

Notes on the bionomics of *Elasmucha grisea* (LINNAEUS 1758) (Heteroptera, Acanthosomatidae) with special regard to joint brood guarding¹

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Abstract: Females of *Elasmucha grisea* are known to guard their eggs and nymphs. We investigated this behaviour in several populations in Germany. While in Scandinavia a high proportion of females have been observed to guard their eggs jointly, in German populations less than 5 % (n=114) of females do so. For the first time, interactions between joint guarding females and nymphs are reported. Observations and data from experiments in the field and in the laboratory reported here contribute to aspects of the distribution pattern of guarding females, selection of oviposition site, host plant shift, mating behaviour, and survival patterns of males and females. We found evidence that in early nymphal instar stages the synchrony of development can become lost. While some nymphs are still in the first instar stage, others already hatched to second instar nymphs and leave the brood leaf. The female then no longer is able to provide an effective shelter for all her nymphs. Consequently, nymphs of different females contact and form mixed groups. In such cases, both single and joint guarding females perform guarding behaviour regardless of whether the nymphs are hers or another female's offspring. So far, joint brood guarding has been studied in terms of predation defence behaviour. We assume that maintaining a „kindergarten“, i.e. a female guarding a mixed group of nymphs, could be an additional factor that promotes joint brood guarding behaviour in *E. grisea*. Nymphs are likely to benefit from such behaviour, in particular when females disappear or die.

Key words: joint brood guarding, maternal care, mate guarding.

Introduction

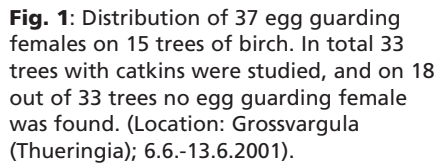
The term parental care describes strategies, in which parents provide postovipositional investment in the offspring. For example, in insects, females insert eggs into protective plant tissues or use chemical or behavioural means to minimise the loss of eggs to predators and parasites. Moreover, females do lay their eggs near the probate resource to provide food for their offspring.

Parental care evolved several times independently within insects and the same is true within the Heteroptera. In fact, Heteroptera do stand out, as numerous examples of parental care have been known for a long time (TALLAMY & WOOD 1986). *Elasmucha* spp. were particularly frequently

investigated (e.g., JORDAN 1958; MELBER & SCHMIDT 1975a, 1975b; MAPPES & KAITALA 1994; KAITALA & MAPPES 1997; MAPPES et al. 1995; KUDO 1990, 2000, 2002; KUDO & NAKAHIRA 1993).

Elasmucha grisea is a phytophagous species. If two generations occur during the year, the first generation invariably feed on birch (*Betula* spp.), the second on alder (*Alnus* spp.) (MELBER et al. 1981). About 40-50 eggs are oviposited as a single clutch on the upper surface of the host plant leaf (MELBER & SCHMIDT 1975a). Each ovary consists of 20-25 ovarioles (FISCHER 1994), with each ovariole only producing a single egg. This character state is considered apomorphic because telotrophic ovaries with seven ovarioles

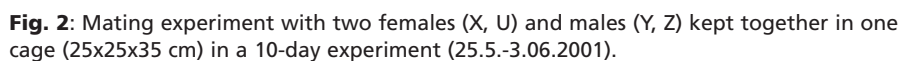
¹Diese Arbeit ist Herrn Ernst Heiss zum 70. Geburtstag gewidmet. Seine charmante und freundliche Art war und ist ein wichtiges Bindeglied für die verschiedenen Generationen der mitteleuropäischen Heteropterologen. Danke dafür!



The female guards her eggs and nymphs by a cascade of defensive behaviours: rapid body jerking, tilting the body toward the source of the disturbance, wing fanning, and finally spraying secretion from the metathoracic and abdominal scent glands toward the disturber (JORDAN 1958; MELBER & SCHMIDT 1975a, 1975b; FISCHER 1995). In most cases, the disturber will be successfully defeated (MELBER & SCHMIDT 1975b; MELBER et al. 1980). As experimental studies have shown the entire offspring is usually lost to predators such as bugs, beetles, earwigs and ants if there is no maternal protection (MELBER & SCHMIDT 1975a; MAPPEs & KAITALA 1994). MELBER & SCHMIDT (1975a) found 10-17% unguarded clutches.

