

Preference and performance are correlated in the spittlebug *Aphrophora pectoralis* on four species of willow

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Abstract. 1. There was a positive correlation between oviposition and feeding preferences and offspring performance in the spittlebug *Aphrophora pectoralis* Matsumura (Homoptera: Cercopoidea, Aphrophoridae) on four species of willow *Salix* sp. (Salicaceae) growing near Sapporo, Japan. Spittlebugs preferred rapidly growing shoots where performance was highest.

2. When the effects of shoot length were removed, egg densities on willow species were associated with offspring performance on three of four species. Egg densities and survival rates were low on *Salix integra* and *Salix miyabeana*. Survival rates were high on *Salix sachalinensis*, which had high egg densities, and *Salix hultenii*, which had low egg densities.

3. *Aphrophora pectoralis* formed mating aggregations almost exclusively on *S. sachalinensis* but then dispersed to other willow species to oviposit.

4. Nymphs dispersed from the oviposition site to feed on nearby shoots within the same plant but they did not disperse to other willow plants. Nymphs had the same preference for rapidly growing shoots as ovipositing females, so they were able to refine the maternal choice by moving to larger shoots near the shoot on which they had eclosed.

5. The spittlebugs were highly aggregated at all life stages so that even at high densities only a small proportion of the most vigorously growing shoots was utilised.

Key words. *Aphrophora pectoralis*, herbivory, host plant variation, intraspecific competition, offspring performance, oviposition discrimination, oviposition preference, *Salix hultenii*, *Salix integra*, *Salix miyabeana*, *Salix sachalinensis*.

Introduction

Understanding the forces that determine the relationship between oviposition and feeding preferences of phytophagous insects for plant resources and their performance on these resources is key to understanding many aspects of insect ecology. Price (1994) proposed that the preference–performance relationship influences the population dynamics of herbivores. Knowledge of the

variation in adaptive strategies such as preference–performance relationships can provide insights into many aspects of herbivore population and community ecology (Ohgushi, 1998; Price *et al.*, 1998; Craig *et al.*, 1999b).

The *naive adaptationist hypothesis* (Courtney & Kibota, 1990) predicts that phytophagous insects will oviposit where the probability of offspring survival is highest. This hypothesis has been supported in a range of herbivores (Whitham, 1980; Leather, 1985; Craig *et al.*, 1989, 1993, 1997; Price, 1994; Ohgushi, 1995) but a lack of correlation between preference and performance has been found in other phytophagous insects (reviewed by Thompson, 1988; Courtney & Kibota, 1990; Thompson & Pellmyr, 1991). Hypotheses are needed that generate testable predictions

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about the causes of the patterns of variation in the strength of the preference–performance relationship. This study was conducted to test predictions of two such hypotheses on the factors that determine the strength of the evolution of the preference–performance relationship: the phylogenetic and resource constraints hypotheses.

The *phylogenetic constraints hypothesis* states that the strength of the relationship between preference and performance depends on the phylogenetic history of the herbivore (Price, 1994). Price argued that groups with the phylogenetic constraint of having ovipositors adapted for laying eggs into living plant tissue, will evolve a strong preference–performance relationship for two reasons. (1) Ovipositor insertion into the tissue in which larvae will develop provides the opportunity to evolve sensitivity to plant cues indicating the quality of the oviposition site for offspring development. (2) Because the female oviposits exactly where the immature stages develop, there is strong selection to evolve the ability to select good oviposition sites. A strong preference–performance correlation has been found consistently in gall-inducing insects (Price, 1994), which have both of these traits. In contrast, when females lay eggs on surfaces away from where larvae develop, there is no opportunity to evolve sensitivity to cues indicating host plant quality. Because offspring develop away from the oviposition site, there is weak selection for the evolution of oviposition site preference. The result is the weak preference–performance correlation found in herbivores that do not oviposit into plant tissue and in which offspring disperse from the oviposition site (Thompson, 1988; Thompson & Pellmyr, 1991; Price, 1994).

In this study, the strength of the preference–performance relationship was examined in a situation in which the two distinct phylogenetic constraints of ovipositing into living tissue and development at the oviposition site are not linked. The spittlebug *Aphrophora pectoralis* oviposits into living plant tissue but its nymphs disperse from the oviposition site. It was predicted that if a strong preference–performance relationship depends only on oviposition into living tissue, a strong relationship would be found, but if development at the oviposition site is also required, a weak relationship would be found. The spittlebug also has the phylogenetic constraint of being adapted to feeding on low-nitrogen-content xylem sap. This nutritionally poor food may influence life-history traits (Strong *et al.*, 1984) that affect the evolution of the preference–performance relationship.

The *resource constraints hypothesis* states that, given a set of phylogenetic constraints, the plant resources that a female encounters will also influence the evolution of the preference–performance relationship (Craig *et al.*, 1999a). For example, if reliable cues about resource quality are lacking, even herbivores that are adapted to ovipositing into living tissue and whose offspring develop at the oviposition site, will fail to develop a strong preference–performance relationship. Resource constraints that prevent the evolution of a strong preference–performance relationship could also include factors such as the spatial

arrangement of plants (Thompson & Pellmyr, 1991), the presence of novel hosts (Chew, 1977), host rarity (Williams, 1983; Williams *et al.*, 1983) and host apparency (Courtney, 1981, 1982a,b), and the complexity of resource variation (Craig *et al.*, 1999a). It was predicted that if variation in a large number of factors influenced offspring performance, *Aphrophora pectoralis* would have a weak preference–performance relationship.

The following specific questions were addressed: (1) Is the oviposition preference of *A. pectoralis* correlated with offspring performance in relation to host species, shoot growth, presence of conspecifics, and natural enemies? (2) What are the dispersal patterns of nymphs from the oviposition site? (3) Do adult mating and feeding preferences influence oviposition preference?

Natural history

Aphrophora pectoralis has been recorded utilising several species of willow host plant including *Salix daisei*ensis, *S. babylonica*, and *S. yuhkii* (Komatsu, 1997). It has also been recorded as occurring in a variety of other plants but it is not known whether it feeds on these plants (Komatsu, 1997). The species is univoltine, and oviposits into the distal portion of current-year shoots starting in late July and continuing until early October (Komatsu, 1997; Nozawa & Ohgushi, 2002a). The portion of the stem with leaves produced during a single growing season is referred to as the shoot. Eggs are oviposited in groups referred to as egg masses. The insertion of egg masses causes mechanical damage that frequently kills the tips of shoots (Nozawa & Ohgushi, 2002b). *Aphrophora pectoralis* overwinters in the egg stage and emerges in mid-May in Hokkaido, Japan. Spittlebugs feed on xylem sap and produce froth in which the nymphs feed. Nymphs frequently live together in the froth, referred to as spittles. The nymphs go through five instars and emerge as adults in late July at the site where this study was conducted. Mating pairs have been observed on the host plant in August and September.

Methods

Aphrophora pectoralis was studied on the willows *Salix hultenii*, *S. integra*, *S. sachalinensis*, and *S. miyabeana* that were growing near (0–0.5 km) the Ishikari River 30 km north of Sapporo, Hokkaido, Japan (43°11'N, 141°23'E). The abundances of the four species among all willows at the Ishikari sites were: *S. miyabeana* 54%, *S. sachalinensis* 26%, *S. integra* 12%, and *S. hultenii* 2% (Ishihara *et al.*, 1999). The spatial distribution of willows was complex: all species grew intermixed, but there was tendency for some species to clump together (T.P. Craig, pers. obs.). *Salix miyabeana* usually grew intermixed with *S. sachalinensis* with their branches frequently touching. *Salix hultenii* were often 3–10 m from other willows and tended to be isolated from *S. sachalinensis* (T.P. Craig, pers. obs.).

