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AGGREGATION BEHAVIOR OF A WILLOW FLEA BEETLE, *ALTICA SUBPLICATA* (COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

This study examined the aggregation behavior of a specialist insect herbivore, *Altica subplicata* (Coleoptera: Chrysomelidae), on its host plant, *Salix cordata*. Mark-recapture experiments were conducted in patches of *S. cordata* growing along the shores of Lake Huron. Beetles aggregated on individual host plants, but did not aggregate in larger areas containing many host plants. Plants colonized by marked beetles had significantly higher abundances of unmarked beetles than did plants that were not colonized by marked beetles.

Experimental manipulations of the number of beetles present on plants showed that colonization rates by marked beetles were higher on plants with conspecifics than on plants which had all beetles removed the previous day. The sex of beetles, however, did not influence colonization behavior; both male and female beetles colonized plants regardless of the sex of beetles already present on plants. These results are discussed with respect to possible explanations for aggregation, and the role of aggregation and movement in influencing insect distributions.

The importance of movement in explaining insect distribution and abundance has been explored both empirically (Kareiva 1985, Turchin 1987, Lawrence 1988) and theoretically (Jones 1977, Taylor and Taylor 1977, Kareiva 1982, Cain 1985, Turchin 1986, 1989). Movement behavior often influences the response of insect herbivores to plant dispersion (Bach 1984, 1988, Cain et al. 1985, Kareiva 1985, Lawrence 1987) and recent reviews emphasize that movement is one of the most important factors influencing how plant spatial pattern affects herbivore populations (Kareiva 1983, Stanton 1983).

Although aggregation behavior is often an important component of movement behavior, it has received little attention. Recent studies have shown the importance of aggregation in influencing insect distributions (Lawrence 1987, 1988, Turchin 1987). For milkweed beetles, *Tetraopes tetraophthalmus* (Förster) (Cerambycidae), conspecific density and sex ratio influence rates of immigration to and emigration from host plant patches (Lawrence 1987, 1988). Turchin (1987) found that the aggregative tendency of the Mexican bean beetle, *Epilachna varivestis* Mulsant (Coccinelidae), strongly influenced response to host plant density.

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Many insect species exhibit aggregated distributions (Kennedy and Crawley 1967, Rowell-Rahier and Pasteels 1986), yet the presence of aggregation pheromones has been confirmed for only a small subset of these species (see review by Birch 1984). For other species, aggregations of one sex often result from response to sex pheromones (Roelofs 1981, Byers 1983, Carde and Baker 1984). Larval aggregations, in contrast, typically are the result of a clumped pattern of egg laying (Stamp 1980, Breden and Wade 1987).

The purpose of this study was to investigate aggregation behavior of a specialist insect herbivore, *Altica subplicata* LeConte (Coleoptera: Chrysomelidae: Alticinae). This flea beetle is a specialist on sand-dune willow, *Salix cordata*, in northern Michigan. Preliminary observations indicated that *A. subplicata* forms aggregations. We examined three specific questions: (1) is there an aggregated distribution of beetles, either on a per plant basis and/or a broader areal basis (aggregation-scale hypothesis)?, (2) do beetles preferentially colonize plants with beetles already present over plants with no beetles present (gregarious behavior hypothesis)?, and (3) do beetles exhibit a sex-specific aggregative response to conspecifics (sex-aggregation hypothesis)?

MATERIALS AND METHODS

The study was conducted at the Nature Conservancy's Grass Bay Preserve on the northern shore of Lake Huron in Cheboygan County, Michigan. This site has three distinct parallel ridges of low sand dunes which differ in age and successional status of vegetation. The sand dune ridge closest to Lake Huron is the youngest dune and was colonized by sand-dune willow for the first time in 1988, whereas the ridge farthest from Lake Huron is the oldest successional stage. Between the dune ridges are interdunal swales, in which *Salix* species do not grow.

The patterns of beetle population dynamics on these three dune ridges are described in detail elsewhere (Bach 1990). All tests for this study were performed on the dune of intermediate age because: (1) first generation beetles completely defoliated the majority of plants on the dune closest to Lake Huron, and (2) there were no beetles present on the dune farthest from Lake Huron. *S. cordata* was more abundant on the intermediate dune than on the other dunes, and was the dominant woody species on that dune.

