

Host plant preference based on salicylate chemistry in a willow leaf beetle (*Chrysomela aeneicollis*)

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Summary. *Chrysomela aeneicollis* (Coleoptera: Chrysomelidae) uses salicin from its host plant (*Salix* spp.) to produce a defensive secretion, salicylaldehyde. Because it requires salicin for this secretion, I predicted that *C. aeneicollis* should be attracted to willows which possess salicin and other salicylates. To test this prediction, I determined the host-plant preferences of *C. aeneicollis* among four potential hosts which occur in the Sierra Nevada range of eastern California. These species have very different salicylate chemistries but do not differ in nutritional quality for *C. aeneicollis*. In oviposition-preference tests, gravid females showed no preference between a salicylate-poor species, *S. lutea*, and a salicylate-rich species, *S. orestera*. However in feeding-choice tests, both larvae and adults preferred *S. orestera* over *S. lutea*. This preference was not affected by the species on which the larvae were reared. In other feeding tests, adults preferred *S. orestera* over two medium-salicylate species, *S. boothi* and *S. geyeriana*, regardless of which host species they had been feeding on in nature. In a final feeding test, adults were stimulated to feed by salicin itself. In nature, the relative abundances of *C. aeneicollis* adults and egg clutches among these species correspond to the adult feeding preference in the laboratory. Additionally, multiple regression analyses showed that adult abundance was not related to among-clone differences in leaf toughness or nutritional quality, but rather to salicin content and plant size. Thus for *C. aeneicollis*, both laboratory and field results demonstrate a preference for salicylate-rich willows which is partly responsible for the increased level of attack on them.

Key words: Chrysomelidae – *Salix* – Salicin – Herbivore feeding preference – Host-plant choice

Several species of willow-feeding leaf beetles (*Chrysomela* spp. and *Phratora* spp.) use host-plant salicin to produce a larval defensive secretion, salicylaldehyde (Rowell-Rahier and Pasteels 1982; Pasteels et al. 1983). Generalist predators are deterred by this secretion under laboratory conditions (Wallace and Blum 1969; Pasteels et al. 1983, 1988; Denno et al. 1990), and in nature, larval survival is frequently higher on salicin-rich willows (*Salix* spp.) than on salicin-poor willows (Rank 1990). The ecological effect of host-plant salicin may evolutionarily favor a preference by the beetles for salicin-rich over salicin-poor willows.

Recent studies indicate that salicin and other salicylates affect host-plant use in willow leaf beetles. Tahvanainen et al. (1985) found that several leaf beetle species preferred to feed on host species which have salicylate profiles similar to their natural hosts, and they also found that the salicin-using leaf beetle *Phratora vitellinae* preferred salicylate-rich over salicylate-poor willows. Moreover, Denno et al. (1990) showed that *P. vitellinae* preferentially oviposits on salicylate-rich willows. The preference for salicin may result in increased attack on salicylate-rich willows in nature, as reported by Smiley et al. (1985) for the montane leaf beetle *Chrysomela aeneicollis*. On the other hand, other factors such as leaf pubescence may also play an important role in a leaf beetle's choice of a host plant (Rowell-Rahier and Pasteels 1982; Rowell-Rahier 1984a, b; Soetens et al. 1991). Rowell-Rahier et al. (1987) and Soetens et al. (1991) found no relationship between the field abundances of adult *P. vitellinae* and the salicylate contents of their potential host plants, while Soetens et al. (1991) found that leaf pubescence was negatively related to abundance. Additionally, although oviposition-choice tests with *P. vitellinae* showed a strong preference for one salicylate-rich willow, *Salix fragilis*, they also showed that few eggs were laid on another salicylate-rich species, *S. dasyclados*, which has very pubescent leaves (Denno et al. 1990).

The positive relationship between host-plant salicin and larval damage in *C. aeneicollis* could result from higher larval survival on salicin-rich willows, a preference

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by adults for salicin-rich willows, or a combination of these two factors. In this study, I determined *C. aeneicollis*'s preferences among four willow species with very different amounts of salicylates. I predicted that *C. aeneicollis* should choose the salicylate-rich species over the salicin-poor ones. To test this prediction, I conducted oviposition- and feeding-preference tests in the laboratory, and I measured the abundances of adults and egg clutches on the same species in the field. I also determined whether salicin itself stimulates *C. aeneicollis* feeding behavior.