Salix integra grew intermixed with *S. miyabeana* and *S. sachalinensis* and a few individuals were found at the edge of the site about 5 m from other species. *Salix subfragilis* and *S. pet-susu* are also host plants at this site but there were too few individuals of these species to be included in the study. All the willows had a shrubby growth form. The willows ranged from <1 m to \approx 3 m in height (T. P. Craig, unpublished).

Preference–performance surveys

To determine the relationship between egg density and performance, *A. pectoralis* were marked and surveyed repeatedly on 20 individuals of each willow species in 1997. These willows are termed the preference and performance willows. *Aphrophora pectoralis* density, shoot diameter, or shoot length utilised, and aggregation were measured in multiple life stages on each willow. Shoot diameter was used instead of shoot length in some surveys because shoot tips had been damaged by oviposition, making accurate shoot length determinations impossible. For some surveys, there were slightly reduced sample sizes (*n*) either because that stage was absent on the plant or because of mistakes that made it necessary to exclude the data. The following seven surveys were conducted.

Egg density. One hundred shoots were selected randomly and the egg masses oviposited in 1996 were counted on these shoots between 3 May and 3 June 1997. If fewer than five egg masses were found, an additional 100 shoot groups were sampled until five egg masses were found or the entire willow had been surveyed.

Early nymphal density. Between 3 and 5 June 1997, the number and size of spittles per 100 randomly selected shoots initiated in 1996 were sampled. First-instar nymphs were found exclusively on 1996 shoots. The number of nymphs per spittle was not counted because disturbing the spittle at this stage caused nymphs to disperse. A correlation between spittle size and nymph number at this stage was obtained from the marked movement survey described below.

Late nymphal shoot preference. Spittle size and number of nymphs during the late (third to fifth) nymphal stage were surveyed between 25 and 29 June 1997. Nymphs were dispersing from the previous year's shoots to the current year's shoot at this time. Five of the current year's shoots with spittles and five shoots without spittles were measured to determine shoot preferences.

Late nymphal density. One hundred of the 1997 shoots were surveyed at random and the number of fifth-instar nymphs was counted between 3 and 7 July 1997. The first emerging adults were seen on the last day of the survey. If five nymphs were not found, additional groups of 100 shoots were surveyed until five nymphs were found or the entire willow had been surveyed.

1997 adult density. Adult density was surveyed on 19 and 20 July 1997. Each willow was surveyed systematically for 90 s and the total number of adults and the number of

mating pairs observed were recorded. If the willow was small, the survey was completed in <90 s. A time survey was used because during this period the adults were very sensitive to disturbance, and the close inspection required to count adults per shoot was not possible.

1998 surveys. Nymph distribution, adult density and activity, egg mass density, and shoot length preference were surveyed on 12 willows of each species of the preference and performance willows in 1998. The number of fifth-instar and newly emerged adults was counted from 1 to 5 July. On 8, 15, and 25 August, surveys of the number of adult spittlebugs per 100 shoots were made. If willows had fewer than 100 shoots, all of the shoots were surveyed. On 15 and 25 August, the number of egg masses was also censused, and on 25 August, the number of matings was also censused. On 9 August, the lengths of 10 shoots with spittlebugs and 10 shoots without spittlebugs were censused on 13 willows.

1998 repeated oviposition. Shoots were marked on 20 willows and surveyed on 9, 13, and 21 August 1998 to determine whether the same shoots received eggs during different time periods.

Egg emergence survey

A survey was conducted between 14 and 24 July 1997 to determine the emergence from eggs on the four willow species and the correlation between the number of egg masses and the number of eggs. One shoot with egg masses was collected from 15 randomly selected willows from each of the four species. The preference and performance willows were excluded from this collection. Hymenopteran parasitoids from two families, Mymaridae and Aphelinidae, were reared from the shoots. Shoots were dissected and classified as having nymphs emerge or having one or the other of the parasitoids.

Marked shoot movement survey

An experiment was performed to follow the fate of individuals derived from a single egg mass. Twenty individuals of *S. integra*, *S. sachalinensis*, and *S. miyabeana* were selected randomly from an area in which they were growing completely intermixed. These were different willows from those used in the preference and performance study. These plants were all <1.5 m tall so all of the spittlebug masses could be reached easily. There were no *S. hultenii* plants growing in this area so they were not included in the survey. One spittle was selected randomly on each willow and a tag on a shoot marked the position adjacent to the mass. In order to follow the individuals from this mass, all other masses were removed from the entire plant, or if the plant was large, all of the spittles on a major ramet were removed. The distance of each spittle from the nearest egg mass was measured and assumed to be the minimum distance that the first-instar

nymphs moved to establish the mass. The size of the shoot from which the nymphs emerged and the size of the shoot to which the nymphs moved were measured, in order to test the hypothesis that nymphs are more likely to move if they emerge on a small shoot. For the spittlebugs that were removed, the size of the spittle and the number of nymphs in each instar were recorded.

The survey was initiated on 27 May 1997 and on 4 June, 11 June, 19 June, and 24 June the position of the marked spittlebugs relative to the tag, the spittle size, and the size of the shoot on which it was found were recorded.

Statistical methods

In all *A. pectoralis* stages, the number of individuals per 100 shoots had standard deviations proportional to the means, and a log transformation was performed before analysing these variables. In analyses in which proportions were used, the data were arc-sin square-root transformed before analysis. Interaction terms between covariates and main effects in ANOVA models that were not significant were omitted from the model.

To measure the influence on willow species, independent of other factors, the full model with covariates was run first. If there were no significant interactions with the covariates, a regression model with the covariates, and without willow species as a factor, was run. A one-way ANOVA with a Tukey's multiple range test was run on the residuals from the regression analysis to examine the species differences.

Results

Adult mating and feeding preferences

Adult preference. Adults were found at the highest density on *S. sachalinensis* (Fig. 1). In 1997, both willow species and the mean shoot diameter of a plant (Table 1) influenced the mean number of adults found per 100 shoots. Once the effects of shoot length had been removed, an analysis of the residuals showed that there was a significant difference among willow species in adult density ($F_{3,78} = 15.73$, $P < 0.001$). A Tukey's test showed that *S. sachalinensis* had a significantly higher adult density than the three other species, while none of the other pairwise comparisons between species showed significantly different densities (Fig. 2). The 19 July 1997 survey was conducted just after adult emergence when only 3.16% of the spittlebugs were observed mating and no egg masses were observed.

There was a strong adult preference for *S. sachalinensis* in all three surveys in 1998 during the mating period (Fig. 3). The same individual willows, almost exclusively *S. sachalinensis*, had adult aggregations in all three periods, as indicated by the correlation among the densities in the three periods (Table 2). A repeated-measures analysis showed that willow species had a significant impact on

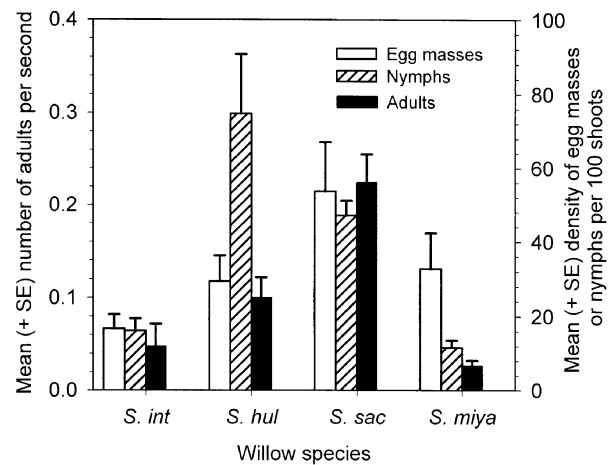


Fig. 1. The density of different life stages at the Ishikari site in the 1997 preference and performance survey. The mean number (+ SE) of egg masses per shoot, nymphs per shoot, and adults observed per second and the mean number of egg masses and nymphs per shoot on four species of willow are shown. The species are *Salix integra* (*S. int*), *S. hultenii* (*S. hul*), *S. sachalinensis* (*S. sac*), and *S. miyabeana* (*S. miya*).