Altica subplicata is a common herbivore on sand-dune willow growing along the shores of Lake Huron. *A. subplicata* is a specialist on willow and has been reported to feed on sandbar willow, *Salix interior*, in South Dakota (DeSwarte and Balsbaugh 1973). At Grass Bay, *A. subplicata* appears to have two generations per year. In late June of 1988, larvae were more common than adults, whereas by mid-July, adults were most common. In August, adults declined in abundance and larvae predominated.

Mark-recapture experiments were carried out in 1988 to examine the three hypotheses relating to aggregation behavior. For all tests, beetles were captured in the afternoon, brought back to the laboratory and marked with Testor's brand enamel paint. Beetles were marked with a particular color pattern that identified each group. On the following morning, beetles were released in the field by placing the container with beetles on the ground and removing the lid. All searches for marked beetles were conducted between 0800 and 1200 hrs using a direct observation method. Direct observation enabled accurate beetle censuses because: (1) very few beetles flew away unless the plant was touched, and (2) the metallic color of the beetles made them very visible and thus easily counted.

Aggregation experiment. To test the aggregation-scale hypothesis, aggregation of both naturally-occurring unmarked beetles and released marked beetles was studied. Twenty beetles were released on 25 July at each of two locations (10 m apart) in the center of the study site. Surrounding each of these release points were host plants

with naturally occurring unmarked beetles on them. On 26 July, a circle with a 5 m radius from each release point was divided into 4 quadrants. For every plant within this sampling area (N = 75 for release area one and N = 109 for release area two), the number of marked beetles, the number of unmarked beetles, and the quadrant number were recorded. On 27 July, these areas were again searched for marked beetles, but data were recorded only for plants with marked beetles. The 5 m radius sampling area was chosen based on preliminary releases of marked beetles (N = 80), which revealed average distances moved in one day to be 5.8 ± 0.6 m.

This experiment allowed us to examine whether: (1) naturally-occurring unmarked beetles aggregated in particular quadrants or on individual plants, and (2) marked beetles preferentially colonized particular quadrants and/or plants. To test for aggregation in particular areas (rather than on particular plants), it was necessary to use an estimate of beetle density which was not confounded by host plant density. Thus, one-way ANOVAs were performed on number of beetles per plant in each quadrant, rather than total number per quadrant, to control for differences between quadrants in the number of available host plants. To examine aggregation on a per plant basis, distributions of beetles on individual plants were analyzed. All data were transformed [ln (x + 1)] prior to analysis to reduce heteroscedasticity of variance.

This experiment also allowed us to test the gregarious behavior hypothesis, by examining whether: (1) the number of marked beetles colonizing a plant was a function of the number of unmarked beetles present, and (2) plants that were colonized by marked beetles had more unmarked beetles present. Regression analyses were used to compare the number of marked and unmarked beetles on plants. Student t-tests were used to compare the mean number of unmarked beetles on plants that were colonized by marked beetles vs. plants not colonized by marked beetles.

To examine aggregation on a finer scale than that of the individual plant, censuses of beetle distributions on individual leaves were conducted on 29 July 1987. The number of beetles on every leaf on one randomly-selected branch from each of 17 randomly-selected plants was recorded.

Response to conspecifics experiment. To examine the gregarious behavior hypothesis under more controlled conditions, groups of beetles were released between eight pairs of relatively isolated *Salix cordata* plants. These pairs of plants were matched as closely as possible for similar beetle densities and plant heights. On 26 July, one of the plants of each pair was cleared of all beetles, whereas beetles were left on the control plant. To control for possible effects of wind direction, the control plant was to the east for half of the pairs, and to the west for the other half of the pairs. Twenty beetles were released at a point equidistant from each plant in the pair. These sixteen plants were searched for beetles for two consecutive days following release, and the number of marked and unmarked beetles was recorded.

