indicate the existence of two reproductively isolated *host races* of the stem galler, one race associated with *S. altissima*, the other associated with *S. gigantea*: (1) flies prefer to mate assortatively with their own host-associated population and females oviposit on their natal host-plant species (Craig *et al.*, 1993), (2) stem gallers that oviposit on the incorrect host plant are penalised with substantially lower offspring survivorship than those that choose correctly (Craig *et al.*, 1997), (3) hybridisation experiments between the two host races suggest that the differences in both plant preference and larval performance have a genetic basis (Craig *et al.*, 1997), (4) there are phenological differences in emergence times between flies reared from the two *Solidago* hosts (Craig *et al.*, 1993; Horner *et al.*, 1999), and (5) allozyme and mitochondrial data indicate that flies from each host plant represent genetically distinct populations (Waring *et al.*, 1990; Brown *et al.*, 1996). Based on the molecular analyses mentioned previously, Waring *et al.* (1990) and Brown *et al.* (1996) have inferred that *S. altissima* is the ancestral host and that the host shift probably occurred in New England.

*Eurytoma gigantea* (Hymenoptera: Eurytomidae) attacks larvae of the stem galler when the gall has reached maximum size (Weis & Abrahamson, 1985; Abrahamson & Weis, 1997). It has been reared from galls associated with both host-plant species, and parasitism rates are similar on both host plants (Brown *et al.*, 1995). *Eurytoma gigantea* has never been reared from other galls and appears to be a specialist of *E. solidaginis* throughout its range (Abrahamson & Weis, 1997; J. T. Cronin, unpublished). In this paper, *E. gigantea* was used to test the hypothesis that parasitoids can exhibit parallel diversification in response to a host shift and subsequent host-race formation by their herbivorous hosts.

## Materials and methods

### Source of parasitoids

In January 1997, galls from *S. altissima* and *S. gigantea* were collected from two sites along the Connecticut River Valley (forms the border between New Hampshire and Vermont, U.S.A.) that were allopatric for one or the other host race. The sites were separated by  $\approx$  60 km. Galls were kept at  $-10^\circ\text{C}$  to maintain inhabitants in diapause until the spring. To break diapause, galls were transferred to an environmental chamber set at a constant  $26^\circ\text{C}$ , 85% RH, LD 14:10 h photoperiod. Emerging adult parasitoids were removed daily and stored in a separate growth chamber set at  $10^\circ\text{C}$  (all other conditions identical). For the experiments that follow, only virgin adult wasps  $\leq$  3 days old were used.

### Parasitoid fitness

Potential fitness differences of *E. gigantea* from the two *Eurosta* host races were determined by obtaining size and egg

load measurements from recently emerged adults. A total of 59–86 parasitoids of each sex and host plant was obtained from the galls above. For each parasitoid, the maximum diameter of the gall (mm) from which it emerged was measured using a pair of dial calipers. A stereoscopic dissecting microscope equipped with an ocular micrometer was then used to measure hind tibia length, wing length, minimum interocular distance, and ovipositor length (mm). Reported values of tibia and wing length are averages of left and right appendages. Female wasps were dissected in insect saline and the number of mature eggs was recorded.

Host-race and sex-specific differences in relative fitness measurements were assessed using ANOVA. Because galls are known to be larger on *S. gigantea* than on *S. altissima* (Lichter *et al.*, 1990; How *et al.*, 1993), and gall size may influence parasitoid fitness, this measure was incorporated as a covariate in the analysis. Separate ANCOVAs were performed for each fitness-related measure. In addition, the relationships among all fitness measures were determined using Pearson's product moment correlations, *R* (Sokal & Rohlf, 1995).

#### Mating preference

Choice trials were used to determine whether female *E. gigantea* derived from *S. altissima* or *S. gigantea* host races exhibited any preference to mate with males from the same or the alternate host race. For each trial, a male wasp from each host race was placed together in a 60-ml clear-plastic container. Pairing a large with a small male parasitoid made it possible to distinguish between the two races. Among trials, the host race that served as the large and small male were alternated. Males were allowed 10 min to acclimate then a female was released into the cage. The cage was then monitored continuously for 1 h, during which time the host-plant origin of the first male to mount the female and the first male to mate successfully was recorded. A total of 193 mating trials was conducted.

