An Attempt to Change Habitat Preference of a Parasitoid, *Cotesia sesamiae* (Hymenoptera: Braconidae), Through Artificial Selection[1]

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Abstract Insect parasitoids are under strong selective pressure to utilize available hosts, which could cause a parasitoid used as a biological control agent to extend its host range. We artificially selected for a change in habitat preference of the braconid parasitoid *Cotesia sesamiae* (Cameron), to test the potential for host range expansion. *Cotesia sesamiae* parasitizes stemborers of maize and sorghum and has potential as a biological control agent of many stemborers. We tested selection for increased attraction to sorghum (a favored plant) and to cabbage (a non-favored plant) through experiments carried out over 4 generations. No change in attraction to either plant was observed, suggesting that this parasitoid may not easily expand its host range through a change in habitat preference.

Key Words Host range, *Cotesia sesamiae, Diatraea saccharalis,* stem borers, artificial selection, habitat preference

When a parasitoid is imported and released as a biological control agent, it is under strong selection to utilize available hosts in a new environment to which it is not adapted. Under this novel selection pressure, a parasitoid may extend its host range beyond what was expected prior to its release (Roderick 1992, Secord and Kareiva 1996). Although expansion of host range may aid the parasitoid in becoming successfully established (Overholt et al. 1994), and being an effective control agent, it may also have a negative impact on non-target host species (Howarth 1991, Asquith 1995, Boettner et al. 2000).

The host-utilization process of parasitoids has been divided into several discrete steps (Vinson 1998): locate the host's habitat, locate the host within that habitat, accept the host and oviposit, and finally the host must be physiologically suitable for the development of the parasitoid larvae. Although this scenario is oversimplified, the potential for host range expansion exists in each of these steps. For example, strains of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) that have been established as a biological control agent against sugarcane borer, *Diatraea saccharalis* F. (Lepidoptera: Pyralidae), have become more physiologically compatible with *D. saccharalis* than have other strains of *C. flavipes* that have not come into contact with this

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host (Wiedenmann and Smith 1995). Changes in habitat preference could also lead to an expansion of host range by a parasitoid; if adult females are attracted to novel plants, parasitoids could utilize hosts that would not have been previously encountered.

For selection to cause a change in habitat preferences of a parasitoid, there must be genetic variation in host preference in the population (Gromko et al. 1991). Heritability in host selection has been found for several parasitoids; Mollema (1991) has shown that variability in the selection of appropriate host species by strains of the braconid *Asobara tabida* Nees was heritable, and Prevost and Lewis (1990) found that flight response to volatile chemicals was heritable in another braconid, *Microplitis croceipes* (Cresson).

Cotesia sesamiae (Cameron) (Hymenoptera: Braconidae) is a short-lived, gregarious parasitoid of noctuid and pyralid stemborers in grasses (Mohyuddin and Greathead 1970). It is native to sub-Saharan Africa, where it is a common parasitoid of stemborers on maize and sorghum (Ullyett 1935, Harris 1962, Bosque-Perez et al. 1994, Kfir 1995). *Cotesia sesamiae* has been collected from hosts in several different grass species, and, therefore, as a species shows a range of plant preferences (Table 1). However, it is not known whether this variation has a genetic basis and is subject to selection pressure. One study of *C. flavipes,* a congeneric and ecologically similar species, showed that the habitat-plant preferences of populations could be changed in as few as 5 generations (Shami and Mohyuddin 1992). In contrast, another study of *C. flavipes* populations from different geographical regions, and from parasitized hosts found in several grass species, suggested that the populations did not differ in habitat plant preferences (Potting et al. 1997). Although generally *C. sesamiae* is not attracted to non-grass plants, in laboratory assays, some individual *C. sesamiae* were shown to be attracted to volatiles produced by non-grass plants (Ngi-Song et al. 1996), such as cabbage (*Brassica oleracea* L.) (Rutledge and Wiedenmann 1999).

To determine whether this variation in host plant preference of *C. sesamiae* is genetically based, we attempted to alter host plant preference in *C. sesamiae* by artificial selection. We tried to select lines of *C. sesamiae* that would prefere sorghum, *Sorghum bicolor* (L.), and lines that would prefere cabbage. Previous testing has shown that sorghum is a highly preferred plant for *C. sesamiae* (Ngi-Song et al. 1996), and it is a primary host plant for several of its stemborer hosts (Kfir 1995, Omwega et al. 1995). In contrast, none of the stemborer hosts of *C. sesamiae* feed on cabbage. The odor of cabbage is not attractive to the majority of *C. sesamiae* females in laboratory choice tests between sorghum and cabbage, but in tests in which female wasps were given a choice between cabbage and air, approximately 16%, of *C. sesamiae* chose cabbage (Rutledge and Wiedenmann 1999). An increase in percentage of individuals who chose cabbage when given a choice between sorghum and cabbage would indicate that the observed preference of individuals who chose cabbage was genetically based. Additionally, if *C. sesamiae* could be selected to respond to cabbage volatiles it would suggest that *C. sesamiae* could greatly expand the range of host plans to which it is attracted, and thus potentially its host range, upon introduction to a new habitat.