In order for this test to be valid, it is necessary that there be minimal re-colonization by unmarked beetles of the experimental plants, and low emigration rates by unmarked beetles from the control plants. By recording the number of unmarked beetles on these plants the day after removal, it was possible to test these assumptions. We decided *a priori* that we would only analyze data from pairs of plants having densities of unmarked beetles on the day after removal which met two criteria: (1) at least 10 beetles on the control plant, and (2) at least twice as many beetles on the control plant as on the experimental plant. Three pairs of plants were excluded from analysis because they did not meet the above criteria, thus analyses included data for the 5 pairs of plants that maintained the predetermined difference in beetle numbers.

Data were analyzed with student t-tests comparing the number of beetles colonizing the experimental vs. the control plant. Beetles were so mobile that only 30% of the marked beetles colonizing plants were from the release between those plants. Thus for each pair of plants, the number of beetles colonizing one plant was independent of the number of beetles colonizing the other plant.

Response to sex of conspecifics experiment. To test the sex-aggregation hypothe-

sis, groups of beetles were released between three pairs of plants on 29 July (these pairs of plants had been previously used in the response to conspecifics experiment). Ten male beetles were placed on one plant of each pair and ten female beetles were placed on the other plant of each pair. Beetles were enclosed in a mesh bag (40 X 25 cm) tied around a branch. Again, the placement of treatments was alternated to control for wind direction. Twenty marked beetles (numbers of each sex varied from 9–11) were released equidistant between each pair of plants. The number and sex of all beetles found on each plant was recorded for three consecutive days. Beetles were sexed by checking for anatomically dimorphic features in the last abdominal sternite, later confirmed by dissection.

To determine if the presence of the mesh bag influenced the results of these experiments, similar experiments were conducted on four additional pairs of plants which had been cleared of beetles. In these experiments, twenty marked male beetles were released at the base of one plant of each pair, and twenty marked female beetles were released at the base of the other plant. The number of unmarked male and female beetles colonizing plants of each pair was recorded on the following day.

Data on marked and unmarked colonists were combined for purposes of analysis, since fewer marked beetles were released because of mortality on route to the site. Thus, comparisons of total number of colonists to plants with male vs. female beetles were made using student t-tests, for the same reasons as previously described for the experiment testing for a response to conspecifics. Paired t-tests were used to compare numbers of males vs. females colonizing individual plants.

To determine the natural sex ratio of beetles, all beetles were collected on three randomly-selected undisturbed plants, brought back to the laboratory and sexed.

RESULTS

Aggregation experiment. There was no significant difference in the average number of marked beetles per plant colonizing the four quadrants for either of the two release areas (Fig. 1A; $F = 1.45$, $F = .54$, $P > 0.05$ for both release areas). There was also no difference in average numbers of unmarked beetles per plant present in the four quadrants (Fig. 1B; $F = 1.81$, $F = 1.68$, $P > 0.05$ for both release areas). Thus, beetles did not appear to aggregate in particular quadrants.

Beetles, however, showed a strong tendency to aggregate on individual plants, as evidenced by the extreme skewness in the frequency distribution of numbers of unmarked beetles on plants (Fig. 2). The number of unmarked beetles on individual plants varied from 0 to 42 for the first release area and from 0 to 220 for the second release area.

Censuses of beetle distributions on individual leaves showed that beetles on average were found on only 20.9% (± 12.0% SEM) of the leaves within a given branch. Thus, beetles were found on only an average of 5.9 (± 4.2 SEM) leaves on each branch, and these leaves were primarily the youngest.

The aggregation of beetles on individual plants appears to result from the preferential colonization of plants with beetles already present. Marked beetles colonized individual plants on the basis of the presence of conspecifics both days after release. On the first day after release, the number of marked beetles on a plant was positively related to the number of unmarked beetles on that plant, both for the first release area ($r = .29$, $N = 75$, $P = 0.012$) and the second release area ($r = .53$, $N = 109$, $P < 0.001$). This relationship between number of marked and unmarked beetles was also significant for just those plants that were colonized by marked beetles, but only for the second release area ($r = .60$, $N = 12$, $P = 0.04$). On the second day after release, the number of marked and unmarked beetles were significantly correlated for the first release area ($r = .72$, $N = 10$ plants, $P = 0.019$). This relationship was also positive for the second release area ($r = 0.96$), although it was not significant ($P = 0.19$), probably because of the small number of plants that were colonized by beetles ($N = 3$).