Because male size can influence host mate choice by females (Grant *et al.*, 1980; Charnov *et al.*, 1981; Jones, 1982), the frequency of females (both host races combined) that were first mounted and mated by large and small males respectively was determined. Whether females were significantly more likely to be mounted or mated by a large or small male was then tested using separate  $\chi^2$  tests for goodness-of-fit (Sokal & Rohlf, 1995). To verify that male size categories were similar between host races (e.g. large male *S. altissima* and large male *S. gigantea*), size measurements were obtained from all males used in the study.

In testing whether there was a female preference for males from one or the other *Eurosta* host race, the effects of male size were minimised by comparing mounting and mating frequencies for large males only. For all trials in which a large male from the *S. altissima* host race was used, the frequency of *S. altissima* males that were first to mount or mate with a *S. altissima* female was determined. In comparison, the frequency of *S. gigantea* males that were first to mount or mate with a *S. altissima* female was determined for trials that

used large male *S. gigantea*. The difference in acceptance frequency of large male *S. altissima* and large male *S. gigantea* parasitoids was assessed using a  $\chi^2$  test-for-independence. A similar procedure was used to examine the preference of female parasitoids from the *S. gigantea* host race.

#### Oviposition preference: no-choice experiment

No-choice experiments were used to determine whether galls on *S. altissima* or *S. gigantea* differed in their susceptibility to attack by *E. gigantea* females. Goldenrod stems bearing galls were collected from the two allopatric field sites along the Connecticut River Valley and transported on ice to the laboratory on the same day. All galls were  $\approx$  6–7 weeks old and 12–18 mm in diameter, which is the age and size of galls that are normally attacked by *E. gigantea* (Weis & Abrahamson, 1985).

An oviposition trial consisted of releasing a recently mated (<48 h previously) female of known *Eurosta* host race into a 300-ml clear-plastic cage containing either a *S. altissima* or *S. gigantea* gall. The time of occurrence of the following two behavioural events was recorded: discovery of the gall by making antennal contact and probing of the gall with the ovipositor. After 1 h, the trial was terminated, the gall was dissected, and the number of eggs laid was counted. A total of 129 trials out of 707 initiated resulted in a parasitoid making contact with a gall.

For all trials involving the same female source and host type, the following indices of host acceptance were computed: proportion of trials in which the gall was discovered, mean time (min) taken for the gall to be discovered, proportion of trials in which a gall was probed with the parasitoid's ovipositor, mean time taken to initiate probing, proportion of discovered galls that was probed, proportion of galls that received a parasitoid egg, and proportion of probed galls that received an egg. Differences between host races in their acceptability to a female parasitoid, based on proportional measures, were assessed using separate  $\chi^2$  tests-for-independence. Differences in mean time to discovery and probing time were determined using separate two-sample *t*-tests.

#### Oviposition preference: choice experiment

In this experiment, female parasitoids were presented with both types of gall at the same time (a choice test) to determine whether they had a preference for galls from a particular *Eurosta* host race/plant species. Four galled stems from each host race were presented together to female parasitoids in 40 × 40 × 25 cm Plexiglas® chambers. The galled stems were placed in two rows at opposite sides of the chamber, with the host race of the gall alternating within each row. Four mated female parasitoids were released into the chamber. The first host-plant species encountered (alighting or walking onto the plant), and the time and host race of the first gall antennated and the first gall probed were recorded for each trial. After the female departed from the probed gall, the trial was terminated

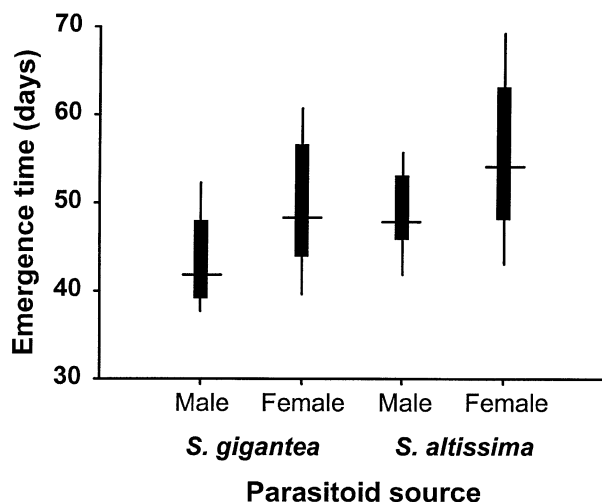
and the probed gall dissected for parasitoid eggs. The remaining stems were then discarded, the inside of the chamber was wiped down with ethanol, and a new trial was initiated. A total of 25 and 29 trials was conducted for female parasitoids from *S. altissima* and *S. gigantea* host races respectively.