With the second instar nymphs becoming larger, the female no longer is able to provide an effective shelter for all her nymphs. Furthermore, in early nymphal instar stages the synchrony of development can become lost. While some nymphs are still in the first instar stage, others have already hatched to second instar nymphs. When second instar nymphs start to move to new food resources, the female follows and attends the aggregation of her nymphs. Variation in nymphal developmental stages brings up a conflict to the female, whether she should remain with the younger nymphs on the brood leaf or should follow her moving nymphs.

MAPPES et al. (1995) reported a new aspect of brood guarding behaviour in *E. grisea*: two or more females oviposit their egg clutches and breed side by side on the same leaf. This is despite the fact, that suitable places for oviposition (birch leaves) are

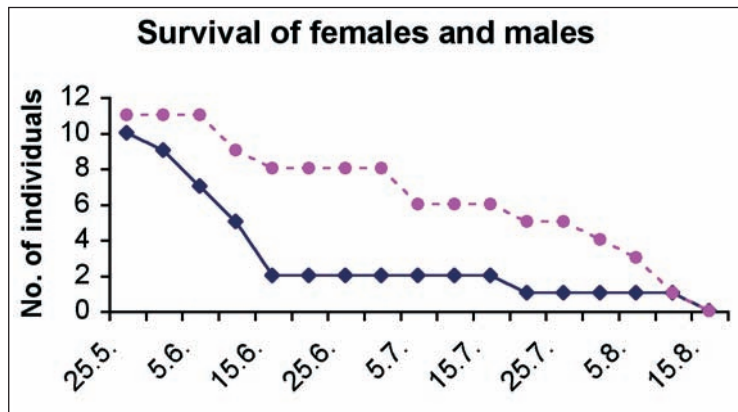


practically unlimited. According to MAPPES & KAITALA (1995) this phenomenon is named joint brood guarding. Remarkably, there seems to be no published information of the females' behaviour during their first contact and circumstances (e.g. time pattern of oviposition) on such shared brood leaves. MAPPES et al. (1995) showed that by joint brood guarding both females nearly double their success to defeat predators compared to single brood guarding females. Consequently, if such joint brood guarding is a successful strategy, one would expect it to be a common phenomenon in *E. grisea*. It is indeed widespread in Scandinavia (MAPPES & KAITALA 1995). However, the latter study only covered the egg-guarding period, and the question remains, whether females and their offspring interact after the hatching of nymphs in joint brood guarding situations.

Here we investigate, for the first time, the whole joint egg guarding until the female finally leaves the nymph aggregation. Our study revealed that in joint brood guarding females their nymphs benefit in terms of optimising their individual development by choosing a female's guarding behaviour according to their developmental status and physiological conditions. We assume that guarding of kin-mixed group of nymphs, has its prerequisites already present in the female's guarding behaviour.

Moreover, the frequency of joint brood guarding of *E. grisea* in central Europe was investigated, and, in contrast to Scandinavian population found to be a rare phenomenon. Factors that promote different proportions in joint brood guarding behaviour in European *E. grisea* populations are not studied yet. But one reason might be a difference in predation risk among European regions.

Additionally, we present and discuss new bionomic and behavioural data of *E. grisea* with regard to oviposition, host plant selection, hibernation, defence and mating behaviour.



Results

1. Distribution pattern of egg guarding females

In June 2001 on a margin of the forest (location: village Grossvargula/Thuringia) 33 birch trees with catkins were chosen to investigate the distribution pattern of egg guarding females. The branches of all trees were carefully checked for egg guarding females or egg clutches of *E. grisea* from ground level up to 2m height. In 15 out of 33 birch trees no females were found, the number of females per tree ranged from 0-5 (Fig. 1). The distribution pattern was analysed in a simple statistical test for Poisson distribution and aggregation (see DYTHAM 1999). The distribution is not significantly different from a Poisson distribution (one sample Kolmogorov-Smirnov-Test (2-tailed): $p=0.552$) and variance > mean ($2.01 > 1.12$), which indicates a clumped distribution. At a different location, near Weimar-Ettersberg (Thuringia), within an area of 2.5 m² 12 females were sitting on a few, mostly non-vital branches (see 3.). It was the maximum number of females found on one single tree in this study.