Natural history

Chrysomela aeneicollis (Schaeffer) occurs at high elevations (2400–3500 m) in the eastern Sierra Nevada of central California. This beetle is univoltine. The adults enter diapause shortly after emergence in late August, and they overwinter in the leaf litter beneath their host plants. In the spring, the adults feed, mate, and oviposit exclusively on willow and aspen foliage (Smiley and Rank 1986). The larvae feed together in groups and they usually do not leave the natal shoot until they molt into the second instar (Rank, personal observations). Even in later instars, the larvae rarely leave the host plant (Smiley and Rank 1986).

Dense populations of *C. aeneicollis* occur along the north fork of Big Pine Creek (37°7' N, 118°29' W). Two sites were used in this study, the Cabin Bog (2840 m) and the Falls Site (2940 m). The Cabin Bog is a wet habitat shaded by lodgepole pine (*Pinus murrayana*), where the two most common willows, *Salix orestera* and *S. lutea*, grow in mixed stands. The Falls Site is a more variable habitat with dry sandy areas, pine woodlands, and open bogs. The most common willows there, *S. boothi*, *S. geyeriana*, and *S. orestera*, occur together in large mixed stands. *Chrysomela aeneicollis* adults and larvae occur naturally on all willow species at the field sites, including other species not discussed in this paper (*personal observation*).

The four species used in this study do not vary in nutritive quality for *C. aeneicollis*. Larvae grow equally well on all of them, and the species do not differ in leaf water content. Only one of the species, *S. boothi*, has pubescent leaves and the mature leaves of all of the species are approximately the same thickness. There is significant among-species variation in leaf toughness as measured by a penetrometer. *Salix lutea* leaves are on average 18% tougher than those of *S. orestera* and *S. boothi*, and *S. lutea* leaves are 46% tougher than those of *S. geyeriana*. However, individual clones also differ in all of these characteristics. These species vary greatly in their phenolglycoside chemistries. *Salix orestera* contains the most salicin (on average, 6% leaf dry weight), *S. geyeriana* has medium levels (3.5% leaf dry weight), *S. boothi* has low concentrations (1.5% leaf dry weight), and *S. lutea* contains only trace amounts of salicin. The total salicylate contents of these species are correlated with their salicin contents, and these differences in leaf chemistry were stable over the summer of 1989 (Rank 1990).

Materials and methods

Choice tests

Oviposition-choice test. I placed one sprig of *S. lutea* and one sprig of *S. orestera* into water-filled plastic cups in the choice arenas. The choice arenas consisted of a paper bucket (18 cm height, 25 cm diameter), with a thin layer of Tanglefoot™ resin along the rim. This resin prevented the beetles from leaving the arena (they rarely fly). I collected gravid *C. aeneicollis* females from a local population (feeding on *S. lemmoni* 50 m above the Cabin Bog). After 48 h, I determined whether the female had laid her egg clutch on *S. lutea* or *S. orestera*. In this test, I used two salicin-rich *S. orestera* clones and three salicin-poor *S. lutea* clones. One clone used in the oviposition-choice tests was *S. lutea* var. *watsoni* (SL3 in Table 1), but the other two were *S. lutea*. Neither variety contains salicin. The sample size for this test was limited by the space required for the choice arenas, and in the statistical analysis I did not include replicates where no clutch was laid. This test was conducted at the Cabin Bog.

Two-species feeding tests. After collecting second-instar *C. aeneicollis* larvae from *S. lemmoni*, I reared them on *S. lutea* and *S. orestera* for 5 days until they molted into the third instar. Then I gave each larva a choice between a *S. orestera* leaf and a *S. lutea* leaf (all of the *S. lutea* clones in the subsequent experiments were *S. lutea* var. *watsoni*). These leaves were placed together into a vial, pointing away from each other distally in a 'V' shape and each larva was placed at their intersection. The choice test lasted for 24 h. Following the test, I reared the larvae on the same species that they had been feeding on before the choice test. When the new adults emerged, I conducted a second choice test between *S. orestera* and *S. lutea*, using the same procedure as in the larval choice test. I used five *S. lutea* clones and five *S. orestera* clones in the larval feeding-choice tests, and I used five *S. lutea* and six *S. orestera* clones for the adult feeding-choice tests. In both tests, each *C. aeneicollis* individual was offered a different choice, i.e. no two individuals were offered a choice between the same two willow clones.