Materials and Methods

Female *C. sesamiae* from a laboratory culture were screened for plant preference, with those choosing sorghum used to start one line, and those preferring cabbage to

Table 1. Host plant and host insect records for *C. sesamiae*

Host plant		
Poaceae	Host	Reference
Sorghum bicolor L.	*Chilo partellus* (Swinhoe)	Omwega et al. 1995
	Busseola fusca Fuller	Kfir 1995, Ullyett 1935
Sorghum arundinaceium (Devs.) Stapf	*Chilo partellus*	Mbapila 1996
Zea mays L.	*Chilo partellus*	Overholt et al. 1994
	Sesamia calamistis Hmps.	Bosque-Pérez et al. 1994
	Busseola fusca	Kfir 1995
Saccharum officinarum L.	*Sesamiae* spp.	Scheibelreiter 1980
Pennisetum purpureum Schumach.	*Chilo* spp.	Mbapila 1996
	Poeonoma sp.	Khan et al. 1997
Pennisetum macrourum Trin.	*Poeonoma* sp.	Khan et al. 1997
Echinochloa pyramidalis (Lam.)	*Phragmataecia boisduvali* (Herrich-Shaeffer)	Khan et al. 1997
Phragmites sp.	*Phragmataecia boisduvali*	Khan et al. 1997

start another. These lines were maintained for three additional generations, with the female wasps that preferred the same plants as their mother used to continue each line (e.g., sorghum in generation 1, sorghum in generation 2, sorghum in generation 3 . . .). To screen female wasps for plant preference, we used a Y-tube olfactometer (Rutledge and Wiedenmann 1999), with the scent of sorghum in one arm, and the scent of cabbage in the other. Newly-emerged, mated, unfed, naive female wasps were used in the experiment. Preliminary experiments showed that the proportion of wasps choosing cabbage and sorghum did not differ between assays in which individual wasps were released into the olfactometer, and those in which groups of 30 wasps were released into the olfactometer. Therefore, to facilitate accumulation of sufficient individuals to perpetuate the selection lines, we released groups of 30 wasps into the base of the Y-tube and they were allowed 15 min to choose one scent or the other. Wasps that crossed beyond the 'fish-trap' baffle at the finish line were collected from each of the arms. This procedure was repeated until all the available female wasps were tested (up to 210 individuals). Wasps choosing a given odor source were caged together for parasitization of hosts.

To start the two lines of wasps, we presented each female wasp with a *D. saccharalis* larva and watched to confirm oviposition. Up to 45 larvae were parasitized for each parasite line per generation. Larval hosts parasitized by wasps from each line were placed in a Petri dish with artificial diet (Martinez et al. 1988). When wasp larvae emerged from the host and formed cocoons, they were separated into individual cocoon masses (one cocoon mass is the offspring from one female wasp) and placed into individual 5-mL cups. To synchronize emergence times, we transferred darkened cocoons (near eclosion) to a refrigerator (10°C) to delay emergence. When the last cocoon masses of that line darkened, the others were removed from the refrigerator and all the cocoons were placed into a 24°C incubator. Newly-emerged adult males and females from the same line were placed into a Plexiglas® cage and allowed to mate.

For each succeeding generation, these newly-eclosed, mated, unfed, naive female wasps were tested for preference, and wasps that had the same preference as their mothers were used to continue the line. The procedure was followed for 4 generations for each pair of lines. In this type of experiment, the cumulative effects of inbreeding, random drift or sampling bias might give the appearance of successful selection for a character (Falconer 1989). We attempted to control for at least some of these factors by setting up 5 replicate lines for each plant species tested.