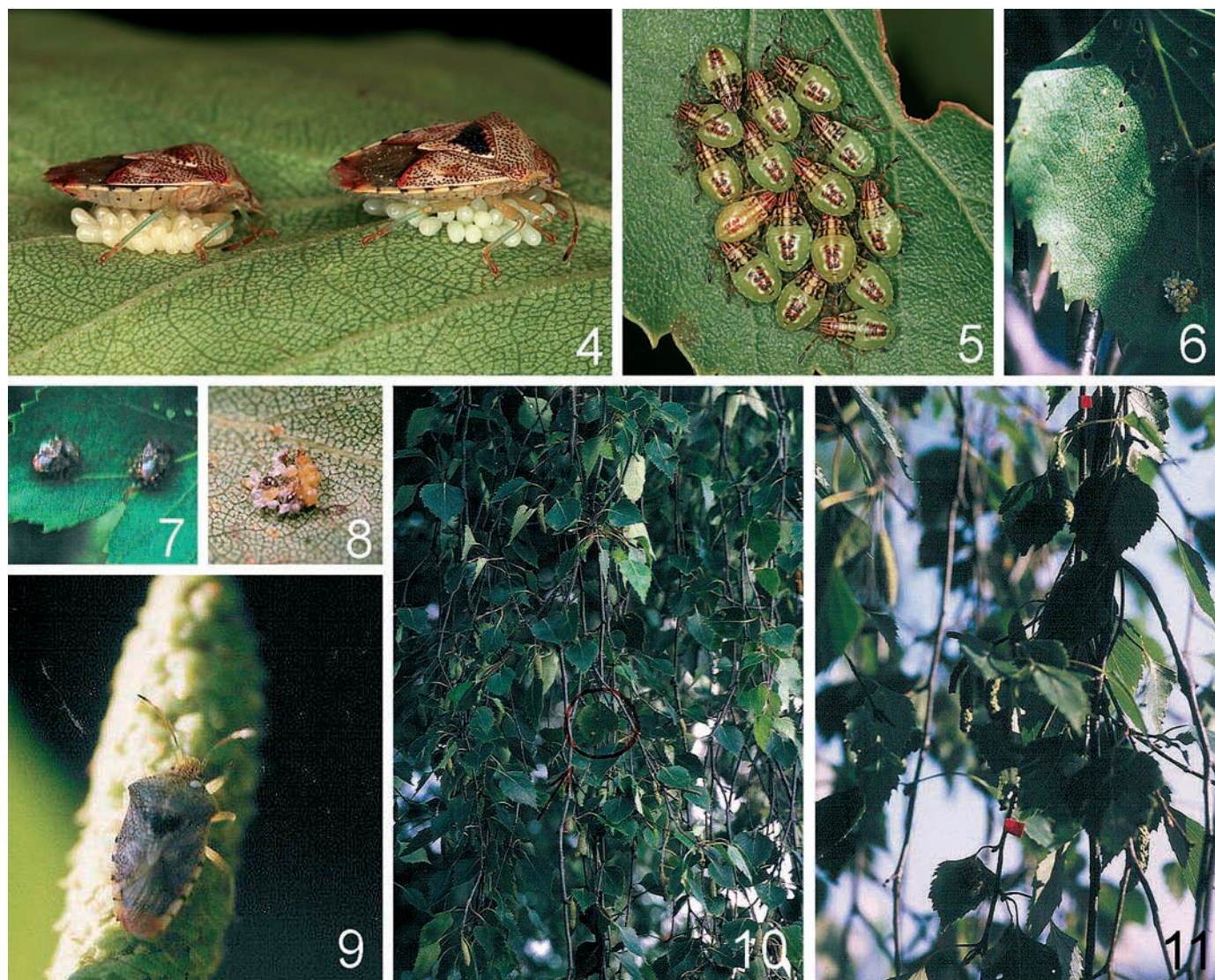
2. Unguarded egg batches

In this study, 17 egg batches were controlled in the beginning and the end of June with regard to guarding females. At the time of the second control three out of 17 egg batches (~17.5%) were unguarded. The reasons for the missing females are unknown but predation or parasitism are assumed.