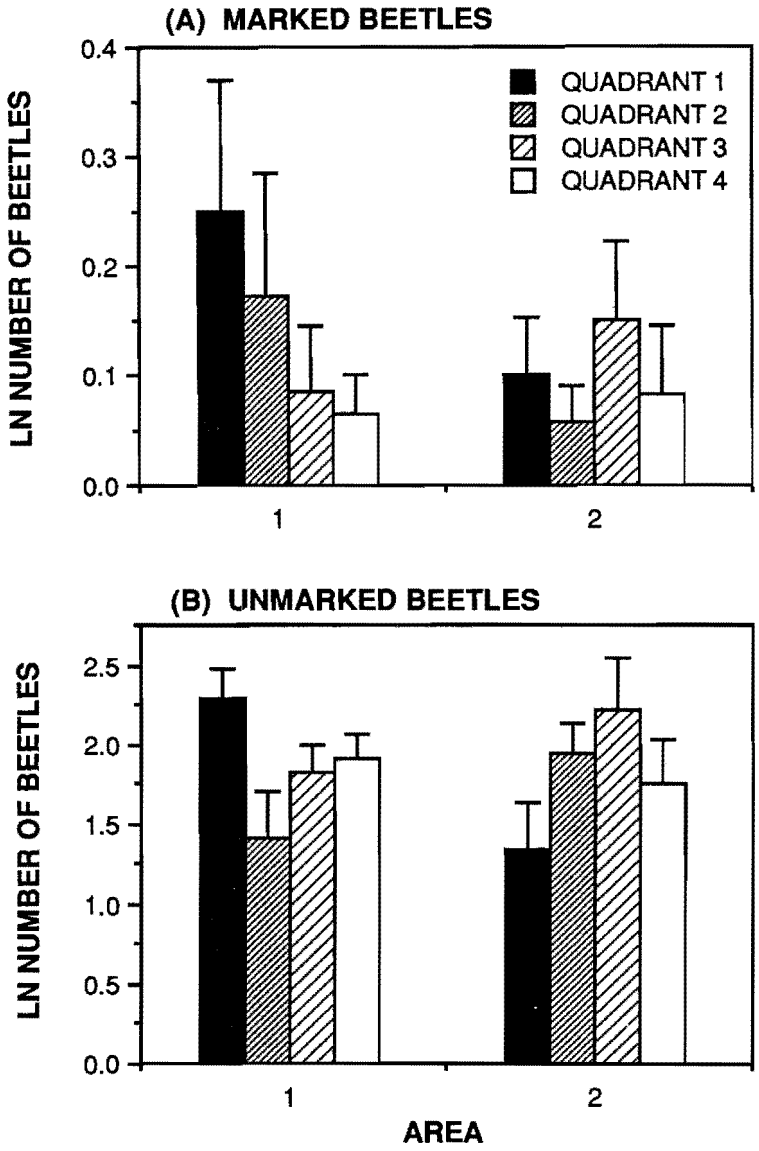

Figure 1. Numbers of beetles per plant in each of the four quadrants for (A) marked beetles and (B) unmarked beetles for releases in each of two areas. Data presented are means and standard error bars of the ln (x + 1) transformed numbers per plant. Sample sizes for the four quadrants for release area 1 were 14, 8, 21, and 32, and for release area 2 were 21, 36, 26, 25.