## Results

### Parasitoid development time and fitness

Parasitoids from each *Eurosta* host race overlapped broadly in the time it took them to eclose as adults following the placement of galls in the incubator (Fig. 1). Most notably, the emergence times for males reared from *S. altissima* galls fell completely within the range of emergence times for females from *S. gigantea* galls. There was less, but still high (47%), overlap between males from *S. gigantea* and females from *S. altissima* galls.

All measures of body size (tibia length, wing length, interocular distance, ovipositor length) were correlated,



**Fig. 1.** Emergence times for *Eurytoma gigantea* from the two *Eurosta* host races following the placement of winter-collected galls in an incubator (26 °C, 85% RH, LD 14:10h photoperiod). Horizontal lines indicate medians, vertical lines show ranges, and wide vertical bars demark the first and third quartiles.

strongly and positively, with each other ( $R \geq 0.69$ ,  $P < 0.001$ ). Less strong, but still significant, positive correlations were also found between body size and female egg load ( $R \geq 0.43$ ,  $P < 0.001$ ) and between gall diameter and all measures of parasitoid fitness ( $R \geq 0.31$ ,  $P \leq 0.05$ ). Because of the close positive relationship among all fitness variables, ANCOVA results are reported for only hind tibia length and egg load (Tables 1 and 2). There were significant differences in parasitoid tibia length between host-plant species and between sexes (Table 1). Among *Eurosta* host races, parasitoids emerging from *S. gigantea* plants were 5% larger on average than parasitoids emerging from *S. altissima* plants (intra-sex comparisons; Table 3). The significant difference in size between host plants was independent of the size of the gall from which the parasitoid emerged (gall size effects were partitioned out in the ANCOVA). Similar results were found for all other body size measurements common to males and females – parasitoids from *S. gigantea* plants were 5–7% larger overall (Table 3). Females from the *S. gigantea* host race had ovipositors that were 8% longer than the ovipositors of females from the *S. altissima* race but the two were indistinguishable with regard to egg loads (Tables 2 and 3).

### Mating preference

Among the 193 mating trials performed, 107 resulted in at least one male mounting a female and 41 resulted in mating. For parasitoids from both *Eurosta* host races combined, large males accounted for 57% of the individuals that made first sexual contact (mounting) with a female. This percentage did not differ significantly from the expectation of random contact (50%;  $\chi^2 = 2.10$ , d.f. = 1,  $P = \text{NS}$ ); however, large males accounted for 71% of the individuals that succeeded in mating with a female, significantly higher than expected by chance ( $\chi^2 = 7.05$ , d.f. = 1,  $P < 0.01$ ). Within a male size class, no differences could be detected in tibia length ( $t = 0.945$ , d.f. = 105), wing length ( $t = 1.211$ , d.f. = 105), or interocular distance ( $t = 0.663$ , d.f. = 105) between the two host races of origin (all  $P = \text{NS}$ ), suggesting that there was no bias in the categorisation of males from each *Eurosta* host race.

There was no evidence for assortative mating between parasitoids from the two *Eurosta* host races. After minimising male size effects by focusing only on the success of the larger member of the male pair, *S. altissima* and *S. gigantea* male parasitoids were equally likely to be the first to mount (49 vs.

**Table 1.** ANCOVA results for the effect of two fixed factors, host-plant origin and parasitoid sex, and the covariate gall diameter on *Eurytoma gigantea* mean hind tibia length.

Source	Sum of squares	d.f.	F-ratio	P-value
<i>Solidago</i> species	0.215	1	8.160	0.005
Parasitoid sex	11.030	1	418.765	<0.001
<i>Solidago</i> species $\times$ parasitoid sex	0.002	1	0.068	0.794
Gall diameter	0.598	1	22.689	<0.001
Error	7.612	289	0.026	

**Table 2.** ANCOVA results for the effect of host-plant origin and gall size on female *Eurytoma gigantea* egg load.

Source	Sum of squares	d.f.	F-ratio	P-value
<i>Solidago</i> species	81.724	1	1.618	0.205
Gall diameter	500.594	1	9.910	0.002
Error	7728.567	153	50.514	

55% respectively,  $\chi^2=0.23$ ,  $P=NS$ ) or mate (73 vs. 68% respectively,  $\chi^2=0.03$ ,  $P=NS$ ) with a female parasitoid from *S. altissima* galls. For female parasitoids from *S. gigantea* galls, males from *S. altissima* and *S. gigantea* also had similar success in mounting (59 vs. 57% respectively,  $\chi^2=0.24$ ,  $P=NS$ ) and mating (80 vs. 65% respectively,  $\chi^2=2.13$ ,  $P=NS$ ) with the female.