Threshold characters are assumed to be controlled by many genes, and thus vary continuously, but also to have a threshold that results in distinct phenotypes instead of a continuously varying phenotype (Falconer 1989). We treated odor preference as a threshold character. The variables produced by our tests were the number of wasps that chose sorghum and the number that chose cabbage in each generation. We used Goodman and Kruskal's *gamma* (1954), a non-parametric statistic, to test if the proportion of wasps that chose a particular source increased over the course of selection for that source. The *gamma* calculation has the same numerator as Kendall's *tau* (1949), and may be tested for statistical significance in a normal approximation by dividing the *gamma* numerator by the root-variance of *tau* (Goodman and Kruskal 1954). Ghent (1993) presented an example and the requisite formulae for this approach in another context. Goodman and Kruskal's *gamma* test showed if there was a directional change within each line in the proportion of female wasps that chose each plant. This test has the advantage of being able to tolerate extremely small numbers (like 1 or 0), so that if numbers of wasps become small after several generations the accuracy of the test will not be affected (A. W. Ghent, pers. com.).

All tests were conducted in a greenhouse room in which temperatures ranged from 24°C to 34°C, but were usually 27-30°C. The test area was enclosed in a white plastic and cloth 'tent' which diffused the natural light, thus avoiding strong directionality in the light, or sharp shadows.

Our Y-tube olfactometer (Rutledge and Wiedenmann 1999) is similar to that of Sabelis and van de Baan (1983), Steinberg et al. (1992) and Ngi-Song et al. (1996), but differed in being positioned upright rather than horizontally. Preliminary trials suggested that the upright position increased response rate of wasps during bioassays. Plant chambers (30 × 30 × 100 cm) were large enough to contain an entire plant and stood in water to complete a seal. Air was pulled through the plant chambers and into the Y-tube and then pulled back into the pump. Total airflow was controlled with flow meters at 2.5 L/min (1.25 L/min in each arm). Air was recirculated through the system and cleaned by charcoal filters. Laminar flow in the Y-tube was assured by two brass baffles in each arm of the Y-tube. CO_2 "smoke" from dry ice was used to provide visual confirmation that air flow though the Y-tube was primarily laminar. The lower baffles in the arms of the Y-tube, the 'fish-trap' baffles, had 4 small holes around their perimeter, such that a gap was created between the screen and the side of the Y-tube. These gaps allowed wasps that chose an odor source in one arm to proceed past the baffle, but made it unlikely that any wasp could return to the main body of the

Y-tube. Wasps that crossed the finish line, in either arm, were therefore trapped and easily collected. To avoid directional effects, we switched odor sources between olfactometer arms after each group of 30 wasps was tested.

Eggs of *D. saccharalis* were obtained weekly from the laboratory of J. W. Smith, Jr., Texas A&M University. Larvae of *D. saccharalis* were reared in Petri dishes on a meridic, wheat-germ diet (Martinez et al. 1988) and were transferred to fresh diet as dishes became contaminated with frass. Host larvae were kept in an incubator at 22°C (45% RH) and 18:6 L:D. Laboratory cultures of *C. sesamiae* were established at Texas A&M University from field collections made at the International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, in 1992. Wasps from the colony at Texas A&M University were used to establish a colony at Illinois Natural History Survey in 1994. The culture has been maintained continuously on *D. saccharalis,* feeding on artificial diet, since establishment. Wasp colonies were maintained following the methods of Wiedenmann et al. (1992).

All plants were grown in the greenhouse in 23-cm diam pots in sterilized soil and were watered twice daily. Plants were fertilized with Peter's Professional fertilizer 20:10:20 (N:P:K) with a 250 ppm concentration weekly (Scotts-Sierra Horticultural Products Company, Marysville, OH). No pesticides were used on plants. Sorghum and cabbage were grown from seed (Funk's Seed cultivar G522DR, and Harris Seed Company, variety 'Market Prize,' respectively). Plants were selected to have similar leaf surface area. All plants were at least 2 weeks old before use, and no plants that had begun to form reproductive structures were used in the experiments.

Cotesia sesamiae is more attracted to the odor of sorghum that has been damaged by *D. saccharalis* than to the odor of undamaged sorghum (Ngi-Song et al. 1996, Rutledge and Wiedenmann 1999). Therefore, sorghum was damaged to increase its attractiveness to the wasps. Third-instar *D. saccharalis* were isolated with pieces of sorghum, and allowed to feed for at least 24 hours in order to clean any artificial diet from the gut. Individual larvae were then placed in a glass vial (5 mm diam, 30 mm length) attached perpendicularly to the stem with Parafilm®. Larvae tunneled into the stem of the sorghum and fed for at least 48 h before the plant was used in the experiments. The damaged plant, with the host in the tunnel and with host frass, was placed into the plant chamber for the experiment. *Cotesia sesamiae* does not distinguish between cabbage and damaged cabbage (Rutledge and Wiedenmann 1999), so undamaged cabbage was used in these experiments. Plants were fitted with a paper collar around the base of stems before they were placed into the plant chamber, which limited the influence of soil on the outcome of the tests. Plants were put into the chambers and allowed to equilibrate for at least a half an hour prior to testing.