Table 1. Analysis of covariance testing the effect of willow shoot diameter and species on the density of adults.

Source	d.f.	MS	F	P
Shoot diameter	1	0.83	6.09	0.016
Willow species	3	2.23	17.43	0.0001
Error	62	0.13		

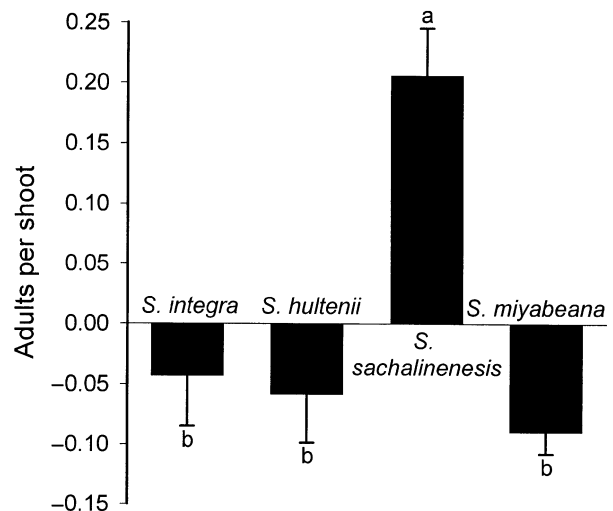


Fig. 2. The residuals for number of adults per shoot, with the effects of shoot length removed, on the four species of willow. Homogeneous groups as indicated by a Tukey's multiple range test are indicated by the lower case letters for each willow species.

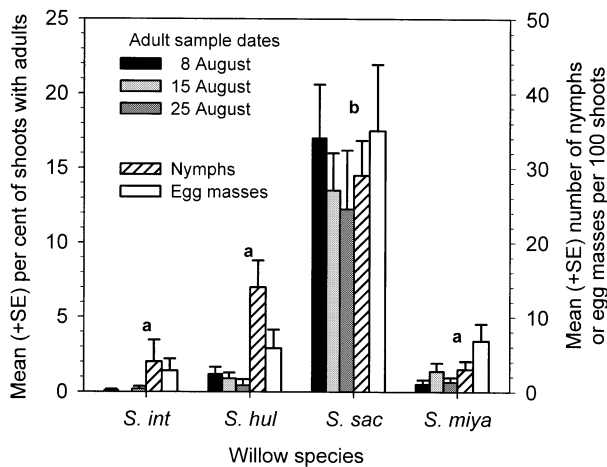


Fig. 3. The density of the different life stages at the Ishikari site in the 1998 survey. The mean per cent (+SE) of shoots with spittlebugs in the 8, 15, and 25 August 1998 surveys, the mean number of nymphs per shoot, and egg masses per shoot on 25 August are given.

adult density (Table 3). To determine species preference, each date was then analysed separately and a Tukey's multiple range test was run to determine pairwise differences in species preference. On each date, the densities differed significantly among species (8 August: $F_{3,45} = 8.22$, $P < 0.001$; 15 August: $F_{3,45} = 6.89$, $P < 0.001$; 25 August: $F_{3,45} = 26.55$, $P < 0.001$), with *S. sachalinensis* having significantly higher adult densities than any of the other species while none of the other pairwise comparisons of densities among the willow species differed significantly. Mating activity was high during this period, with 21.55 and 38.27% of the spittlebugs observed mating during the 8 August and 25 August surveys respectively.

Long shoots were preferred by adults: the 9 August 1998 survey showed that shoots with spittlebug adults were significantly longer than shoots without adults on 13 plants (mean length \pm SE with adults = 28.11 ± 4.1 cm; without adults = 17.56 ± 1.75 cm; paired t -test, $t = 3.85$, $P < 0.01$).

Egg masses

Both shoot diameter and willow species were significant predictors of the number of egg masses per shoot (Table 4) in 1997. *Salix sachalinensis* and *S. hultenii* had the largest shoot diameters (Fig. 4) but differed in the density of egg

Table 2. Correlations among spittlebug densities on 8, 15, and 25 August 1997.

	8 August density	15 August density
15 August density	0.61	
P -value	0.0001	
25 August density	0.81	0.47
P -value	0.0001	0.002

masses (Fig. 1). To isolate the effect of willow species on egg mass density, the residuals of egg mass number were analysed, when the effects of shoot length had been removed. In pair-wise comparisons of all species, only *S. sachalinensis* and *S. hultenii* differed significantly in egg mass densities (Fig. 5). In 1998, egg mass density in August was significantly higher on *S. sachalinensis* than on any of the other host species ($F_{3,44} = 10.36$, $P < 0.001$; Fig. 3).

The 1997 preference and performance survey showed that large diameter shoots, which constituted only a small proportion of available shoots, had the highest density of egg masses (Fig. 6). Only a small proportion of even the largest shoot diameter classes received egg masses (Fig. 6), indicating that large diameter shoots were not a limiting resource. In the preference and performance survey, shoots with egg masses had greater shoot diameters than randomly selected shoots on the same plant (Fig. 4). In the marked movement survey, paired t -tests showed that in all three species, shoots with egg masses had significantly larger diameters than randomly selected shoots (mean \pm SD for differences in diameters: *S. integra*: 0.83 ± 0.66 mm, $T = 5.43$, $P < 0.001$, $n = 19$; *S. sachalinensis*: 0.90 ± 1.11 mm, $T = 3.55$, $P < 0.01$, $n = 20$; *S. miyabeana*: 0.98 ± 0.53 mm, $T = 6.20$, $P < 0.001$, $n = 20$). The mean diameter of shoots with egg masses was a significant predictor of the mean diameter of all shoots on the plant ($y = 91.6 + 0.979x$, $r^2 = 42.1\%$, $P < 0.001$), indicating that even if nymphs disperse from the oviposition site, they are likely to encounter shoots similar to those where oviposition occurred.

Egg masses were much more highly aggregated among shoots than if they had been distributed at random (goodness-of-fit to a Poisson distribution, d.f. = 9, $\chi^2 = 401.60$, $P < 0.001$, d.f. = 3; Fig. 7). The egg emergence survey showed that the number of egg masses was correlated highly with the number of eggs ($y = -4.71 + 13.9x$, $r^2 = 71.2\%$, $P < 0.001$, d.f. = 61). The mean number of eggs per shoot \pm SD was 65.02 ± 49.82 (range three to 239). When only shoots that had egg masses were considered, there was also strong aggregation among egg masses (goodness-of-fit to a Poisson distribution $\chi^2 = 57.28$, $P < 0.001$). There was a significant difference among willow species in the mean number of egg masses per shoot when only shoots with egg masses were considered (one-way ANOVA, $F_{3,524} = 9.94$, $P < 0.001$; mean \pm SD: *S. integra* =

Table 3. Repeated measures analysis testing the effect of species and date on adult density. Willow individual is nested within species. The data are from 45 willows of four species sampled on 8, 15, and 25 August 1997.