#### Oviposition preference: no-choice experiment

Based on no-choice oviposition trials, a preference by female parasitoids for galls derived from their natal host plants could not be detected. Probability that a gall was discovered, probed with the ovipositor, probed given discovery, oviposited within, oviposited within given that it was probed, and the time taken to discover or probe a gall were all remarkably similar between galls formed on *S. altissima* and *S. gigantea* (Fig. 2). Furthermore, there was no indication that female parasitoids from one host race of origin were more likely to accept a gall than were females from the other host race. When gall origin was ignored (*S. altissima* and *S. gigantea* galls pooled), female parasitoids reared from *S. altissima* had a greater probability of discovering a gall than did parasitoids from *S. gigantea* (22 vs. 15%,  $\chi^2=6.531$ , d.f.=1,  $P<0.05$ ), but once a gall was discovered, *S. gigantea* females were more likely than *S. altissima* females to probe it with their ovipositors (69 vs. 48%,  $\chi^2=5.594$ , d.f.=1,  $P<0.05$ ). No other differences between females originating from the two *Eurosta* host races were evident.

**Table 3.** Fitness-related measures (mean  $\pm$  SE) for male and female *Eurytoma gigantea* from two host-plant races: *Solidago altissima* and *Solidago gigantea*. All size measurements are in mm.

	Female <i>E. gigantea</i>		Male <i>E. gigantea</i>			
	<i>S. altissima</i>	<i>S. gigantea</i>	<i>S. altissima</i>	<i>S. gigantea</i>		
Gall diameter	21.10 $\pm$ 0.24	NS	20.84 $\pm$ 0.31	18.95 $\pm$ 0.35	NS	19.09 $\pm$ 0.46
Tibia length	1.32 $\pm$ 0.02	*	1.36 $\pm$ 0.02	0.86 $\pm$ 0.02	*	0.92 $\pm$ 0.02
Wing length	3.29 $\pm$ 0.05	**	3.48 $\pm$ 0.04	2.35 $\pm$ 0.04	**	2.56 $\pm$ 0.03
Interocular distance	0.86 $\pm$ 0.01	*	0.90 $\pm$ 0.01	0.73 $\pm$ 0.01	**	0.78 $\pm$ 0.01
Ovipositor length	5.98 $\pm$ 0.12	**	6.48 $\pm$ 0.11	–	–	–
Egg number	15.14 $\pm$ 0.73	NS	16.38 $\pm$ 0.95	–	–	–

Significant differences between the two host races of the same sex are denoted by \* $P<0.05$ , \*\* $P<0.01$ , or NS=no significant difference between means. For measures common to males and females, differences were assessed using the Specify command in the GLM Module of Systat 8.0 (SPSS Inc., 1998) and are based on the ANCOVA model described in Table 1. Differences in means between female-specific characters were assessed as a main effect in an ANCOVA model (see Table 2).