Three-species feeding test. I collected *C. aeneicollis* adults from four clones of *S. orestera*, *S. geyeriana*, and *S. boothi*. These were newly emerged adults which had probably fed as larvae on the plants from which I collected them. After depriving them of food for 24 h, I offered them foliage from the same three willow species, represented by a randomly selected leaf from one of four individual clones. Each dish received a different combination of these clones. In this experiment, I placed the three leaves into separate vials in a 12.5 cm petri dish before adding three beetles. After 24 h, I replaced each leaf with a new one from a different willow to make a second measurement.

Salicin-feeding test. I used Millipore™ filters (Millipore Corporation, 2.5 cm diameter, type SC, pore size 8.0 μm) as artificial leaf disks. After soaking the filters in the solutions, I cut them into halves. I then positioned the filters at a slightly upward angle from their point of attachment, and added three beetles that had not fed for 24 h to each dish. This choice test ran for 48 h.

All of the feeding-choice tests were conducted at White Mountain Research Station, about 45 km from the field site, using a Percival incubator (20° C, photoperiod 14:10 L:D). I used an image analysis system to measure the leaf area consumed in the Cabin Bog choice tests (facility at the James Reserve of the University of California Natural Reserve System, Idyllwild, California). For the Falls Site and the salicin-feeding tests, I photocopied the samples onto 1 mm² graph paper and counted the number of squares within the area consumed.

Statistical analysis of feeding tests. In all feeding tests, *C. aeneicollis* had been simultaneously offered two or more choices. The amount of any one item eaten was therefore not independent of the amount eaten of the others. To analyze the two-way Cabin Bog and salicin-feeding tests (Zar 1984), I used Wilcoxon signed-ranks tests (for

paired comparisons). However, I used multivariate analysis of variance (MANOVA) to analyze the three-way Falls Site feeding-choice test, where the amount of each willow test species eaten represented a separate dependent variable. The dependent variables in the MANOVA need not be independent measurements (SAS 1988), and similar analyses have been used in other studies of host-plant choice in herbivorous insects (e.g. Thompson 1988b, c). Before the analysis, I took averages of the amount of each test species eaten over the 2 days and log-transformed those averages to remove the positive relationship between the mean and standard deviation. The MANOVA tested for: (1) differences among the three test species (within-subjects factor; preference among the three species), (2) differences in overall feeding rates among the beetles that had been collected on each species (between-subjects factor; source of the beetles), and (3) differences in preference among the beetles from the different willow species (test species by beetle source interaction). The last test indicates whether the species of willow from which I collected the beetles affected their subsequent feeding preference. I report three commonly used MANOVA test statistics: Hotelling-Lawley Trace, Pillai's Trace, and Wilks' Criterion.

Adult and egg clutch distributions

I selected 10–15 pairs of willows of different species in which one willow's nearest neighbor was an individual of the other species. The two individuals of each pair were approximately equal in size, and I used morphological, phenological, and gender differences to distinguish individual clones. At the Cabin Bog, I compared adult abundance on *S. orestera* and *S. lutea* (10 July 1989), and at the Falls Site, I made three pair-wise comparisons between *S. orestera*, *S. geyeriana*, and *S. boothi* (adult abundance on 23–26 June 1989, egg abundance on 15–17 July 1989). I counted adult beetles on each tree for 2 min (cf. Rowell-Rahier 1984a), and I recorded the number of beetles in copula. To determine the egg abundances, two observers counted clutches on a tree for 5 min.

Finally, in addition to the species comparisons, I used multiple regression analysis to determine the effects of salicin content, plant size, water content, and leaf toughness on adult abundance at the Falls Site. Plant size was estimated by measuring the plant's height and diameter, and calculating the cylindrical volume. The salicin contents were determined from samples collected on 23–26 June 1989, and the water contents and leaf toughness measurements were obtained from samples collected in early July 1989 for a growth rate experiment (see Rank 1990 for a more detailed description of the methods). Only a subset of the willows used in the abundance comparisons were used in the growth experiment, and because abundance on one willow from a pair is correlated with abundance on its neighbor (see below), I dropped one of the willows from each plant-pair before the regression analysis. Thus, 20 plants were used in the regressions (6 *S. boothi* clones, 7 *S. geyeriana* clones, and 7 *S. orestera* clones). Before the regressions, the abundances and plant volumes were log-transformed to normalize them. Unless otherwise noted, all measures of dispersion reported in this paper are standard errors.