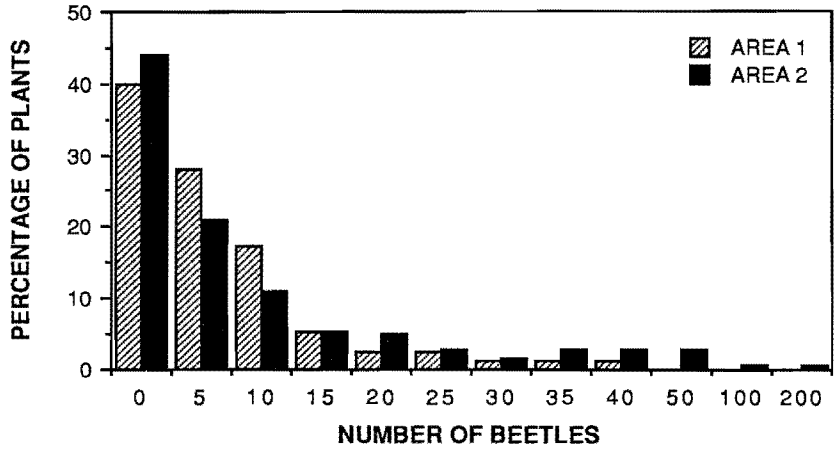

Figure 2. Percentage distribution of numbers of beetles per plant for the areas surrounding each of the two release plants. Sample size was 75 for release area 1 and 109 for release area 2.

Table 1.—Number of unmarked beetles on plants that were colonized by marked beetles and on plants that were not colonized by marked beetles, for each of the two release areas. Means ± standard errors are shown for the ln (x + 1) transformed numbers per plant. Sample sizes are in parentheses. Results from student t-tests (values of t-statistic and significance levels) are also presented.

	Number of unmarked beetles on plants that were:			
	Colonized	Not colonized	t	P
Area 1	2.49 ± .21 (11)	1.80 ± .11 (64)	2.51	0.014
Area 2	3.88 ± .26 (12)	1.61 ± .12 (97)	6.28	<0.001

Because the number of marked beetles colonizing plants varied only from 1 to 3, we also compared the number of unmarked beetles on plants that were colonized by marked beetles vs. plants that were not colonized by marked beetles. For both release areas, the plants that were colonized by marked beetles had significantly more unmarked individuals present than those plants that were not colonized by marked beetles (Table 1).

Because other factors may have varied between the plants that were colonized by marked beetles (with many unmarked beetles) and the plants that were not colonized by marked beetles (with few unmarked beetles), it was necessary to conduct more controlled experiments in which the number of beetles present was manipulated.

Response to conspecifics experiment. In these controlled experiments, a significantly greater number of marked beetles colonized the control plant than the experimental plant from which all beetles had been removed the previous day (Fig. 3; $t = 2.39$, $P = 0.044$). There was also a significantly greater number of colonists on plants with beetles present than on plants with no beetles present on the second day after release ($t = 2.35$, $P = 0.047$). Not surprisingly, numbers of unmarked beetles were also greater on the control plants than on the experimental plants for both days

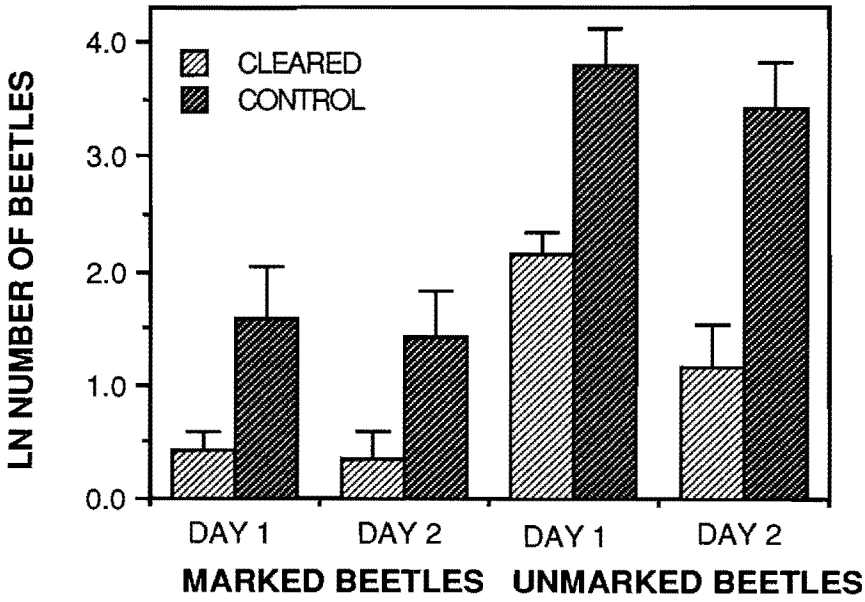

Figure 3. Numbers of marked beetles and unmarked beetles on plants from which all beetles had been removed (=cleared) vs. control plants. Means and standard error bars for ln (x + 1) transformed data are shown for the five replicate plants of each type for each of the two days after manipulation.