Source	d.f.	MS	F	P
Willow species	3	0.767	56.32	0.0001
Willow individual	41	0.013	1.44	0.31
Date	3	0.011	8.68	0.40
Species \times date	6	0.015	0.92	0.27
Error	70	0.012		

Table 4. Analysis of covariance testing the effect of shoot diameter and willow species on the number of egg masses per 100 shoots.

Source	d.f.	MS	F	P
Shoot diameter	1	1.90	7.45	0.008
Willow species	3	0.80	2.79	0.030
Error	74	0.25		

4.04 ± 1.9 ; *S. hultenii* = 4.20 ± 1.90 ; *S. sachalinensis* = 5.54 ± 3.14 ; *S. miyabeana* = 4.59 ± 2.16).

The clumping of eggs was due at least partially to females ovipositing egg masses during different oviposition bouts on the same shoot. Results from the 1998 repeated-oviposition survey showed that new egg masses were added to 32.0% of the shoots between the first and second surveys and 60.0% between the first and third surveys.

Nymphs

Nymphs often moved away from the oviposition site, and continued to move during the entire nymphal period. In the marked movement survey, all nymphs moved from the egg mass where they eclosed to establish the first spittle (mean \pm SD = 29.70 ± 31.07 cm). The maximum move recorded was 132.0 cm, however this may be an underestimate, because it was assumed that all nymphs had originated from the nearest egg mass, and it is possible that nymphs moved further than this. There was relatively little movement of groups recorded between the first and second survey (8.62%; Fig. 8). In all subsequent periods, a large proportion of the surviving nymphs moved (11 June, 43.8%; 19 June, 38.8%; 24 June, 47.6%; 5 July, 40.0%). Many of the groups split into smaller groups (Fig. 8). During each survey period, increasing numbers of groups were either found dead or were missing. The missing groups either died or dispersed so far that they moved out of the area that had been cleared of spittlebugs. Although the latter may have occurred, it seems unlikely to have accounted for most disappearances. Spittles had been removed from most of the plants in the area and only rarely were spittles that could possibly have originated from a marked group observed on adjacent plants.

Nymphs had a preference for rapidly growing shoots. In the marked movement survey plants, the shoots with spittles were larger than randomly sampled shoots; for two species this difference was highly significant, for one species it was not significant (mean \pm SD for differences in diameters: *S. integra*: 0.43 ± 0.40 mm, $T = 3.82$, $P < 0.01$, $n = 13$; *S. sachalinensis*: 0.32 ± 0.75 mm, $T = 1.90$, $P = \text{NS}$, $n = 20$; *S. miyabeana*: 0.43 ± 0.72 mm, $T = 2.46$, $P < 0.05$, $n = 17$). Nymphs were found on large diameter shoots both because these shoots were chosen for oviposition and because first-instar nymphs moved to larger shoots. In 32 out of 60 willows, the first-instar nymphs were found on a different shoot from that on which the egg mass was located. The diameters of these shoots were significantly

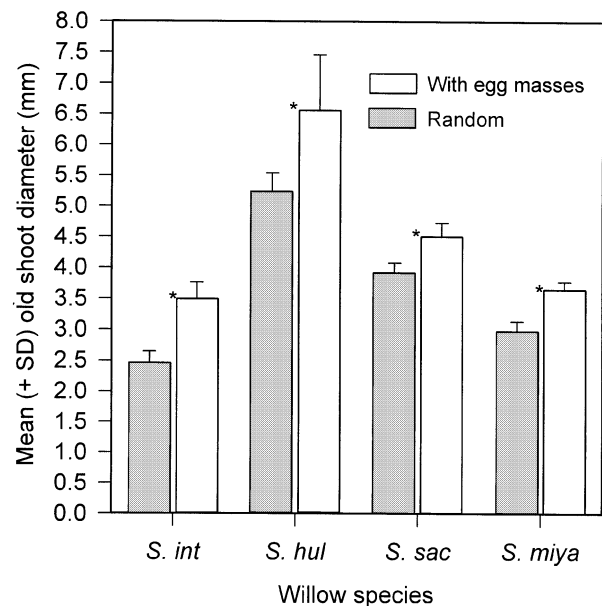


Fig. 4. The mean diameter (\pm SE) of shoots initiated in spring 1996 with nymphs, and randomly selected shoots without nymphs. The species are *Salix integra* (*S. int*), *S. hultenii* (*S. hul*), *S. sachalinensis* (*S. sac*), and *S. miyabeana* (*S. miya*).

larger than that of the shoot with the egg mass (mean difference \pm SD = 0.70 ± 1.10 mm, paired $T = 3.36$, $P < 0.01$).

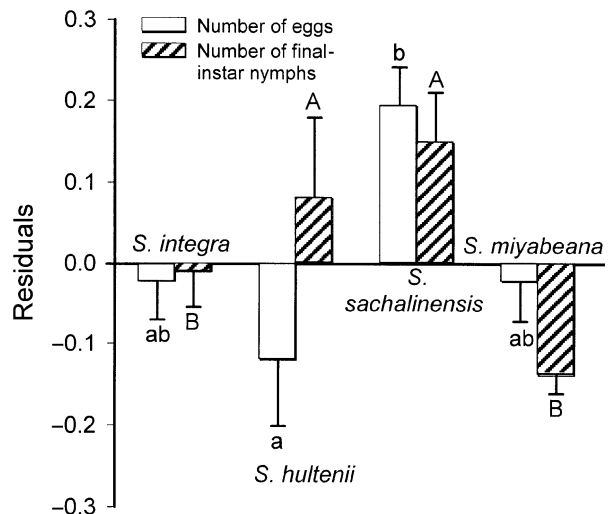


Fig. 5. The residuals for number of egg masses per shoot on the four willow species when the effects of shoot length on density have been removed. Homogenous groups as determined by a Tukey's multiple range test are indicated by the lower case letters above or below the bars for each willow species. The residuals for number of final-instar nymphs are when the effects of egg density and shoot length have been removed. Homogeneous groups as determined by a Tukey's multiple range test are indicated by the upper case letters for each willow species.

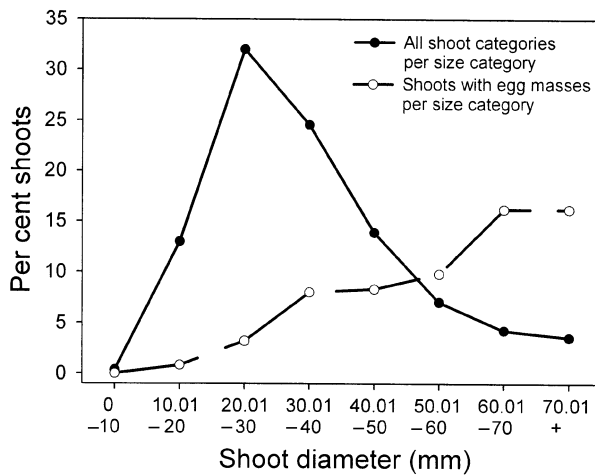


Fig. 6. The distribution among size diameter categories of randomly sampled shoots, and shoots with egg masses. The data from all willow species are pooled.

Nymphs moved from the previous year's shoots to rapidly growing new shoots as they became available in the preference and performance survey. All nymphs fed initially on the previous year's shoots then moved to new shoots: on 13 June $50.4 \pm 37.7\%$ (mean \pm SD) were on new shoots and on 25 June $83.5 \pm 24.9\%$ were on new shoots. These new shoots were significantly greater in diameter than randomly selected shoots on all four willow species (Fig. 9).

