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### HOST-PLANT SELECTION AND PREDATION RISK FOR OFFSPRING OF THE PARENT BUG

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Herbivores, especially specialists, must adapt to characteristics of their host to survive and reproduce successfully (Hardin and Tallamy 1992). If offspring survival among different hosts varies, natural selection should lead females to choose egg-laying sites where performance of the progeny will be highest. This is especially true when newly hatched larvae cannot move to another host (Singer 1986), or when searching for new hosts would cause heavy mortality (Singer and Mandracchia 1982).

A number of studies have shown that females that search for oviposition sites respond to plant characteristics that are correlated with the nutritional quality of plants for their offspring (e.g., Myers 1985, Damman and Feeny 1988). Also, secondary chemicals of plants play an essential part in determining whether the plant is suitable for oviposition (e.g., Feeny et al. 1985). Furthermore, females may detect visually or chemically the presence of other conspecific and nonconspecific competitors already on a potential host (Rothschild and Schoonhoven 1977, Rausher 1979, Mappes and Mäkelä 1993).

However, one of the most important selective agents driving the evolution of behavioral adaptations of prey animals is predation (Endler 1991), and for herbivorous insects, natural enemies commonly represent the major source of mortality (Myers 1981, Feeny et al. 1985). Thus, predation as well as plant characteristics could influence both oviposition behavior and offspring performance on the host (Bernays and Graham 1988). At the moment, however, there is very little empirical ev-

idence about the ability of ovipositing insects to discriminate among host plants based on the risk of predation or parasitism (but see Ohsaki and Sato 1994).

Parent bugs (*Elasmucha grisea*) may choose oviposition sites based on predation risk. Parent bugs guard their eggs and small nymphs against predators (Jordan 1958, Melber and Schmidt 1975). Without maternal protection, predators kill almost all nymphs (Melber and Schmidt 1975, Melber et al. 1980, Mappes and Kaitala 1994). Ants are the main predators of *E. grisea* (Melber et al. 1980, Mappes and Kaitala 1994). Adult bugs disperse from their natal trees and overwinter in the ground litter (J. Mappes and A. Kaitala, *personal observation*). In June, a female lays one clutch, of 40–58 eggs ( $\bar{X} = 50$ ), usually on the lower surface of birch leaves in the beginning of June (A. Kaitala and J. Mappes, *unpublished data*). Both adults and nymphs suck liquids of developing birch seeds; breeding parent bugs are found on birches (*Betula pendula* and *Betula pubescens*) with plenty of young catkins (Jordan 1958). However, parent bugs use only a few of the birches with catkins (J. Mappes and A. Kaitala, *personal observation*). It is obvious that some environmental characteristics associated with the hosts affect host selection in this species.

The purpose of the present study was to test how selection of oviposition site affects breeding success of the parent bug and what is the possible mechanism behind the preference of certain birch trees.

#### Methods

The experiment was conducted in 1993 in a woodland near the Tvärminne Zoological Research Station, southern Finland. Six trees (3 *Betula pendula* and 3 *B. pubescens*) were designated as controls which means that those trees were used naturally by parent bugs. Usually, these trees contained some 30–40 parent bugs. We chose nine trees (5 *B. pendula* and 4 *B. pubescens*) that were not used by any bugs as the “experimental” trees. These trees were located intermingled between the control trees. We collected female–male pairs from the control trees. All females (including controls) were marked and weighed individually in a laboratory before transplantation back to the control trees and to the experimental trees. Six randomly chosen female–male pairs were placed in each tree on randomly chosen

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branches with catkins. There were at least 10 female catkins on each chosen branch, which represents enough food for nymphs, and the branch was covered by a net. After oviposition we removed the net and counted the number of eggs in the clutch. We also recorded the number of eggs remaining just before hatching and number of nymphs reaching the third instar. Third instar stage nymphs are very mobile and

TABLE 1. Results of two-way ANOVAs measuring effect of experimental treatment (bug transplantation and tree species) on parent bug egg-laying date, clutch size, and offspring survival parameters.

Dependent variable	Categories		
	Treatment	Tree species	Treatment × tree species
Egg-laying date			
$F_{(1,11)}$	0.34	2.10	1.94
$P$	0.572	0.175	0.191
Clutch size			
$F_{(1,11)}$	0.01	0.47	0.72
$P$	0.906	0.509	0.414
Number of nymphs surviving			
$F_{(1,11)}$	47.42	0.33	1.20
$P$	0.000	0.576	0.297
Number of ants			
$F_{(1,11)}$	8.03	0.10	1.0
$P$	0.016	0.757	0.338