3. Selection of oviposition site

We tested if host plant vitality affects the choice for oviposition. In a cage, females

Fig. 3: Number of surviving females (n = 11) and males (n = 10) of *Elasmucha grisea* in the laboratory in May-August 2001. Males = solid line, Females = dotted line.



Figs 4-11: (4) Joint guarding pair of *Elasmucha grisea* at Naturpark Schlaubetal (Brandenburg) (5) Group of third instar nymphs, note one nymph still being in the second instar stage (6) Leaf with female C and the remaining egg shell of her egg clutch (very close by to the female). Below the larger egg batch of female D, which has left the leaf with her nymphs (3.7.2001) (7) Joint guarding pair II with female C (right) and the parasitized female D (left) on the same leaf (1.7.2001) (8) Detail of the egg clutch of parasitized female D after hatching and leaving of the female (3.7.2001) (9) Parasitized female D. Note, the egg of a Tachnidae parasite on the pronotum of the bug (6.7.2001) (10) View of the branches of the birch tree with the leaf with joint breed females C and D in the centre (indicated by arrow) (3.7.2001). *Elasmucha grisea* oviposits frequently in dense and hanging branches (11) Position of female C (below red mark) and female E (above red mark) ca. 24 h after interaction (6.7.2001). Note, the low distances between females which easily allow contact and nymph interchange. Photos: 4-5 Jürgen Deckert, 6-11 Wolfgang Adaschkiewitz.

were given the choice of selecting either fresh and vital or old and dry birch branches. Few females (2 out of about 30) selected old, non-vital birch branches with dry leaves and old, dry catkins as oviposition sites. The mortality of the nymphs of such clutches was very high (>90 %). In the field (location Weimar-Ettersberg- see 1.), 12 females had also chosen old, non-vital birch branches as oviposition sites. Immediately (i.e. within 36 hours) after hatching, all females moved with their accompanying nymphs to upper parts of tree.

4. Second generation and host plant shift

In *E. grisea*, the first generation invariably feed on birch, the second on alder and nymphs did not survive a shift from catkins of one host plant to another (see MELBER et al. 1981). Therefore, it can be assumed that females of the second generation prefer alder for oviposition and maybe also as copulation sites. We tested the hypothesis whether reproduction behaviour is restricted to alder. At the end of August 2001, 30

Tab. 1: Diary of joint brood guarding females of group I. Behaviour of the two interacting females A and B. Interactions of different kinds are shown in *italic-bold*.

| Phase | Date | Hour | Female A | Nymphs of Female A | Female B | Nymphs of Female B |
|-------|---|-------------|---|--|---|--|
| I | 16.6.-25.6. | | guards her eggs/nymphs on brood leaf | stay on brood leaf | guards her eggs/nymphs on brood leaf | stay on brood leaf |
| II | 25.6. | 07.00 | left brood leaf with her nymphs | left brood leaf with female A | guards her eggs/nymphs on brood leaf | stay on brood leaf |
| III | 25.6. | 09.15-10.45 | stays within a distance of 20 cm to brood leaf | <i>return from feeding tour to brood leaf but move to and stay with female B</i> | stays on leaf, guards own nymphs <i>and nymphs of female A</i> | stay on brood leaf <i>(mixing (?) with nymphs of female A)</i> |
| IV | 25.6. | 10.45 | stays within a distance of 20 cm to brood leaf | all (?) nymphs leave brood leaf and walk to female A | stays on brood leaf | stay on brood leaf |
| V | 25.6. | 18.00 | returns to brood leaf with her nymphs | return to brood leaf with female A | stays on brood leaf | stay on brood leaf |
| VI | 25.6. | 20.00-22.00 | <i>left brood leaf and branch together with her own nymphs and some nymphs of female B</i> | all (?) nymphs left leaf and branch with mother, <i>mixing with some nymphs of female B</i> | stays on brood leaf | some nymphs stay on brood leaf, <i>other nymphs left leaf with female A</i> |
| VII | 26.6.-30.6. 26.6. 27.6. 28.6. 30.6. | | female A lost contact to nymphs female A disappears | nymphs split in small groups and spread over tree | left brood leaf with remaining nymphs last observation | left brood leaf with female B last observation |