Results and Discussion

Approximately 70 to 74% of wasps that were selected for sorghum preference chose sorghum over the four generations (Table 2). Of the lines of wasps that were selected for attraction to sorghum, one replicate showed a significant increase in the proportion of wasps that chose sorghum with increasing numbers of generations; the four other replicates showed no significant trends (Table 2).

Approximately 25 to 27% of wasps that were selected for cabbage preference chose cabbage over the four generations (Table 3). One of the lines of wasps selected for attraction to cabbage showed a significant increase in the proportion of wasps that chose cabbage with increasing numbers of generations; however, another replicate showed a significant decrease in the proportion of wasps that chose cabbage (Table 3). Finally, the three other replicates showed no significant trends (Table 3).

The artificial selection regimen did not change preferences of *C. sesamiae* for plant volatiles; in most selection lines, the percentages of wasps choosing sorghum and cabbage remained consistent across four generations. Three lines, however, did show significant trends. In one of the lines selected for increased attraction to cabbage there was an increase in the proportion of wasps choosing cabbage. In two lines there was an increase in the proportion of wasps choosing sorghum; one line had been selected for attraction to sorghum, and one had been selected for increased attraction to cabbage. There was no connection between the direction of artificial selection and the direction of change in preference. Examination of those individual lines that showed significant trends revealed unusual proportions of wasps choosing sorghum and cabbage in the first generation, followed by a return to typical proportions in successive generations (for example, see Replicates 2 and 3 in the cabbage line). Thus, it seems likely that significant changes in the proportions were due to the unusual proportions of wasps choosing sorghum and cabbage in the first generation.

Artificial selection may have failed to alter host-plant preference in *C. sesamiae* for several reasons. First, the selection regimen may not have been long enough; if changes in preference were subtle and accumulated gradually, they could have escaped detection in a study only four generations long. Yet, if habitat preference were strongly heritable, the response to selection should be sharply reduced after the first generation, and additional generations would show only minor change (Falconer 1989). Therefore, if habitat preference were strongly heritable, we should have seen response in the course of four generations.

Second, choice of cabbage in the olfactometer may not have reflected true attraction; individual wasps may have arbitrarily chosen that side of the olfactometer. Cabbage is not a host plant for any of the hosts of *C. sesamiae,* and cabbage odor may, therefore, not be recognized by *C. sesamiae.* By selecting cabbage as the alternative plant, we were testing an extreme range of potential plant hosts. If *C. sesamiae* indeed could have been selected for increased attraction to cabbage, then the potential range of released *C. sesamiae* would be very large. However, failure of the selection regimen to increase *C. sesamiae* attraction to cabbage does necessarily preclude less-drastic shifts. We know that *C. sesamiae* is sensitive to sorghum odors, so the failure of the selection regimen to increase the numbers of individuals attracted to sorghum is more suggestive of a fixed, non-heritable, preference for plant species than the failure of the selection regimen to increase the number of individuals attracted to cabbage.

Third, selection pressure may not have been strong enough to cause a measurable change in preference. Weak selection would result from arbitrary choice of olfactometer arms rather than responding to attractive odors. Even if many of the wasps made choices based on olfaction, a few wasps that did not could hinder selection. Although it was not apparent from preliminary experiments, it is possible that crowding of wasps in the Y-tube caused some individuals to enter the cabbage arm. Although male wasps were not selected for habitat preference, this is unlikely to have reduced selection pressure because males receive their genetic material from their mothers, which had already been tested for host plant preference.

Fourth, our culture of *C. sesamiae* may not have had sufficient genetic variability in habitat preference to respond to selection. Wasps for this study were from a

Table 2. Results of selection for attraction of *C. sesamiae* to sorghum volatiles. The proportions of female wasps preferring sorghum to cabbage in each line for each generation is shown, with the gamma (γ) value for each line. N shows the number of females tested. The sign of γ indicates the overall trend: if γ is positive, the proportion of female wasps preferring sorghum increased, if negative, there was an overall tendency toward cabbage. A value of P less than 0.05 indicates that there was a significant trend across the four generations