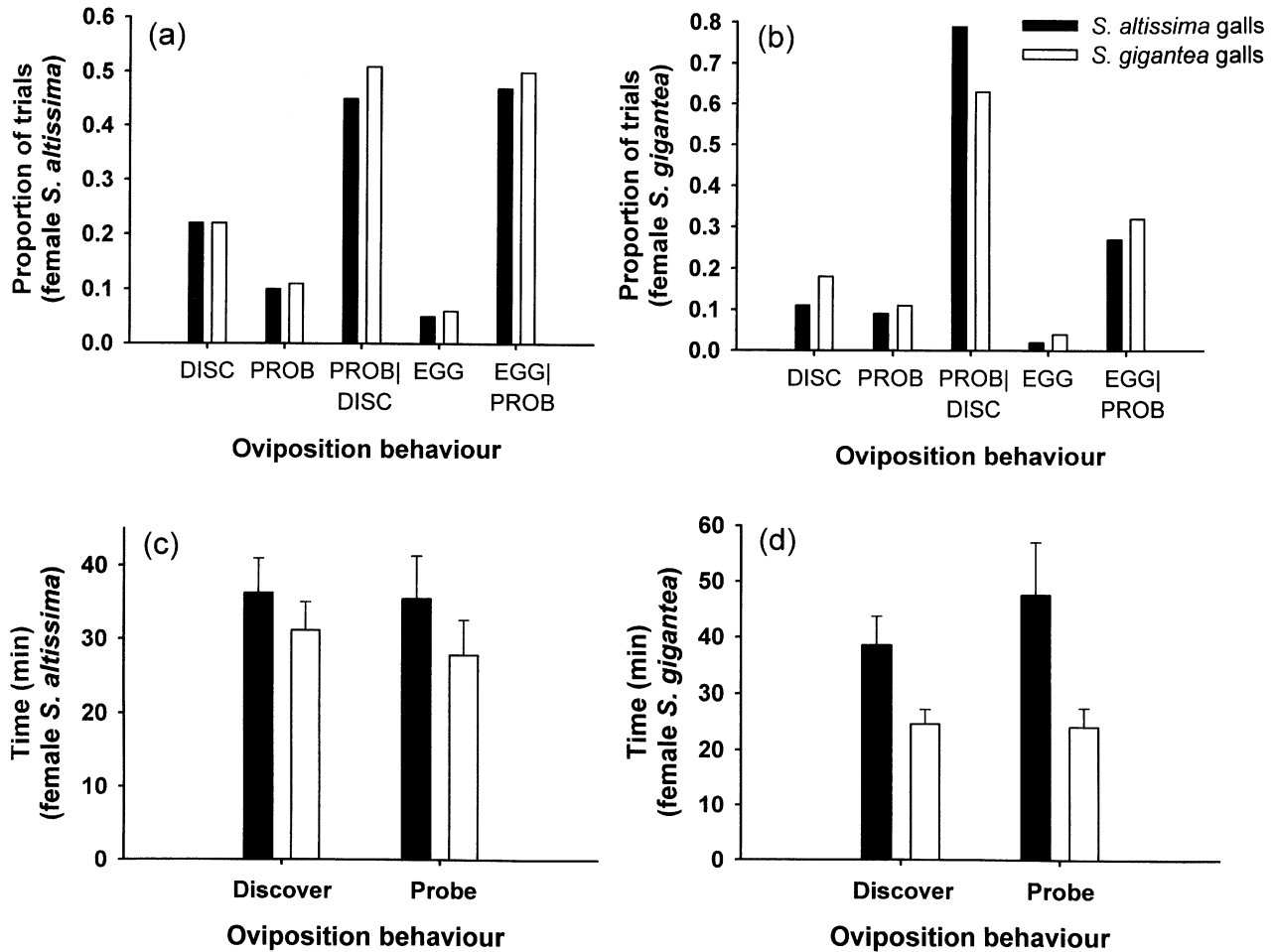
#### Oviposition preference: choice experiment

In support of results from the no-choice experiment, *E. gigantea* females exhibited no significant preference for *S. altissima* or *S. gigantea* stems or galls, irrespective of the origin of the female. Female parasitoids from both host races had a slightly, but not significantly, higher probability of first encountering *S. altissima* than *S. gigantea* host plants within the cages (56 vs. 44% for parasitoids from *S. altissima*,  $\chi^2=0.36$ , d.f.=1,  $P=NS$ ; 58 vs. 42% for parasitoids from *S. gigantea*,  $\chi^2=0.86$ , d.f.=1,  $P=NS$ ). The proportion of trials in which a *S. altissima* or a *S. gigantea* gall was first to be discovered, probed with the ovipositor, probed given that the gall was discovered, and the time taken to discover or probe galls from either host race, also did not differ significantly (Fig. 3). There were insufficient oviposition events to test whether females laid more eggs on one or the other *Eurosta* host race.

#### Discussion

Ecological specialisation, particularly through the incorporation of a novel host into the diet, is regarded as a primary initial step promoting the diversification of herbivore and parasitoid taxa (e.g. Mayr, 1976; Price, 1980; Futuyma & Moreno, 1988). The evidence to date provides compelling support for the idea that *E. solidaginis* expanded its host range from the ancestral host plant, *S. altissima*, to include *S. gigantea* (see Introduction). Since that time, stem-galling flies associated with each host plant have undergone molecular, behavioural, and physiological divergence to the extent that they are considered distinct host races. The specialist parasitoid, *E. gigantea*, however, shows no behavioural evidence of a parallel evolutionary response to the host-plant shift.