adults of the second generation were collected on one alder tree by stick beating sampling. In cage experiments, 5-7 females and the same number of males were kept with a) alder catkins, b) birch catkins and c) birch catkins and the odour of alder catkins (i.e. alder were in separate part of the cage and not accessible for the bugs). In all three treatments, copulation and oviposition occurred (data were not analysed quantitatively). Moreover, in Thuringia a large temporal overlap of fresh catkins of both host plants occurred from June until September 2001. Therefore, even if a shifting of host plant may optimise the reproduction efficiency of the species, such shifting is not obligatory for reproduction.

5. Studies on the joint brood guarding behaviour of *E. grisea*

Frequently, egg-guarding females of *E. grisea* can be found in close neighbourhood to each other (see above). In these clusters, only a single egg-guarding female is present on one birch leaf. Here we address several aspects of joint brood guarding. A special focus is given to the interactions between guarding females and their nymphs. These

results are presented in a diary in order to show interactions of each female and their offspring (Tab. 1, 2).

5.1 Frequencies of joint brood guarding behaviour in central European *E. grisea* populations

In 2001, the occurrence of this phenomenon was investigated at three different locations in Germany. In the central part of Thuringia, a total of 89 egg guarding females were found in May and June. Joint brood guarding was only observed in two cases, i.e. a proportion of less than 5 %. Two other sites in Germany were briefly checked for egg guarding females and egg clutches. In Hannover (Lower Saxony) we found 7 brood guarding females, and in the Schorfheide (Brandenburg) another 18 females with egg clutches. Joint brood guarding did not occur in any of these additional 25 observations.²

5.2 Interactions of joint breeding females

In 2001, two groups of joint brood guarding females were investigated. Our observations cover the period from egg guarding to the disappearance of the females or

²After finishing the manuscript, we got knowledge of another two pairs of joint brood guarding *E. grisea* in Germany (Jürgen Deckert, pers. comm.). These pairs were found breeding on birch leaves at Naturpark Schlaubetal (4 km southwest of Eisenhüttenstadt, Brandenburg). Jürgen Deckert kindly provided fine photographs of these joint brood guarding females (Fig. 4).

Tab. 2: Diary of joint brood guarding females of group II. Number of guarded nymphs and behaviour of the three interacting females C, D, and, E at different observation phases. Note that female C and D perform joint brood guarding on the same leaf. The brood leaf of the female E was in a distance of 1 m to the leaf with female C and D. Females could be discriminated by colour pattern and parasitization of female D. Number of nymphs were estimated by countings both in the field and recountings by using photographs. Arrows indicate that nymphs have changed from one female to another female(s). (n.a. = data not available)

| Phase | Date | Hour | Female C Behaviour | No. of nymphs guarded | Female D Behaviour | No. of nymphs guarded | Female E Behaviour | No. of nymphs guarded |
|-------|---------------|-------------------------------|---|--------------------------|--|---------------------------------------|--|--------------------------|
| I | 26.6.-2.7. | | guards her nymphs ^a on brood leaf | > 30 | guards her nymphs on brood leaf | < 30 | n.a. | n.a. |
| II | 3.7. | 13.00 | guards her nymphs ^a on brood leaf | 8 all small in size | left brood leaf with nymphs ^b for 1 hour | ~ 42 most of them large in size | n.a. | n.a. |
| III | 3.7. | 20.00 | left brood leaf | 8 | guards walking and feeding nymphs | ~ 42 | n.a. | n.a. |
| IV | 4.7. | 8.00-20.25 | guards her walking and feeding nymphs | 8 | guards walking and feeding nymphs | ~ 42 | n.a. | n.a. |
| V | 4.7. | 20.30-20.45 20.30 20.45 | female lost contact to her larvae gets close to female D and attacking her gets close to female E and attacking her by darkness, female C stays on the same catkin as female E | 8 | no nymphs | ~ 42 | guards her walking and feeding nymphs attacking female C attacking C, by darkness stay C on the same catkin as female E | ~ 32 |
| VI | 5.7. | 18.00 | guards walking and feeding nymphs | 47 | sitting in same area as on 4.7. but no guarding | no nymphs | guards her walking and feeding nymphs | 35-40 (>32) |
| VII | 6.7. | | guards her walking and feeding nymphs some nymphs left female | 47 | sitting in same area as on 5.7. but no guarding female D disappeared last observation | no nymphs | guards her walking and feeding nymphs | 35-40 |
| | 7.7. 10.7. | | | | | | | last observation |