Nymphs were highly clustered among shoots. First-instar nymphs were much more highly aggregated (mean \pm SD = 4.5 ± 6.6 , range 1–49) than expected if they had been distributed at random when only shoots with nymphs were considered (goodness-of-fit to a Poisson distribution, $\chi^2 = 2317$, $P < 0.001$). Late-instar nymphs were also highly aggregated (mean \pm SD = 3.3 ± 3.0 , range 1–12) when only shoots with nymphs were considered (goodness-of-fit to a Poisson distribution, $\chi^2 = 2054$, $P < 0.001$).

There was a significant difference among willow species in the group sizes of nymphs. In the first nymphal instar, there were significant differences among species in the spittle length in the preference and performance plants (one-way ANOVA, $F_{3,65} = 21.2$, $P < 0.001$; mean \pm SD: *S. integra* 9.90 ± 2.60 mm; *S. hultenii* 16.70 ± 5.20 mm; *S. sachalinensis* 10.21 ± 3.02 mm; *S. miyabeana*: 7.20 ± 2.88 mm). Nymphs in these samples were not counted in order not to disturb them. The mean spittle length was a highly significant predictor of the number of nymphs in the spittle ($y = 4.27 + 72.2x$, $r_2 = 44.8\%$, $P < 0.001$, d.f. = 568). In the late nymphal stages, there were significant differences among willow species in the number of nymphs per spittle (one-way ANOVA, $F_{3,74} = 4.13$, $P < 0.01$; mean \pm SD of number of nymphs: *S. hultenii* = 5.0 ± 3.2 ; *S. integra* 2.6 ± 1.1 ; *S. sachalinensis* 3.3 ± 2.4 ; *S. miyabeana* 2.8 ± 1.7). *Salix hultenii* and *S. sachalinensis* had the largest

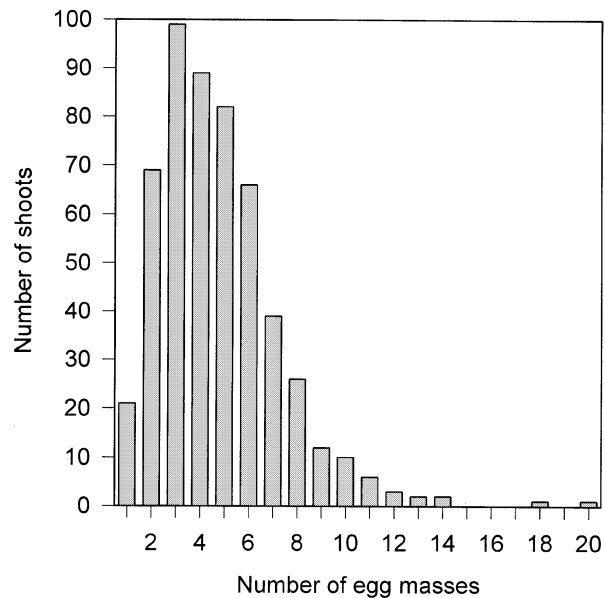


Fig. 7. The distribution of numbers of egg masses per shoot in the preference and performance survey. Shoots without egg masses were excluded.

spittles in the early survey and also had the highest mean number of nymphs during the later survey.

Performance. In the marked movement survey plants, there was a significant relationship between the shoot diameter on which an egg mass was found and the survival of the nymphs that originated from that mass. Survival dropped precipitously through the nymphal period (Fig. 10). As the survival dropped, the mean diameter of shoots on which the survivors had originated (the *egg-mass shoots*) increased, indicating that groups that had originated on shorter shoots had high mortality rates. The egg-mass shoots for nymphs that reached the adult stage were more than twice the diameter of egg-mass shoots in which the nymphs were dead or missing after the first time period.

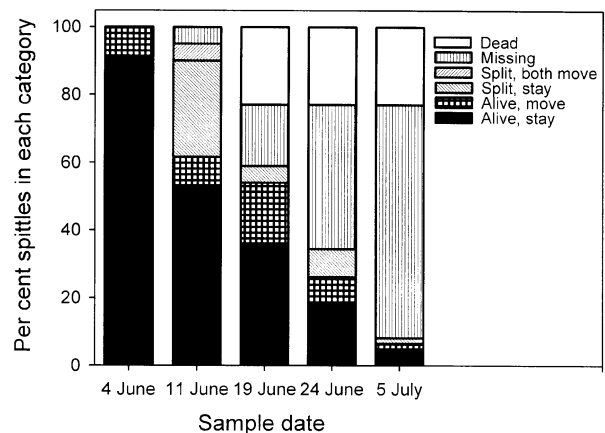


Fig. 8. The percentage of spittle masses classified into each of the categories on each of the sample dates.

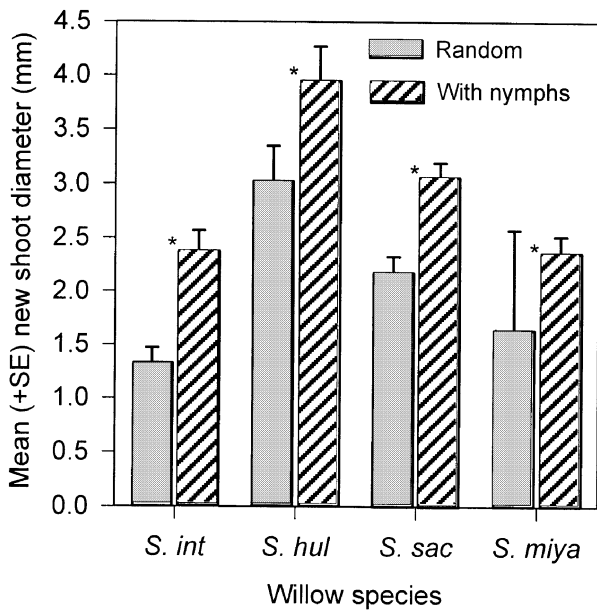


Fig. 9. The mean diameter (+SE) of shoots initiated in spring 1997 with nymphs and randomly selected shoots without nymphs. The species are *Salix integra* (*S. int*), *S. hultenii* (*S. hul*), *S. sachalinensis* (*S. sac*), and *S. miyabeana* (*S. miya*).

The willow species had no effect on the length of time for which nymphs survived.

Nymph density per shoot in 1997 differed widely among species (Fig. 1). Willow species influenced the number of nymphs that survived until the final instar per 100 shoots in the 1997 preference and performance survey but the mean shoot diameter of a plant did not (Table 5). The number of egg masses per 100 shoots was used as a covariate

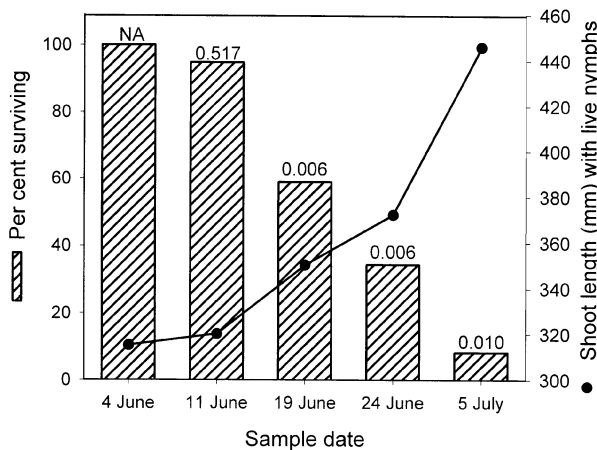


Fig. 10. The per cent of spittlebugs with survivors on each sample date (left axis). The solid line shows the mean diameter of shoots with surviving nymphs on each sample date. The numbers above each column show the *P*-value for the significance of a *t*-test for the difference between the means of the shoots with and without surviving nymphs on each sample date.