Results

Oviposition-choice test

Gravid females displayed no consistent preferences among the two Cabin Bog species. In one comparison (SO1 versus SL3) all of the clutches were laid on the *S. orestera* clone, but in another (SO2 versus SL1), all of the clutches were laid on *S. lutea* (Table 1). When the choices between SO1 and the three *S. lutea* clones were pooled, the preference for SO1 over the *S. lutea* clones was not

Table 1. Number of ovipositions on *Salix orestera* and *S. lutea* by different gravid *Chrysomela aeneicollis* females

	<i>S. lutea</i> clone #		<i>S. orestera</i> clone #	
	SO1		SO2	
	# Clutches SO	# Clutches SL	# Clutches SO	# Clutches SL
SL1	2	2	0	3
SL2	2	1	2	2
SL3	2	0	2	2
Total	6	3	4	7

Each willow species is represented by its two-letter abbreviation, and the individual clones are labeled by their identification number

statistically significant ($G=1.02$, $P>0.2$), nor was the preference for the *S. lutea* clones over SO2 ($G=0.83$, $P>0.3$). Altogether, equal numbers of clutches were laid on each species (Table 1).

Feeding-choice tests

In the two-way choice test between *S. lutea* and *S. orestera*, the larvae consumed nearly 4 times as much *S. orestera* foliage ($4.73 \pm 0.68 \text{ cm}^2$) as *S. lutea* foliage ($1.16 \pm 0.44 \text{ cm}^2$), and this difference was highly significant (Wilcoxon signed-ranks test, $P<0.001$). Indeed, of the 20 larvae tested, 13 avoided *S. lutea* foliage entirely and only 2 consumed more *S. lutea* foliage than *S. orestera* foliage (Fig. 1). There was no apparent effect of larval experience on larval preference. Larvae that had fed on *S. lutea* before the choice-test consumed a slightly higher proportion ($86 \pm 9.4\%$) of *S. orestera* foliage than the larvae that had fed on *S. orestera* ($79 \pm 7.9\%$), but this small difference was not statistically significant (Mann-Whitney test, $P=0.38$).

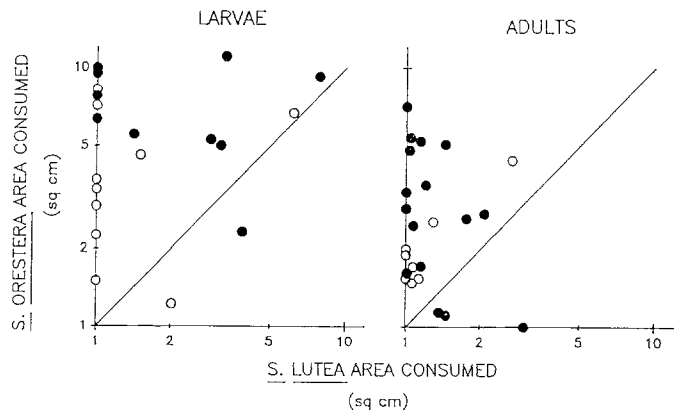


Fig. 1. Amounts eaten by *Chrysomela aeneicollis* larvae and adults feeding on *Salix lutea* and *S. orestera*. Each point represents a single individual. The color of the point denotes which species the larvae were reared on before the choice test: open, *S. lutea*; closed, *S. orestera*. The three adults that consumed more *S. lutea* foliage than *S. orestera* foliage were different individuals from the two that had chosen *S. lutea* as larvae. The line of equal preference is indicated

As adults, these *C. aeneicollis* individuals consumed nearly 6 times more *S. orestera* foliage ($1.87 \pm 0.34 \text{ cm}^2$) than *S. lutea* foliage ($0.29 \pm 0.09 \text{ cm}^2$), and this difference was highly significant (Wilcoxon signed-ranks test, $P < 0.001$). Yet fewer adults rejected *S. lutea* foliage (7 of 24 individuals) than larvae ($G = 5.76$, $P = 0.016$). Adults that had been reared on *S. lutea* consumed $89\% \pm 4.4\%$ *S. orestera* foliage, versus $77\% \pm 8.3\%$ for those that had been reared on *S. orestera*, but this difference was not statistically significant (Mann-Whitney test, $P = 0.69$). Hence, for adults as for larvae, the feeding preference was not conditioned by larval food plant experience.