In the laboratory, female *E. gigantea* do not mate assortatively with males that originate from the same host plant. Based on the phenology of parasitoid emergence from galls in an environmental chamber, males and females from



**Fig. 2.** Female *Eurytoma gigantea* oviposition preference behaviour (no-choice experiment) for galls from both *Eurosta* host races. For females originating from (a) *Solidago altissima* or (b) *Solidago gigantea* galls, the proportion of trials in which a gall was discovered (DISC), probed with the ovipositor (PROB), probed given that the gall was discovered (PROB|DISC), oviposited within (EGG), and oviposited within given that the gall was probed (EGG|PROB) did not differ in the presence of *S. altissima* and *S. gigantea* galls (separate  $\chi^2$  tests for independence,  $P = \text{NS}$ ). Time taken to discover the gall or probe it with the ovipositor also did not differ between the two gall host races for female parasitoids derived from (c) *S. altissima* or (d) *S. gigantea* galls (paired  $t$ -tests,  $P = \text{NS}$ ).

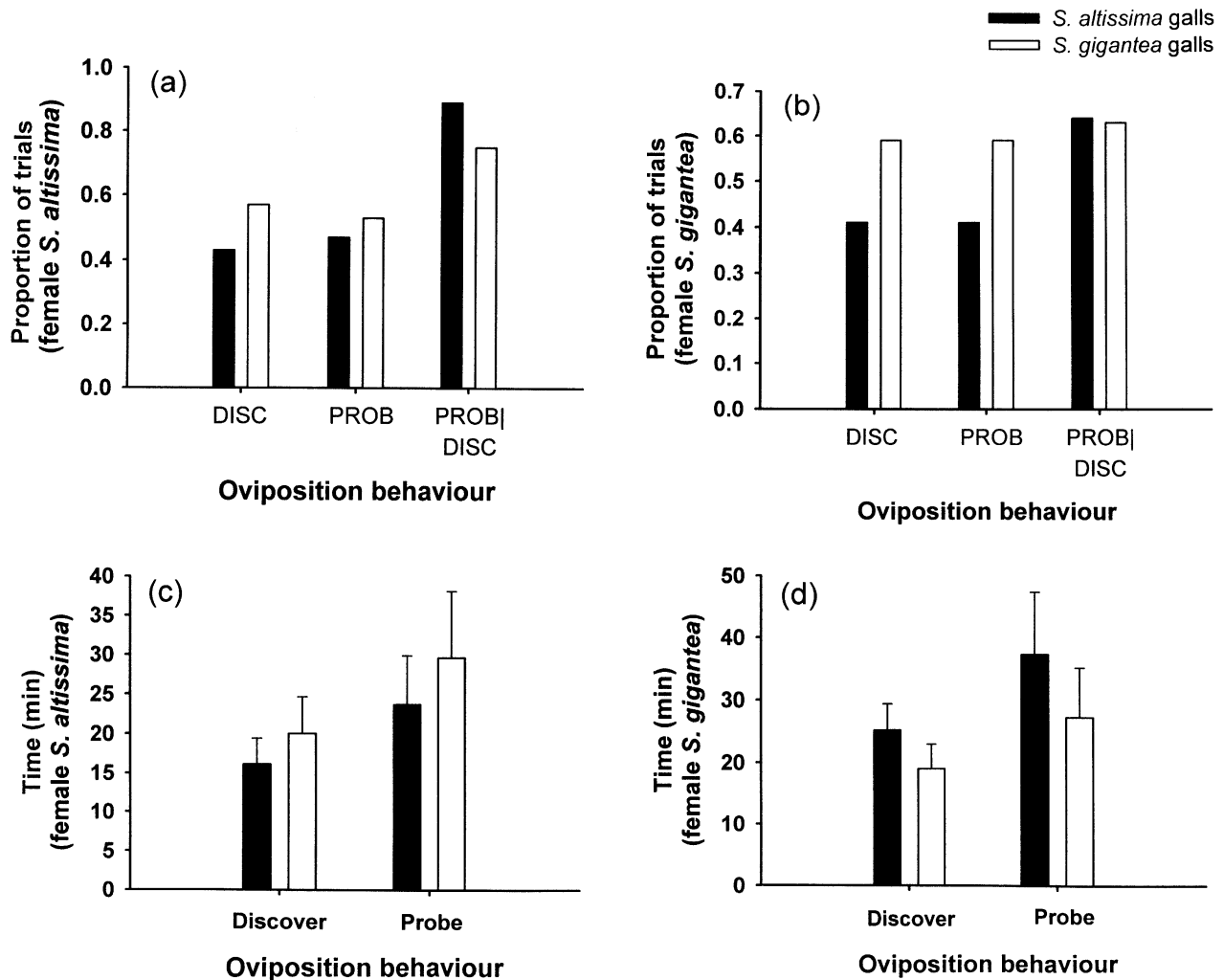
both *Eurosta* host races overlap broadly in emergence times. A lack of allochronic isolation suggests that in the field, males from both host races may vie for mating opportunities with females of either host race. In contrast, allochronic isolation is evident in the braconid parasitoids that attack sympatric host races of the apple maggot fly *Rhagoletis pomonella* (Feder, 1995), suggesting that assortative mating may be likely in this system.