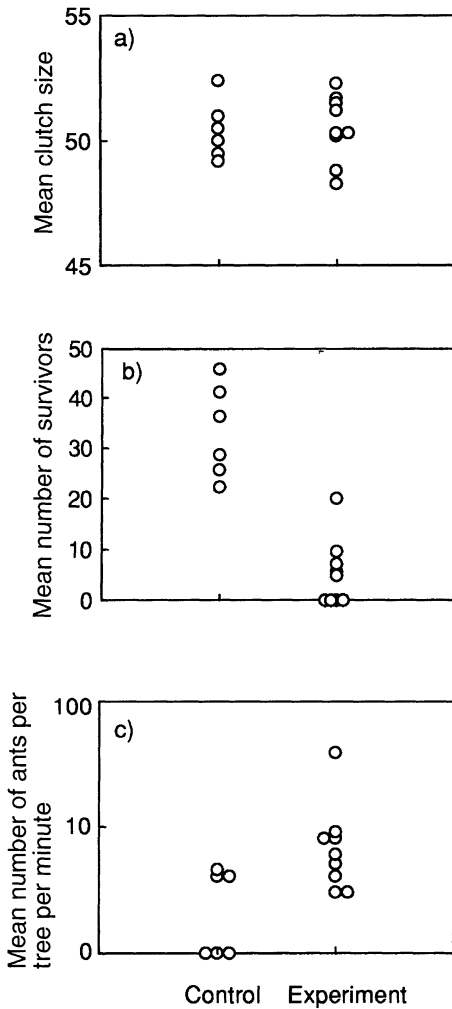


FIG. 1. (a) The mean number of eggs per clutch on control trees and experimental trees. Each circle represents the average clutch size on each tree, with six females per tree. The range of standard errors in the control group is 1.1–1.9 and in the experimental group 0.8–3.3. (b) The mean number of surviving nymphs (later stage of second instar) on control trees and experimental trees. The range of standard errors in the control group is 6.2–11.6 and in the experimental group 0–10.8. (c) The visitation frequency of ants to control trees and experimental trees. The range of standard errors in the control group is 0–2.6 and in the experimental group 1.0–3.2. See Table 1.

may disperse widely, and thus reliable counts of larger nymphs of each individual female were not possible.

We located foraging routes of ants on each birch trunk. We counted the number of ants (*Myrmica* sp. and *Formica* sp.) that climbed up the trunk during 1 min on three different days (20 and 25 June and 7 July) between 1100 and 1400. These days were sunny and air temperature varied between 15° and 20°C. Because number of ants varied only slightly between days we used the mean values in statistical analyses.

Data from the experiment were analyzed with a two-way ANOVA. In these tests, the mean values from each individual host tree (six clutches in each tree) were used to assure statistical independence of the observations. The number of ants patrolling in trees were log-transformed to normalize the data before analysis. All statistical tests were performed using the PC version of SPSS (SPSS 1988).

Results

Host species (*B. pendula* vs. *B. pubescens*) and the treatment did not affect egg-laying date ( $8.9 \pm 2.2$  d and  $9.6 \pm 2.4$  d after 1 June) and clutch size ( $50.4 \pm 1.2$  and  $50.5 \pm 1.3$  eggs) (mean  $\pm$  1 SD in control trees and experimental trees, respectively) (Fig. 1). There were no significant interactions between treatment and tree species (Table 1). However, after the egg-guarding period, the number of surviving nymphs differed significantly between treatment groups; it was higher on the control trees (mean =  $33.2 \pm 9.3$  nymphs) than on the experimental trees ( $5.2 \pm 6.6$  nymphs), but there were no significant differences between tree species (Table 1). Predation rate was highest during the egg stage; 98% of disappearances took place during that period.

The number of ants per tree did not differ between

*B. pendula* and *B. pubescens*, but was significantly lower on the control trees ( $2.1 \pm 2.3$  ants) than on the experimental trees ( $9.4 \pm 11.3$  ants) (Table 1).

#### Discussion

Female parent bugs, *Elasmucha grisea*, seem to prefer to oviposit on the sites where the survival of nymphs is highest. They seem to discriminate against trees where offspring mortality is high, most likely because of high ant predation. In some cases, the appearance of highly mobile predators, such as wasps and spiders, might be impossible to predict when females search food plants (Rausher and Papaj 1983). For example in the *Battus philenor* butterfly (Rausher and Papaj 1983), and in the *Eurytides marcellus* butterfly (Damman and Feeny 1988), the major mortality source for caterpillars was predation. However, oviposition in relation to predator occurrence on the plant was random. In *E. grisea*, ant predation is a predictable risk, which is possible to avoid. Feeding activity of ants usually starts in southern Finland in late April (Rosengren and Sundström 1987), which is 1–3 wk before parent bugs start to emerge on the birches in the same area. Moreover, worker ants use the same routes as in previous years, and the traffic intensity does not vary markedly within season or even during the day (Rosengren and Sundström 1987). Thus, the risky habitats (birches with ants) may be easy to discriminate from the safe birches.

The species that lay all of their eggs on a single or only a few plants, such as *E. grisea*, or lay only a few eggs during their lifetime, would be expected to evaluate food plants more carefully than insects that disperse their eggs over space and time (Damman and Feeny 1988). Although Melber and Schmidt (1975) have shown that maternal brood care in parent bugs is highly effective against invertebrates, ants are superior predators, and high ant densities can cause the death of both mother and the whole brood (present study). Moreover, few females can lay another clutch after the loss of their initial brood (A. Kaitala and J. Mappes, unpublished data). Thus, the cost of predation is extremely high and selection of a host plant with low predator density is crucial for survival of parent bugs.

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