(Fig. 3; day 1: $t = 4.39$, $P = 0.002$; day2: $t = 3.92$, $P = 0.004$). However, there was no significant difference between the number of beetles on each member of the pair on the day on which beetles were removed ($t = 1.58$, $P > 0.05$), nor was there any difference in the size (measured by height) of the members of each pair ($t = 1.54$, $P > 0.05$). Thus, differences in colonization by marked beetles can be attributed solely to differences in presence/absence of unmarked beetles.

Response to sex of conspecifics experiment. Beetle aggregation was not influenced by sex. There was no significant difference in the number of female vs. male beetles colonizing plants with either bagged female beetles present (Fig 4A; $t = 1.9$, $t = 3.2$, $t = .78$; $P > 0.05$ for all three days) or plants with bagged male beetles present (Fig 4B; $t = .58$, $t = .54$, $t = 1.4$; $P > 0.05$ for all three days). Furthermore, the total number of beetles colonizing plants with female beetles present vs. plants with male beetles present did not differ significantly for any of the three days after release ($t = 2.1$, $t = .04$, $t = .68$; $P > 0.05$ for all).

Results from the experiments in which male and female beetles were released at the base of the plant showed the same patterns as the experiments using mesh bags (Table 2). There was no difference in the number of males vs. females colonizing plants with female beetles ($t = .94$, $P > 0.05$) or plants with male beetles ($t = .88$, $P > 0.05$). The total number of beetles colonizing plants with males vs. plants with females also did not differ significantly ($t = .04$, $P > 0.05$).

The close correspondence to a 1:1 sex ratio found in both the experiments with mesh bags and the experiments with releases of beetles at the base of the plant agrees