Assortative mating by *E. gigantea* may still be possible in nature if mating takes place in association with the host plant of origin, as it does for the gall-inducing fly (Craig *et al.*, 1993). Newly eclosed female *E. gigantea* have a brief teneral period ( $\approx 1\text{--}3$  h) during which they do not mate but are quite active and mobile (J. T. Cronin, unpublished). It is very likely that these parasitoids emigrate from their emergence sites prior to mating. In a sympatric site where galls of both *Eurosta* host races are inter-mixed, it is possible that males and females

gravitate towards the plant species of their origin and thus mate assortatively as a result of habitat preference. No information on the mating behaviour of *E. gigantea* in the field is available; however, because female parasitoids exhibit no preference in the laboratory to walk or alight on one host plant species or the other, this possibility seems unlikely.

While pre-mating barriers do not appear to exist between *E. gigantea* parasitoids emerging from the two host races, post-mating barriers preventing the production of viable offspring remain a possibility. Matings between parasitoids from the two host races can yield adult offspring (J. T. Cronin, unpublished) but the fitness of these offspring relative to those derived from pure within-host-plant matings is unknown.

The data presented here suggest that large male *E. gigantea* are more likely to procure a mate than are small male *E. gigantea*. This is in accord with other studies that indicate a greater preference by females for, or a higher mating success



**Fig. 3.** Oviposition preference (choice experiment) by female *Eurytoma gigantea* for galls from *Solidago altissima* and *Solidago gigantea*. Separate trials were performed for females from each *Eurosta* host race. Regardless of female origin, there was no difference in the proportion of trials in which (a) a *S. altissima* gall or (b) a *S. gigantea* gall was discovered (DISC), probed with the ovipositor (PROB), or probed given that the gall was discovered (PROB|DISC) (separate  $\chi^2$  tests for independence,  $P = \text{NS}$ ). Time taken to discover the gall or probe it with the ovipositor also did not differ between the two gall host races for female parasitoids derived from (c) *S. altissima* or (d) *S. gigantea* galls (paired  $t$ -tests,  $P = \text{NS}$ ).

rate of, larger males (Grant *et al.*, 1980; Charnov *et al.*, 1981; Jones, 1982; but see King, 1988). Because parasitoids emerging from *S. gigantea* are larger on average than those emerging from *S. altissima*, it is likely in nature that a greater percentage of females from both host races will be mated by males emerging from galls of the *S. gigantea* host race.

With both choice and no-choice oviposition experiments, female *E. gigantea* from both *Eurosta* host races accepted either gall type with equal probability, despite the potential fitness advantages associated with *S. gigantea* galls. Measurements on recently enclosed individuals indicate that *E. gigantea* achieves a significantly larger body size by developing in galls on *S. gigantea* as opposed to *S. altissima* plants, a 5–7% increase. Large body size can enhance fitness by increasing longevity or egg load (for a review, see Godfray,

1994), although this is only known to be true for egg load for *E. gigantea*. Moreover, the increase in ovipositor length associated with female parasitoids emerging from *S. gigantea* galls may enhance reproductive success greatly by allowing females access to a greater fraction of the gall population. Studies have shown that short ovipositor lengths in *E. gigantea* prevent parasitoids from attacking all but the smaller galls (Weis & Abrahamson, 1985; Weis *et al.*, 1985).