Table 5. Analysis of covariance testing the effect of shoot diameter and species on the number of late-instar nymphs. The number of egg masses per shoot is included to adjust for initial differences among individual willows in egg densities.

Source	d.f.	MS	<i>F</i>	<i>P</i>
Shoot diameter	1	0.04	0.30	0.5880
Egg mass density	1	2.17	14.03	0.0001
Willow species	3	1.34	8.68	0.0001
Error	70	0.15		

Table 6. Analysis of covariance testing the effect of egg density, shoot diameter, and willow species on per cent parasitism.

Source	d.f.	MS	<i>F</i>	<i>P</i>
Total number of eggs	1	0.00	0.00	0.965
Shoot diameter	1	0.03	0.90	0.346
Willow species	3	0.07	2.90	0.112
Error	57	0.03	0.15	

to account for the variance among willows in the density of eggs, which is equivalent to calculating the survival rate of nymphs per egg mass. A significant difference among species in survival to the final nymph stage was indicated, when the effects of the covariates for shoot length and the initial egg mass density had been removed by analysis of residuals (one-way ANOVA, $F_{3,62} = 12.62$, $P < 0.001$; Fig. 5). A Tukey's multiple range test showed that there were two homogeneous groups that differed in survival rates: *S. integra* and *S. miyabeana* had low survival rates; *S. sachalinensis* and *S. hultenii* had high survival rates (Fig. 5).

Nymph density per shoot differed significantly among species in 1998 ($F_{3,44} = 14.74$, $P < 0.001$; Fig. 3) and a Tukey's test indicated that *S. sachalinensis* had significantly higher densities than all other species.

Natural enemies

Host plant species, shoot size, and egg density did not influence survival during the egg stage (Table 6). All of the mortality detected during the egg stage was due to parasitism by two unidentified species of hymenopteran parasitoid from the families Mymaridae and Aphelinidae. Parasitism rates were high (mean \pm SD: *S. integra* $38.4 \pm 17.6\%$; *S. hultenii* $43.02 \pm 16.5\%$; *S. sachalinensis* $49.9 \pm 18.4\%$; *S. miyabeana* $51.2 \pm 14.8\%$) in eggs found on all willow species.

Discussion

The preference–performance relationship

A positive relationship was found between oviposition preference and offspring performance in *Aphrophora*

pectoralis, which has been seen in many other herbivores with other feeding strategies (Price, 1994). This is the first time, however, that this relationship has been seen in a xylem-sap feeding herbivore. Adults, nymphs, and ovipositing females were all found at higher densities on rapidly growing shoots, and nymphal survival was highest on these shoots. Females oviposited preferentially on rapidly growing shoots, and because the diameter of shoots with egg masses was correlated with the mean shoot diameter of the plant, dispersing nymphs encountered shoots similar to the one chosen by the female. Therefore an oviposition preference for rapidly growing shoots would be adaptive even though oviposition kills all or part of the shoot, forcing the nymph to move in order to feed (Nozawa & Ohgushi, 2002b,c). Because willow species differed in mean shoot size, the preference for willow species with rapidly growing shoots also assured nymphs of an abundant supply of rapidly growing shoots. Nymphs had a limited dispersal ability, and they refined the oviposition preference for rapidly growing shoots by choosing the largest shoots for feeding within the region of the plant where they eclosed. Adults also chose the largest shoots for feeding and mating, although adult movement made it impossible to assess the impact of this choice on adult performance. Because all spittlebug life stages chose to aggregate on a few long shoots, this resulted in only a small proportion of even the most vigorous shoots being utilised.

The distribution of eggs, nymphs, and adults among shoots within a host plant can be regarded as a true measure of host preference, which has been defined as: '... non-random oviposition on plant resources that are offered simultaneously or sequentially; a preferred oviposition site is one that is attacked at a higher rate than if attack were random' (Craig *et al.*, 1989). Because both nymphs and adults could search among a highly heterogeneous range of shoot lengths within a willow, they were being offered a range of shoot sizes simultaneously or sequentially.

Preference among willow species

There was a match between egg density and performance on species with the exception of *S. hultenii*. The limited dispersal ability of nymphs did not allow them to make choices among willow species, so female oviposition preference among willow species influenced nymphal survival. The effects of preference and performance due to shoot growth rate and species effects independent of shoot size were subdivided. Because shoot size differs among host species, it is also a species characteristic. The effects of shoot size on preference were so strong that they may largely have determined the preference among species. A measure of the effects of willow species on performance, with the effects of shoot length eliminated, was obtained through an analysis on the residuals of nymph density. This analysis indicated that three of the four species showed a preference and performance correlation (Fig. 5). *Salix sachalinensis* had a high nymphal survival rate and high egg densities. *Salix integra* and *S. miyabeana* both had low survival rates and

low egg densities. *Salix hultenii* was the exception to the pattern, having high survival rates and low egg densities.

Natural enemies had a strong impact on egg survival, but because there was no difference in parasitism rates among host plant species or among shoot sizes, there is no indication that they would exert selection on oviposition preference. There was no evidence of natural enemy mortality during the nymphal stage.

Movement among species

The distribution of *A. pectoralis* among host species was influenced both by survival rates on that host and by dispersal. The high ratio of adults to nymphs (Figs 1 and 3) on *S. sachalinensis* indicates that when spittlebugs reached the adult stage, they moved from all other hosts to this species. In particular, there was a high survival rate to the final nymphal instar on *S. hultenii* but a very low density of adults in both 1997 and 1998, indicating that adults moved from this host to *S. sachalinensis*. After mating, many females oviposited on *S. sachalinensis*, but there was significant dispersal to other host species for oviposition: there was a high ratio of eggs to adults in 1998 on all of the other species (Fig. 3). Because the distribution of adults in the 1996 generation that oviposited the egg masses observed in 1997 was not recorded, definite conclusions cannot be drawn about movement in that generation. If, however, mating was almost exclusively on *S. sachalinensis* as it was in 1997 and 1998, the large proportion of eggs on other species (Fig. 1) indicates dispersal from the mating site for oviposition during 1997.

Phylogenetic constraints hypothesis

The spittlebug has the phylogenetic constraint of being adapted for ovipositing into living tissue but it lacks the constraint of developing at the oviposition site. The results indicate that immobile, immature stages are therefore not critical for the development of a strong preference–performance relationship. Dispersal by spittlebug nymphs from the oviposition site indicates that selection for precision in oviposition preference is weaker than for an internal plant feeder. For example, if *A. pectoralis* oviposited on a shoot where nymphs could not survive, which was near a high quality shoot, nymphs could disperse to the better shoot and survive. In the same situation, immature gall-inducing insects would die. The limited nymphal dispersal of *A. pectoralis*, however, indicates that there is selection for the evolution of oviposition preference for host species, host plants, and regions of a host plant where offspring would have high performance. This contrasts with the extreme where females cannot assess host quality and offspring may have to disperse to find suitable food. A useful comparison is the study by Pires *et al.* (2000) of the neotropical spittlebug *Deois flavopicta*. It oviposits into the soil rather than in the host plant, and there is no oviposition preference–offspring performance linkage.