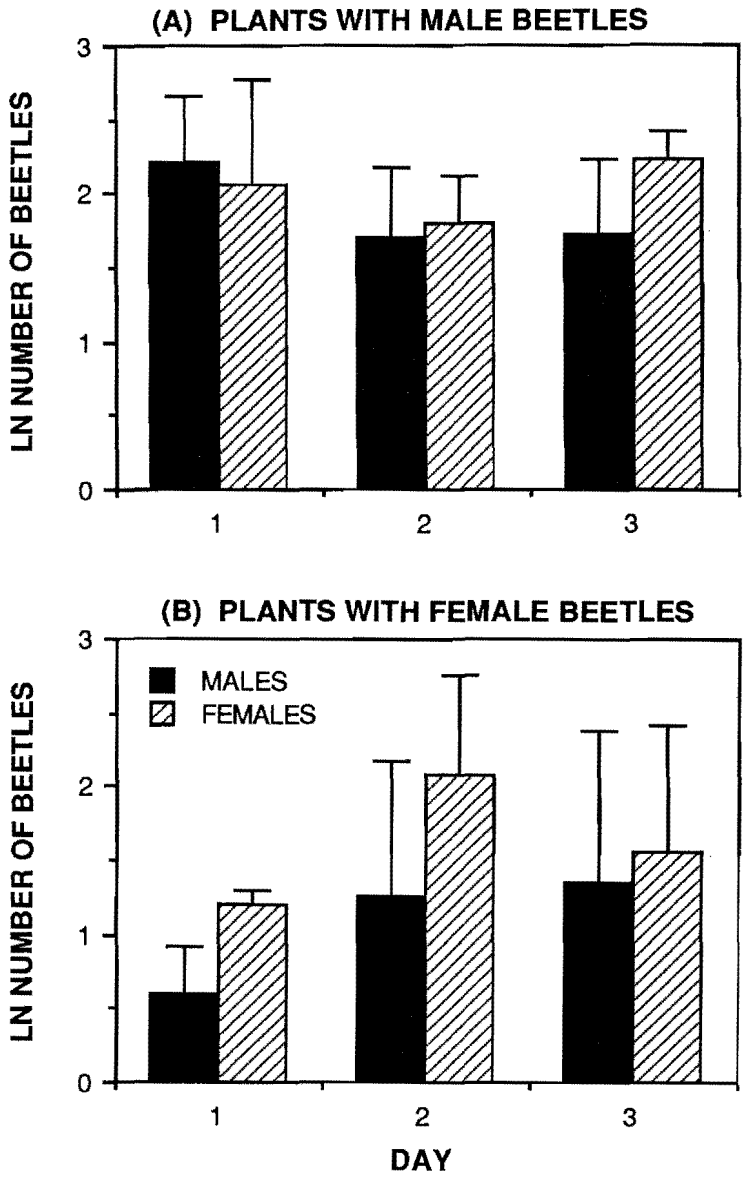

Figure 4. Numbers of male and female beetles colonizing plants containing (A) male beetles and (B) female beetles. Means and standard error bars for ln (x + 1) transformed data are shown for the three replicate plants containing beetles of each sex.

Table 2.—Number of male and female beetles colonizing plants which either had male or female beetles released at the base of the plant. Means ± standard errors are shown for the ln (x + 1) transformed numbers per plant. Sample sizes were 4 for each treatment. Total beetles colonizing each type of plant are also presented.

	Number of colonists		
	Male	Female	Total
Plants with males present	1.87 ± .50	1.64 ± .60	2.33 ± .62
Plants with females present	1.90 ± .53	1.72 ± .72	2.37 ± .70

with the natural sex ratio of beetles on undisturbed plants, which ranged from 0.93:1.00 to 1.08:1.00.

DISCUSSION

Patterns of aggregation. Like other species of insects, *A. subplicata* exhibits an aggregated spatial distribution (Kennedy and Crawley 1967, Turchin 1987). This pattern is typical of chrysomelids, which tend to aggregate on plants (Rowell-Rahier and Pasteels 1986). Baker et al. (1972) report that a closely-related species, *Haltica* (=*Altica*) *carduorum* Guerin, also exhibits aggregation. Although other studies show distinct aggregation in certain areas, our study found aggregation on a per plant basis, but not on a per unit area basis, at least as determined for areas of approximately 20 square meters. Beetles also did not appear to be aggregating as a function of either magnetic or wind direction.

The clumped distribution of *A. subplicata* appears to be explained by gregarious behavior, since individuals clearly responded to the presence of conspecifics. This species, however, does not exhibit spaced-out gregariousness, as shown for the sycamore aphid, *Drepanosiphum platanoides* (Schank) (Homoptera: Aphididae), (Kennedy and Crawley 1967). Although distances between individuals were not measured, observations during sampling revealed that there was often physical contact between beetles on individual leaves, both for adults and larvae.

The preferential colonization of plants with conspecifics reported in this study agrees with results from Turchin (1987), who found that Mexican bean beetles have more rapid immigration rates and greater probabilities of stopping on plants with larger numbers of conspecifics. Turchin (1987) also reports that the tendency to aggregate is stronger in patches with high plant density because there is more intra-patch movement. It seems possible that the differences in the degrees of aggregation exhibited by willow flea beetles in the two release areas (see Fig. 2) may result from differences in plant dispersion in these two areas.

Although aggregation may result from visual or auditory communication, the results from this study are consistent with the existence of an aggregation pheromone, which are well documented for other beetle species (chrysomelids—Rowell-Rahier and Pasteels 1986, scolytids—Birch 1984). It is very unlikely that the preference for plants with conspecifics results from any possible differences in plant odor/quality, since treatments were systematically assigned to plants to control for possible effects of wind direction.