Brown *et al.* (1995), working in the same area where this study was performed, detected no difference in per cent parasitism by *E. gigantea* on the two *Eurosta* host races. Together with the lack of allochronic isolation, assortative mating, and oviposition preference, these results suggest that *E. gigantea* does not prefer one host race over the other, and has probably not diverged into two distinct races in association

with the host races of *Eurosta*. This does not, however, preclude the possibility that parasitoids differ in their performance on the two host races or that there are trade-offs associated with the use of these hosts. For example, high performance on the host plant of origin may come at a cost of low performance on the alternative host (see Gould, 1979; Via, 1991; Mackenzie, 1996). An experiment with *E. gigantea* to evaluate this hypothesis was attempted (J. T. Cronin and W. G. Abrahamson, unpublished) but the rearing of parasitoids to adult eclosion was largely unsuccessful; however, without some reproductive isolation, allowing for the build-up of genetic adaptations to one *Eurosta* host race or the other, performance trade-offs seem unlikely. Finally, there is no evidence to suggest that the host shift by *Eurosta* was facilitated by lower rates of *E. gigantea*-induced mortality on the derived, *S. gigantea*, vs. the ancestral, *S. altissima*, host plant (Holt, 1984; Holt & Lawton, 1994; Berdegue *et al.*, 1996). The absence of an oviposition preference for the *S. gigantea* host race, and the equivalent rates of parasitism on the two *Eurosta* host races (Brown *et al.*, 1995), vitiate this possibility for *E. gigantea*.

The absence of a host-race affiliation by *E. gigantea* is in contradiction to the findings for the other major natural enemies of the goldenrod gallmaker. Brown *et al.* (1995) found that the specialist parasitoid *E. obtusiventris*, which was derived primarily from *S. altissima* galls, landed and spent more time on *S. altissima* than on *S. gigantea* plants. The net result was significantly higher rates of parasitism of galls on the former than on the latter plant species. While these data show a clear preference by the parasitoid for one *Eurosta* host race, they are only suggestive of a preference or adaptation to the host race from which the parasitoid originated (reciprocal experiments with parasitoids derived from *S. gigantea* galls would have to be performed). In comparison, M. Eubanks, C. Blair and W. G. Abrahamson (unpublished) have recently found evidence that *Mordellistena convicta* (Coleoptera: Mordellidae), a gall/stem-boring beetle that feeds facultatively on *Eurosta*, shows a strong preference for the plant species/gall host race from which it emerges. Allozyme differences have also been shown between beetles from each host race.

One possible explanation for why *E. obtusiventris* and *M. convicta* show evidence of differentiation on *Eurosta* host races, while *E. gigantea* does not, is that the former two species probably use different search cues from the last species. *Eurytoma obtusiventris* attacks its host before the gall becomes visible and probably locates the host via host-plant cues (see also Brown *et al.*, 1995). *Mordellistena convicta* is an omnivore, feeding primarily on plant tissue and secondarily on *Eurosta*. Host-plant cues therefore may be more important in host choice than the cues derived from the *Eurosta* prey. In contrast, *E. gigantea* attacks fully formed galls and may rely on visual cues from the gall or volatiles released from *Eurosta* alone. These studies suggest that some, but not all, specialist natural enemies of the goldenrod gallmaker may have responded to the formation of distinct races in their host.

The absence of a response by *E. gigantea* to the host shift by *Eurosta* suggests that specialisation and subsequent diversification by parasitoids, as a result of specialisation and

subsequent diversification by their hosts, may not be the primary diversification mechanism within the parasitic Hymenoptera. Parasitoids are often thought to be more highly specialised than predatory or saprophytic species (because of their intimate dependencies on one or few host types) and are thus expected to exhibit more extensive diversification (e.g. Mayr, 1976; Price, 1980). Yet, Wiegmann *et al.* (1993) found that carnivorous parasitic insects (including parasitoids) exhibited less diversification than predatory or saprophytic sister taxa. It is possible that some component of the environment other than the presence of distinct host populations is a more important agent of selection favouring the diversification of parasitoid species. To understand the evolutionary diversification of natural enemies of herbivores better, more studies are needed that focus on the response of natural enemies to herbivore host-plant shifts.

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