Replicate	Gen. 1	Gen. 2	Gen. 3	Gen. 4	δ, P
1	0.69 (N = 111)	0.75 (N = 119)	0.80 (N = 172)	0.77 (N = 140)	$\gamma = 0.118$, $P = 0.114$
2	0.47 (N = 98)	0.75 (N = 107)	0.60 (N = 241)	0.76 (N = 149)	$\gamma = 0.218$, $P = 0.001$
3	0.90 (N = 82)	0.74 (N = 43)	0.75 (N = 124)	0.84 (N = 128)	$\gamma = -0.057$, $P = 0.569$
4	0.86 (N = 88)	0.63 (N = 126)	0.76 (N = 222)	0.70 (N = 135)	$\gamma = -0.078$, $P = 0.280$
5	0.68 (N = 71)	0.71 (N = 162)	0.78 (N = 214)	0.63 (N = 134)	$\gamma = -0.038$, $P = 0.589$
Totals	0.71 (N = 450)	0.72 (N = 557)	0.73 (N = 973)	0.74 (N = 686)	

Table 3. Results of selection for attraction of *C. sesamiae* to cabbage volatiles. The proportions of female wasps preferring cabbage to sorghum in each line for each generation is shown, with the gamma (γ) value for each line. N shows the number of females tested. The sign of γ indicates the overall trend: if γ is positive, the proportion of female wasps choosing sorghum increased; if negative, there was an overall tendency toward cabbage. A value of P less than 0.05 indicates that there was a significant trend across the four generations

Replicate	Gen. 1	Gen. 2	Gen. 3	Gen. 4	γ, P
1	0.31 (N = 111)	0.26 (N = 231)	0.24 (N = 229)	0.22 (N = 195)	$\gamma = 0.102$, $P = 0.106$
2	0.53 (N = 98)	0.22 (N = 65)	0.28 (N = 72)	0.28 (N = 25)	$\gamma = 0.356$, $P = 0.0003$
3	0.10 (N = 82)	0.34 (N = 41)	0.29 (N = 110)	0.28 (N = 144)	$\gamma = -0.204$, $P = 0.027$
4	0.14 (N = 88)	0.19 (N = 16)	0.00 (N = 7)	—	$\gamma = 0.067$, $P = 0.841$
5	0.32 (N = 71)	0.34 (N = 30)	0.13 (N = 32)	0.27 (N = 11)	$\gamma = 0.235$, $P = 0.124$
Totals	0.29 (N = 450)	0.27 (N = 383)	0.25 (N = 450)	0.25 (N = 375)	

laboratory colony that has been in culture for 4 yrs (approximately 70 generations) and may well have gone through several genetic bottlenecks. *Cotesia sesamiae* are sibling maters (Kimani and Overholt 1995), and inbreeding can lead to low levels of heterozygosity in populations (Graur 1985). Hymenoptera in general have low heterozygosity when compared to other insects (Metcalfe et al. 1975, Pamilo et al. 1978), although the solitary Hymenoptera have a somewhat higher level of heterozygosity than the social Hymenoptera (Graur 1985).

Low levels of genetic variability in preference for plant species in *C. sesamiae* may be a consequence of ecological conditions. *Cotesia sesamiae* is native to grasslands, and is faced with little variation in the habitat plants available to it. *Cotesia sesamiae* does favor certain grass species more strongly than others, but it is not attracted to non-grass plants (Ngi-Song et al. 1996, Rutledge and Wiedenmann 1999). It seems likely that the cues *C. sesamiae* is using to locate host habitats are cues that are common to many grasses, and could therefore adequately equip *C. sesamiae* to find hosts in a variety of grasses. Our findings were consistent with those of Potting et al. (1997), who detected no variation in volatile chemical preference in geographically distinct populations of *C. flavipes* that utilize different host habitats.

Given the qualifications discussed above, these results have limited power to address the question of genetic heritability of plant preference in *C. sesamiae.* However, in combination with previous olfactometer testing of *C. sesamiae* plant preferences (Ngi-Song et al. 1996, Rutledge and Wiedenman 1999) and with previous tests of geographic variation in plant preferences of *C. flavipes* (Potting et al. 1997), these results suggest that *C. sesamiae* is unlikely to expand habitat preferences beyond grasses, particularly where hosts are available in grasses. This further implies that impact on non-target host species in non-grass plants would be unlikely. On the other hand, inflexibility in host plant preference suggests that *C. sesamiae* may not adjust readily to a new habitat, and may have a more difficult time establishing than would more flexible parasitoid species (Overholt et al. 1994).

Parasitoid species that search in diverse habitat types, or that have longer life spans than *C. sesamiae,* might be more genetically variable in habitat preferences. Therefore, more species of parasitoids, with different ecologies, would have to be subjected to selection regimens for habitat preference before we can generalize these results to parasitoids outside of the *C. sesamiae–C. flavipes* species complex.

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