INTRODUCTION

Subsociality has been reported in many taxonomic groups within the Heteroptera, especially in the Pentatomomorpha (Melber and Schmidt 1977, Tachikawa 1991). In the family Acanthosomatidae, maternal care has been recorded for more than 10 species of three genera, Anaxandra, Sastragala and Elasmucha (Tachikawa 1991). However, the adaptive significance of this behavior has been confirmed by field experiments in only a few species (Melber and Schmidt 1975b, Honbo and Nakamura 1985, Kudô et al. 1989). There have been some observations of maternal attendance of offspring in Elasmucha signoreti Scott (Tachikawa 1991). Nevertheless, a detailed report of its reproductive history remains unavailable. In the present paper, we describe oviposition and patterns of maternal behavior, as well as show the effects of the maternal behavior on survival of the offspring under field conditions.

MATERIALS AND METHODS

Observations and experiments were conducted in a forest in Toyotaki, Sapporo, Hokkaido, northern Japan, from August to September in 1991 and during August in 1992. At the study site, host...
plants of *E. signoretii*, the vine *Hydrangea petiolaris* Sieb., grow on pine tree supports. The *E. signoretii* population was rather small: less than 30 females with offspring were discovered on the host plant during the two-year research period. We marked individual females attending the offspring with quick-drying paint, tagged oviposition sites, and then monitored the females and offspring. To count the eggs, females were temporarily removed from the clutches; however, this did not disturb the subsequent behavior of the females.

In many subsocial insects, brooding females show specific defensive behavior when disturbed (e.g., Eberhard 1975). To observe behavior against disturbance in the field, females with offspring, females that had left the offspring and males were stimulated by shaking a small black ball (4 mm in diameter) in front of them at a distance of about 5 mm. Five females with eggs were brought into the laboratory and placed with a potential predator, an asopine bug nymph, for detailed observations.

To examine ovarian development during the period of maternal care, we dissected females with eggs (n=11), females with late 1st-instar nymphs (n=5) and those that had just left 2nd instar nymphs (n=3).

In 1992, to evaluate the adaptive significance of female attendance, 7 females were removed from their egg masses in the field. Another 5 females with eggs were kept intact as controls. Six days after the removal, the number of surviving eggs or nymphs were counted in each of the clutches and the survival rate was compared between the two groups.

**RESULTS AND DISCUSSION**

Oviposition usually occurred in early August. Eggs were laid in a compact mass usually on the undersurface of host leaves, but one egg mass was found on the sepal. The number of eggs per clutch was, on average, 33.79 (SD=4.35; range, 21–36; n=19). Females always straddled their offspring (Fig. 1). Of 11 females monitored in 1991, one disappeared from her egg mass, and another was confirmed to have been killed by a web building spider. These two egg masses which were left without a female were completely destroyed before hatching, while the other nine clutches with a female successfully hatched. First instar nymphs always form a
Fig. 1. An *Elasmucha signoreti* female with 1st-instar nymphs on a leaf of the host plant, *Hydrangea petiolaris*.

tight aggregation and probably do not feed. After molting to the 2nd instar, nymphs moved from the oviposition site to the inflorescence in aggregations, to feed on fruit. We observed three marked females straddling newly-molted 2nd-instar nymphs which remained at the oviposition site. However, no females attended 2nd- or later-instar nymphs that had left the oviposition site. In other *Elasmucha* spp., parent females often attend the 2nd- or later-instar nymphal aggregation away from the oviposition site (Frost and Haber 1944, Melber and Schmidt 1975a, Honbo and Nakamura 1985, Kudô et al. 1989). Thus, *E. signoreti* females probably desert their offspring at the earliest developmental stage among the related species. Five marked females were observed alone on the host at least once after deserting the offspring from the middle to the end of August in 1991. Although males were found on the host before the females disappeared, no copulation was observed. Moreover, none of the females produced additional clutches.

Females with offspring probably took no food: their ovaries had no chorionated eggs and contained only undeveloped oocytes (the largest oocyte was always less than 0.1 mm long) during the period of maternal care.
When disturbed, brooding females showed almost the same aggressive behavior as in other *Elasmucha* spp. (Melber and Schmidt 1975a, Melber et al. 1980, Kudô et al. 1989, Kudô 1990): jerking the body rapidly, tilting the body toward the source of the disturbance, and wing fanning. In the laboratory, *E. signoretii* females with eggs dealt with an asopine bug approaching them by employing various combinations of the responses described above. Against a disturbance made by a small black ball in the field, all of the females with eggs (n=10), those with 1st-instar nymphs (n=8) and those with 2nd-instar nymphs remaining at the oviposition site (n=3) responded with some of the above behaviors. However, solitary females that left offspring (n=4) and males (n=12) retreated from the disturbance or dropped from plants without displaying any aggressive behavior.

Maternal brooding in *E. signoretii* was highly effective in protecting offspring from predation. Five out of the seven clutches from which females were removed were attacked and disappeared from the leaves within six days, while most of the offspring survived in the five control clutches. The offspring survival in the experimental group (Mean=0.270, SD=0.461) was significantly lower than that in the control group (Mean=0.978, SD=0.036) (Mann-Whitney U test, p=0.0065). Several spiders and predatory bug nymphs (Asopinae and Nabidae) were observed to feed on eggs and nymphs. Ants, which were often observed on host plants, probably preyed on *E. signoretii* eggs because no chorion remained on leaves from which eggs disappeared. Egg parasitoids have often been recorded as an important mortality agent of subsocial bugs (ex., Eberhard 1975, Ralston 1977, Nakamura 1990). However, as in other studies determining egg mortality agents of *Elasmucha* (Melber and Schmidt 1975b, Melber et al. 1980, Honbo and Nakamura 1985, Kudô et al. 1989), no egg parasitism was observed in *E. signoretii* even when parent females were removed from eggs.

The maternal behavior in *E. signoretii* apparently functions as physical defense of offspring against arthropod predators. This is also the case in other *Elasmucha* spp. (Melber and Schmidt 1975b, Melber et al. 1980, Honbo and Nakamura 1985, Kudô et al. 1989) and other subsocial bugs (e.g., Tallamy and Denno 1981). Predation pressure is probably the primary selective factor leading to the maternal care commonly observed in *Elasmucha* bugs.
Reproductive behavior in the subsocial bug *Elasmucha signoreti* is described. Females usually deposited eggs in a compact mass on a leaf of the host plant, *Hydrangea petiolaris*, and straddled the offspring until the 2nd instar when they left the oviposition site. While attending offspring, a female’s ovaries were invariably undeveloped. When disturbed, attending females showed aggressive responses. Effectiveness of maternal behavior against arthropod predation was demonstrated by a female removal experiment in the field.

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