The combined effects of adult and immature preference, such as in *A. pectoralis*, should result in better offspring performance than when either adult or offspring alone can express preference. This prediction has rarely been tested but a limited number of studies supports this prediction. A strong preference–performance relationship was found in a free-feeding ladybug, *Epilachna niponica*, with limited dispersal where the preferences of both adult and larvae influenced performance (Ohgushi, 1995). In addition, Carr *et al.* (1998) found that a free-feeding sawfly that was not constrained to develop within the oviposition site, but with extremely low dispersal, had a strong preference–performance relationship.

The phylogenetic constraint of being adapted to feeding on nitrogen-poor xylem sap may have led to aggregation for mating, which subsequently influences egg distribution. *Aphrophora pectoralis* have a long pre-oviposition period, they mature eggs slowly, and oviposit over an extended time period (Nozawa & Ohgushi, 2002a); all of these characteristics are probably due to feeding on extremely nitrogen-poor xylem sap. Spittlebugs have been observed to mate repeatedly (T. P. Craig and A. Nozawa, unpublished), and mating aggregations persist over an extended period of time (this study). This suggests that females may be limited in their ability to store sperm and must mate repeatedly as they obtain enough nitrogen to mature eggs. Aggregation on *S. sachalinensis* may facilitate this repeated mating but this aggregation may make it costly to disperse and search for the best oviposition sites if they occur on other species.

The resource constraints hypothesis

The distribution of high-quality oviposition sites in relation to adult mating and feeding sites may constrain the evolution of a strong preference–performance relationship. Spittlebugs aggregate on *S. sachalinensis* for mating, and alternate host plants distant from *S. sachalinensis* populations may have received few eggs despite their potential for high offspring performance. For example, *S. miyabeana* had higher egg densities than *S. hultenii* although performance on *S. hultenii* was much higher. *Salix miyabeana* may have been favoured, despite lower performance on this species, because of its abundance and proximity to *S. sachalinensis*. Thus dispersal would have been less costly to *S. miyabeana* than to *S. hultenii*. *Salix hultenii* may serve as a population source, with low oviposition rates and high nymphal survival rates, and *S. miyabeana* as a population sink, with high oviposition rates and low nymphal survival rates.

The benefits of dispersing from mating sites on *S. sachalinensis* to other host species for oviposition sites are not clear. The data indicate that females could maximise their fitness by ovipositing only on *S. sachalinensis*: this would minimise the mortality due to dispersal and maximise offspring performance. It seems unlikely that spittlebugs are dispersing to avoid intraspecific competition, as there is a preference for aggregation in all stages. There may

be benefits to dispersion that were not measured. More information on the spatial distribution of host species and the costs and benefits of dispersal are needed before the oviposition and mating strategies of *A. pectoralis* can be understood completely.

The distribution of host species may be a resource constraint that interacts with the phylogenetic constraints of xylem feeding, and oviposition into living tissue. If the willow species where performance was highest were located nearest the species where mating occurred, there would be a strong preference–performance relationship, but this does not occur at the Ishikari site. This illustrates that a set of phylogenetic constraints will determine the range of preference–performance relationships that can evolve, but the resource constraints modify the strength of this relationship.

Aphrophora pectoralis maintains a strong preference–performance relationship while responding to one potential resource constraint: the difficulty that polyphagous herbivores may have in evolving oviposition preference in response to complex resource variation (Craig *et al.*, 1999a). A strong preference–performance correlation has frequently evolved in monophagous herbivores where preference evolves in response to a single factor that has a strong influence on performance: plant module growth rate (Price, 1994). Among polyphagous herbivores, the preference–performance relationship varies from weak (Chew, 1977; Courtney, 1981, 1982a,b; Williams, 1983; Legg *et al.*, 1986) to relatively strong (Wiklund, 1977, 1981; Rausher, 1982; Leather, 1985; Singer *et al.*, 1988, 1994; Craig *et al.*, 1993; Rank *et al.*, 1998). Polyphagous herbivores, such as *A. pectoralis*, must respond to complex variation: within plant modules, among plant modules within a plant, among individual plants within a species, among species (Thompson & Pellmyr, 1991) and natural enemies (Attsatt, 1981; Denno *et al.*, 1990; Feder, 1995; Yamaga & Ohgushi, 1999). *Aphrophora pectoralis* may have evolved a strong preference–performance relationship in spite of these multiple sources of variation because of the predominance of a single factor in determining performance: shoot growth.

Mechanisms explaining host preference

Spittlebug performance may be best on rapidly growing shoots and on *S. sachalinensis* and *S. hultenii* for several reasons. First, large shoots may have higher concentrations of nitrogen, resulting in increased survival of nymphs feeding there. Xylem sap feeders encounter very low concentrations of nitrogen in their food (Wiegert, 1964; Mattson, 1980; Llewellyn, 1983). More rapidly growing, large diameter shoots may provide higher concentrations of nitrogen. Nitrogen and other minerals concentrations were found to be higher in xylem sap from rapidly growing trees with long branches than on slowly growing trees with short branches in conifers (Stark & Spitzner, 1985). Spittlebugs prefer plants with high nitrogen content (Thompson, 1994; Hartley & Gardner, 1995). Horsfield

(1977) found that *Philaenus spumarius* preferred young leaves where the amino acid concentrations in the xylem were higher than in old leaves. He also found that the higher the amino acid concentration, the higher the nymphs' survival rate. More rapidly growing shoots may have more xylem sap to be excreted as froth, which serves as a defence and prevents desiccation (Weaver & King, 1954; Whittaker, 1970). A third reason why large shoots may be favoured is that it may be easier to oviposit into large shoots and these shoots may be better able to withstand the high winds and heavy snow at the study site. Small shoots with many eggs may also have a greater tendency to break and fall off the willow, leaving the emerging nymphs far from their feeding site (Nozawa & Ohgushi, 2002c). Shoot terminals are killed by oviposition, and subsequent resprouting on vigorous shoots produces larger, more numerous lateral shoots (Nozawa & Ohgushi, 2002b) for feeding by the nymphs. This is a form of resource regulation (Craig *et al.*, 1986), in which the offspring benefit from the alteration in plant growth induced by the actions of the previous generation. Lastly, nymphs prefer to feed in groups, and large shoots may provide a cue that facilitates aggregation. In support of this hypothesis is the pattern that the highest survival rates were found on the species with the largest mean spittlebug group sizes.

Aggregation for mating may have influenced oviposition preference for willow species by increasing the probability that willows near aggregation sites would receive egg masses. *Salix miyabeana* was abundant and grew in close proximity to *S. sachalinensis*, and had higher egg densities than would be predicted on the basis of nymphal performance. Nymphal performance was high on *S. hultenii* but had low egg densities, possibly because it was rare and frequently grew isolated from *S. sachalinensis*.