In the three-way Falls Site choice tests, beetles collected on all three species preferred *S. orestera* over the

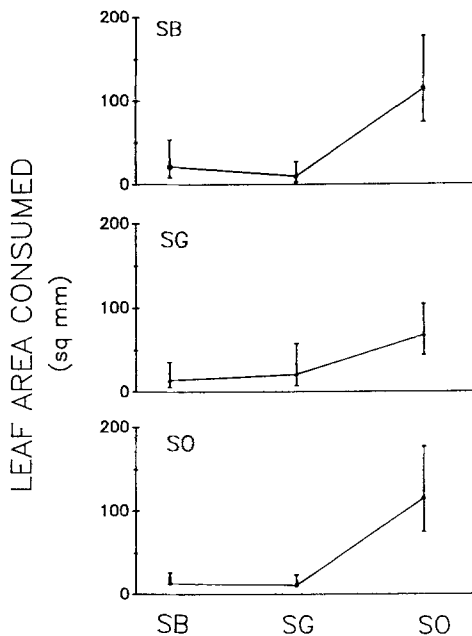


Fig. 2. Amounts of *S. boothi*, *S. geieriana*, and *S. orestera* eaten by adult beetles which were collected on each of those species in the field. Error bars represent the 95% confidence limits of the back-transformed means of the amounts consumed. Lines are drawn between the means to indicate the source \times test species interaction

Table 3. Average abundances of *C. aeneicollis* eggs and adults on four species of willows at the Cabin Bog and the Falls Site

Site Species	Adult abundance			Egg abundance		
	Mean (SD)		$P <$	Mean (SD)		$P <$
	<i>n</i>	(# adults)		<i>n</i>	(# clutches)	
Cabin Bog						
SO	13	3.5 (3.0)	0.001			
SL	13	0.2 (0.6)				
Falls Site						
SO	11	19.7 (12.1)	0.001	9	17.2 (14.4)	0.094
SB	11	3.8 (3.2)		9	7.7 (7.3)	
SO	15	26.5 (15.6)	0.005	10	41.3 (12.6)	0.014
SG	15	11.2 (10.8)		10	23.8 (17.7)	
SG	14	8.7 (4.8)	0.005	8	11.3 (6.2)	0.500
SB	14	4.1 (5.5)		8	8.9 (8.2)	

The two-letter abbreviations denote the initials of the species name. The sample size was the number of pairs of willows for that species comparison

Table 2. Amounts eaten by adult *C. aeneicollis* on leaf disks with a salicin solution versus a control solution

Test solution	<i>n</i>	Amount eaten Test solution mean (SD) mm ²	Amount eaten Control solution mean (SD) mm ²	$P <$
0.01 M Salicin	6	11.2 (4.0)	3.2 (4.0)	0.016
0.1 M Salicin	17	10.2 (8.9)	2.3 (3.7)	0.005

Results were statistically analyzed using a one-tailed Wilcoxon signed-ranks test (Zar 1984)

lower-salicin *S. boothi* and *S. geieriana* (Fig. 2). The differences in the amount fed on the three species were highly significant (MANOVA within-subjects factor $F_{2,20} = 25.5$, $P = 0.0001$; Hotelling-Lawley Trace, Pillai's Trace, and Wilks' Lambda), but the beetles' source species had no significant effect on the overall amount fed (between-subjects factor $F_{2,21} = 0.11$, $P = 0.89$). Moreover, the beetles from different source species did not differ in their preferences (source-species by test-species interaction: Hotelling-Lawley Trace $F_{4,38} = 0.78$, $P = 0.54$; Pillai's Trace $F_{4,42} = 0.83$, $P = 0.52$; Wilks' Lambda $F_{4,40} = 0.80$, $P = 0.53$), suggesting that there was little or no conditioning of adult preference by previous adult or larval experience.

Adults were stimulated to feed by the salicin in the leaf disks (Table 2). For both salicin solutions, over 75% of the total area consumed by the beetles was from the disk which contained salicin. There was no difference between the solutions in the amount of feeding stimulation (Mann-Whitney test, $P = 0.80$).