Beetle colonization of plants was not different for plants containing male beetles and plants containing female beetles. These results contrast with those of Lawrence (1987), who reports a change in milkweed beetle movement behavior as a function of the sex ratio of beetles within a patch. Although sex pheromones are known for many insects (Roelofs 1981), particularly beetles (see review by Carde and Baker 1984), our results do not suggest the existence of a sex pheromone. We observed beetles mating

from mid-July until the end of the study in early August, thus the experiments were conducted at a time when at least a portion of the population was mating.

Hypotheses explaining aggregation. Two aspects of the aggregation behavior exhibited by *A. subplicata* need to be explained: (1) Why do beetles aggregate?, and (2) Why do beetles occur on particular plants and avoid other plants? A number of hypotheses have been proposed to answer the first question. One possible explanation is that animals aggregate for purposes of mating (Snead and Alcock 1985), and that the probability of mating increases in larger groups. Although *A. subplicata* adults were not differentially attracted to plants with members of the opposite sex, there could still be a greater probability of mating in aggregations. A second possible explanation for aggregation behavior is that survivorship is greater in larger groups, as shown for the imported willow leaf beetle, *Plagiodera versicolora* (Laicharting) (Chrysomelidae) (Breden and Wade 1987). The increased survivorship in larger groups could result from an increase in feeding efficiency (Ghent 1960), or from lower rates of predation (Lawrence 1990) or parasitism (Morris 1976). For *A. subplicata*, however, it seems much more likely that larger groups would experience greater competition for food. Beetle densities sometimes reached 36 beetles per leaf and host plant defoliation was not uncommon.

It is also possible that larger groups of beetles would have an advantage in terms of overcoming chemical defenses, as shown for other aggregating insects (Birch 1984). Several studies have shown that plant chemistry of willows (specifically, concentrations of phenolic glycosides) strongly influences herbivore distributions (Tahvanainen et al. 1985, Rowell-Rahier et al. 1987). It is more likely, however, that beetles specializing on willow would use these chemicals as feeding stimulants and/or attractants. If *S. cordata* increases levels of phenols in response to herbivory, as has been shown for closely-related poplars (Baldwin and Schultz 1983), then aggregations may simply result from an increase in the amounts of attractants in plants with beetles present.

Finally, many aposematic insects aggregate (Crowson 1981) and many Chrysomelidae are aposematic (Rowell-Rahier and Pasteels 1986). Although it is not conclusively known whether *A. subplicata* is toxic to predators, this seems likely, since many other willow-feeding chrysomelids possess defensive compounds that protect them from predators and competitors (Raupp et al. 1986, Rowell-Rahier and Pasteels 1986).

It seems most likely that the answer to the second question about why beetles aggregate on particular plants involves resource quality differences between plants. Plant-plant differences that could affect beetles include: plant size or age, nutritional quality, and/or amounts of secondary compounds. Bach (1990) found that *A. subplicata* preferentially colonizes taller host plants and tends to be more abundant on plants with higher levels of nitrogen. Smiley et al. (1985) report that neighboring individuals of *Salix lasiolepis* vary by 100-fold in salicin concentration and that abundance of the imported willow leaf beetle, *Plagiodera versicolora*, is positively correlated with concentration of salicin. Although other studies have demonstrated genetic differences in willows in susceptibility to herbivory (Fritz et al. 1986, Fritz and Price 1988), it seems unlikely that the differences in abundance of these willow flea beetles on neighboring plants result from genetic differences between plants, since *S. cordata* sprouts prolifically and neighbors are likely of clonal origin. However, somatic mutations in clonal plants have been shown to be an important influence on insect herbivore aggregations in other systems (Whitham and Slobodchikoff 1981, Whitham 1983). The predominance of beetles on young leaves agrees with results for a closely related species, *Haltica* (=*Altica*) *lythri* Aubé, which prefers young over old foliage (Phillips 1976).

In conclusion, *A. subplicata* exhibits aggregated distributions which result from gregarious behavior. The large differences in the spatial dispersion of beetles on host plants certainly have a profound impact on the resultant effects of herbivory on plant fitness. There were dramatic differences in the amounts of beetle damage to

different plants of *Salix cordata* at this study site (Bach 1990). Thus, aggregation behavior appears to be a major factor influencing the dynamics of this herbivore-plant system.

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