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References

- Attsatt, P. (1981) Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia*, **48**, 60–63.
- Carr, T.G., Roininen, H. & Price, P.W. (1998) Oviposition preference–larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. *Environmental Entomology*, **27**, 615–625.
- Chew, F.S. (1977) Coevolution of pierid butterflies and their cruciferous host plants. II. The distribution of eggs on potential foodplants. *Evolution*, **31**, 568–579.
- Courtney, S.P. (1981) Coevolution of pierid butterflies and their cruciferous foodplants. III. *Anthocharis cardamines* (L.) survival, development and oviposition on different host plants. *Oecologia*, **51**, 91–96.
- Courtney, S.P. (1982a) Coevolution of pierid butterflies and their cruciferous foodplants. IV. Hostplant apparency and *Anthocharis cardamines* oviposition. *Oecologia*, **52**, 258–265.
- Courtney, S.P. (1982b) Coevolution of pierid butterflies and their cruciferous foodplants. V. Habitat selection, community structure and speciation. *Oecologia*, **54**, 101–107.
- Courtney, S.P. & Kibota, T.T. (1990) Mother doesn't know best: selection of hosts by ovipositing insects. *Insect–plant Interactions* (ed. by E. A. Bernays), pp. 161–188. CRC Press, Boca Raton, Florida.
- Craig, T.P., Itami, J.K., Abrahamson, W.G. & Horner, J.D. (1993) Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution*, **47**, 1696–1710.
- Craig, T.P., Itami, J.K., Abrahamson, W.G. & Horner, J.D. (1999a) Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. *Oikos*, **86**, 119–126.
- Craig, T.P., Itami, J.K. & Horner, J.D. (1997) Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. *Evolution*, **51**, 1552–1560.
- Craig, T.P., Itami, J.K. & Price, P.W. (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology*, **70**, 1691–1699.
- Craig, T.P., Itami, J.K., Schantz, C., Abrahamson, W.G. & Horner, J.D. (1999b) The influence of host plant variation and intraspecific competition on oviposition preference in the host races of *Eurosta solidaginis*. *Ecological Entomology*, **25**, 1–12.
- Craig, T.P., Price, P.W. & Itami, J.K. (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology*, **67**, 419–425.
- Denno, R.F., Larsson, S. & Olmstead, K.L. (1990) Role of enemy-free space and host plant quality in host-plant selection by willow beetles. *Ecology*, **71**, 124–137.
- Feder, J.L. (1995) The effects of parasitoids on sympatric host races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Ecology*, **76**, 801–813.
- Hartley, S.E. & Gardner, S.M. (1995) The response of *Philaenus spumarius* (Homoptera: Cercopidae) to fertilizing and shading its moorland host-plant (*Calluna vulgaris*). *Ecological Entomology*, **20**, 396–399.
- Horsfield, D. (1977) Relationship between the feeding of *Philaenus spumarius* (L.) and the amino acid concentration in the xylem sap. *Ecological Entomology*, **2**, 259–266.
- Ishihara, M., Hayashi, T. & Ohgushi, T. (1999) Life cycle of the willow leaf beetle, *Plagioderma versicolora* (Coleoptera: Chrysomelidae) in Ishikari (Hokkaido, Japan). *Entomological Science*, **2**, 57–60.
- Komatsu, T. (1997) A revision of the froghopper genus *Aphrophora* Germar (Homoptera, Cercopoidea, Aphrophoridae) from Japan, Part 2. *Japanese Journal of Entomology*, **65**, 369–383.
- Leather, S.R. (1985) Oviposition preferences in relation to larval growth rates and survival in the pine beauty moth, *Panolis flammea*. *Ecological Entomology*, **10**, 213–217.

- Legg, D.E., Shenk, T.C. & Chiang, H.C. (1986) European corn borer (Lepidoptera: Pyralidae) oviposition preference and survival on sunflower and corn. *Environmental Entomology*, **15**, 631–634.
- Llewellyn, M. (1983) The energy economy of fluid-feeding herbivorous insects. *Proceedings of the 5th International Symposium on Insect-plant Relationships* (ed. by J. H. Visser and A. K. Minks), pp. 243–251. Pudoc, Wageningen, The Netherlands.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.
- Nozawa, A. & Ohgushi, T. (2002a) Life-history and oviposition preference of the willow spittlebug *Aphrophora pectoralis* (Homoptera: Aphrophoridae). *Entomological Science* (in press).
- Nozawa, A. & Ohgushi, T. (2002b) How does spittlebug oviposition affect shoot growth and bud production in two willow species? *Ecological Research* (in press).
- Nozawa, A. & Ohgushi, T. (2002c) Shoot characteristics affect oviposition preference of the willow spittlebug *Aphrophora pectoralis* (Homoptera: Aphrophoridae). *Annals of the Entomological Society of America* (in press).
- Ohgushi, T. (1995) Adaptive behavior produces stability in herbivorous lady beetle populations. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P. W. Price), pp. 303–319. Academic Press, San Diego, California.
- Ohgushi, T. (1998) Bottom-up population regulation of a herbivorous lady beetle: an evolutionary perspective. *Insect Populations in Theory and in Practice* (ed. by J. P. Dempster and I. F. G. McLean), pp. 367–390. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Pires, C.S.S., Price, P.W. & Fontes, E.G. (2000) Preference-performance linkage in the neotropical spittlebug, *Deois flavopicta* and its relationship to the phylogenetic constraints hypothesis. *Ecological Entomology*, **25**, 71–80.
- Price, P.W. (1994) Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. *Researches on Population Ecology*, **36**, 1–12.
- Price, P.W., Craig, T.P. & Hunter, M.D. (1998) Population ecology of a gall-inducing sawfly, *Euura lasiolepis*, and relatives. *Insect Populations in Theory and in Practice* (ed. by J. P. Dempster and I. F. G. McLean), pp. 323–340. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Rank, N.E., Kopf, A., Julkunen-Tiito, R. & Tahvanainen, J. (1998) Host-preference and larval performance of the salicylate-using leaf beetle *Phratora vitellinae*. *Ecology*, **79**, 618–631.
- Rausher, M.D. (1982) Population differentiation in *Euphydryas editha* butterflies: larval adaptation to different hosts. *Evolution*, **36**, 581–590.
- Singer, M.C., Ng, D. & Thomas, C.D. (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution*, **42**, 977–985.
- Singer, M.C., Thomas, C.D., Billington, H.L. & Parmesan, C. (1994) Correlates of speed of evolution of host preference in a set of twelve populations of the butterfly *Euphydryas editha*. *Ecoscience*, **1**, 107–114.
- Stark, N. & Spitzner, C. (1985) Xylem sap analysis for determining the nutrient status and growth of *Pinus ponderosa*. *Canadian Journal of Forestry Research*, **15**, 783–790.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants*. Harvard University Press, Cambridge, Massachusetts.
- Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia experimentalis et applicata*, **47**, 3–14.
- Thompson, J.N. & Pellmyr, O. (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology*, **36**, 65–89.
- Thompson, V. (1994) Spittlebug indicators of nitrogen-fixing plants. *Ecological Entomology*, **19**, 391–398.
- Weaver, C.R. & King, D.R. (1954) Meadow spittlebug. *Ohio Agricultural Experiment Station Bulletin*, **741**, 1–100.
- Whitham, T.G. (1980) The theory of habitat selection: examined and extended using *Pemphigus* aphids. *American Naturalist*, **115**, 449–465.
- Whittaker, J.B. (1970) Cercopid spittle as a microhabitat. *Oikos*, **21**, 59–64.
- Wiegert, R.G. (1964) The ingestion of xylem sap by meadow spittlebugs, *Philaenus spumarius* (L.). *American Midland Naturalist*, **71**, 422–428.
- Wiklund, C. (1977) Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lep. Pieridae). *Oikos*, **28**, 56–58.
- Wiklund, C. (1981) Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. *Oikos*, **36**, 163–170.
- Williams, K.S. (1983) The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants. III. Oviposition behavior and host plant quality. *Oecologia*, **5**, 336–340.
- Williams, K.S., Lincoln, D.E. & Ehrlich, P.R. (1983) The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants. II. Maternal and host plant effects on larval growth, development, and food-use efficiency. *Oecologia*, **56**, 330–335.
- Yamaga, Y. & Ohgushi, T. (1999) Preference-performance linkage in an herbivorous lady beetle: consequences of variability of natural enemies. *Oecologia*, **119**, 183–190.

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