Field distributions of adults and eggs

Both adults and eggs were more abundant on the willow species that contained more salicylates. The higher adult abundance on the salicin-rich species was statistically significant in all four comparisons (Table 3). Of the three egg abundance comparisons, only the one between

Chrysomela aeneicollis does not appear to discriminate among willow species through its oviposition behavior. However, if willow leaf beetles have time to feed before ovipositing, the distribution of egg clutches should reflect the feeding preference. When I offered non-gravid females a choice between one *S. orestera* and one *S. lutea* clone, 23 of 26 egg clutches were laid on *S. orestera*, which was defoliated before the *C. aeneicollis* adults began feeding on *S. lutea* (Rank, unpublished data). Furthermore, Denno et al. (1990), who used non-gravid *Phratora vitellinae* in oviposition tests, documented the same ranking of host species as revealed by the feeding preferences tests conducted by Tahvanainen et al. (1985). However, the absence of an oviposition preference in the gravid females in this study indicates that the apparent specificity in oviposition actually reflects a feeding preference. This laboratory result is supported by the observation that, in the field, egg clutches are not as concentrated on the salicin-rich willows as the adults were. If the larval plant were determined by an oviposition preference rather than a feeding preference, the reverse would have been the case.

Willow leaf beetles appear to locate favorable hosts through their adult feeding behavior. In this respect, they differ from butterflies, sawflies, and many drosophilids which are commonly very selective in their oviposition behavior (Wiklund 1974, 1975; Smiley 1978; Stanton 1979, 1982; Rausher 1980; Singer 1983; Singer et al. 1988; Jaenike 1988; Scriber 1988; Thompson 1988a, b, c; Roininen and Tahvanainen 1989). This difference probably results from the greater role of the larval host plant in the life cycle of many leaf beetles. Butterflies, for example, usually do not use the larval host plant for the adults' nutrition (Wiklund 1977; Strong et al. 1984), while willow leaf beetles use the same hosts as adults and larvae (Brown 1956; Raupp and Denno 1983; Wade and Breden 1986; Pasteels et al. 1988). In at least one other insect which uses the same plant as larvae and adults, the agromyzid fly *Liriomyza sativae*, adults show both a feeding and an oviposition preference, and the two preferences correspond well (Via 1986).

Conditioning of adult feeding or oviposition by the larval food plant has seldom been demonstrated (Wiklund 1974; Futuyma and Mayer 1980; Papaj and Rausher 1983; but see Via 1986). Nevertheless, conditioning of adult preference by previous adult experience may be more common (Papaj and Rausher 1983; Rausher 1983; Jaenike 1988). This type of conditioning may promote host-based genetic divergence of an herbivore (Jaenike 1988). In the case of willow leaf beetles, Rowell-Rahier (1984b) determined that adults of *P. vitellinae* were conditioned by previous adult food plant experience. For *C. aeneicollis*, neither larval food plant experience (Cabin Bog tests), nor previous adult experience (Falls Site tests), had an effect on subsequent preference. However, the likelihood of conditioning almost certainly depends on the range of host plants offered. In the case of *C. aeneicollis*, the plants offered varied greatly in their salicylate chemistries, and if there was any conditioning of preference between them, it was minimal. On the other hand, in Rowell-Rahier (1984b)'s choice tests with

P. vitellinae, both hosts were salicylate-rich species. When both potential host species already possess the favored chemicals, conditioning between them may be more important.

It appears unlikely that *C. aeneicollis* is genetically subdivided among its host species. In order for populations to diverge onto different hosts, gene flow among them must be greatly restricted (Futuyma and Mayer 1980). This could happen if (1) populations on different hosts were temporally isolated and/or (2) populations were so tightly associated with their natal host species that inter-host matings seldom occur. However, at the Falls Site, the host species grow together so that their foliage is often in physical contact, and adults occur and mate on all of the host species at the same time. Moreover, the difference between the adult and egg clutch distributions suggests that adults occasionally move between species. Thus it does not appear that *C. aeneicollis* populations on different willow species are temporally isolated. Additionally, no willow is completely unacceptable to *C. aeneicollis*, and both laboratory and field data suggest that *C. aeneicollis* is less selective in oviposition than in feeding. Although the Falls Site feeding tests did not distinguish between environmental and genetic influences on preference, the universal feeding-preference for *S. orestera* also indicates that adults were not tightly associated with their natal host species. It thus appears that *C. aeneicollis* populations on different species are not sufficiently isolated to promote genetic divergence among them. Indeed, an electrophoretic survey indicates that like other willow leaf beetles (e.g. *Plagioderma versicolor*, McCauley et al. 1988) they are often significantly differentiated among individual trees, but that there is no additional differentiation across host species (Rank 1992).

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