^a egg batch of female C with 8 empty egg shells and one egg was not developed; ^b egg batch of female D with 13 empty egg shells and 16 eggs was not developed; ^c the 8 nymphs of female C were found without any guarding female at time phases VI and VII

nymphs. In order to make the results of the two groups comparable, we categorise the period of observation as phases.

From mid to end of June group I with two females A and B breeding on the upper side of the same birch leaf were studied in Mönchenholzhausen (Thuringia) (Table 1). Remarkable, interactions of the two females and their offspring, were 1) that the nymphs of female A returned to female B on the brood leaf, whilst female A did not return (phase III), and 2) nymphs both female A and B established mixed groups and left brood leaf attended by female A (phase VI) (Table 1).

At Stausee Hohenfelden (Thuringia) three females oviposited in close neighbourhood to each other and were observed from end of June to mid of July (group II, Table 2). In fact, females C and D performed joint brood guarding and another female E oviposited her egg clutch in a distance of 1 m above this broodleaf. Female D had been parasitized by a tachinid fly before oviposition.

Observations of interactions are given in detail in Table 2, but the following aspects deserve some specific notes. We observed that females were attacking each other in a similar way as females attack predators (wing-fanning – see MELBER & SCHMIDT 1975b) (phase V, Table 2). During the next day a complete exchange of nymphs of all females occurred (phase V). We did not directly observe this process, but the take-over can be interfered from photographs. Female D had been parasitized before guarding the egg clutch, laid about 30 eggs, which is less than the average from 40-58 eggs per female in *E. grisea*. Female D had fewer and smaller nymphs than female C. Moreover, 16 eggs of the clutch of female D were not developed. This clearly indicates a reduced fitness of female D. Eventually; female D lost all of her nymphs to female C (see phase IV). Remarkably, some nymphs of female C joined female D, when female C left the brood leaf (see Tab. 2, phase II).

6. Mating behaviour

In this study, we focused on three aspects of the mating behaviour: copulation time, remating, and postcopulation guid-

ance. The copulation time is long and can last several days (Tab. 3). This can be interpreted as prolonged mating (mate guarding). The typical copulation position is tail-to-tail (Figs 12-14). If the copulation is interrupted the male sits on the back of the female with his antennae attached to the female pronotum. The time between the termination of the copulation and oviposition varies from 4-12 hours (Tab. 3).

Two pairs of *E. grisea* were kept together in cages (34 cm x 18 cm x 46 cm). Remating with several males occurred frequently (Fig. 2). In some cases, however, pairs remained in copula for several days, and females did oviposit without remating (female X – Fig. 2). In other cases, females remated with another male before oviposition (female U – Fig. 2). Although no choice experiments were carried out these observations suggest that premating mate choice is not very strong in *E. grisea*.

In *E. grisea*, both adult males and females hibernate. In spring or early summer females produce new egg-clutches. In theory, mating can occur before or after hibernation, or both.

As soon as the first individuals of *E. grisea* appeared in 2001, females were collected in order to study oviposition and egg fertility in the laboratory. From May 18-20, six females, three from Hannover and three from Thuringia, were kept separately in cages without males. In the field copulation was not observed before May 25. While three females died without any oviposition, three females laid eggs of which two had fertile eggs.

In early spring of 1993, five females of *E. grisea* were dissected to study the female genitalia (see FISCHER 1994). In all studied females, no sperm were found in the spermatheca. This may indicate that there was either no mating in autumn or sperm was reabsorbed during hibernation.

7. Survival of males and females

Males live shorter than females (Fig. 3). In late autumn of 2001, 38 individuals were collected. Their survival in a garden experiment (i.e. bugs were kept in cages with foliage and mosses outside during winter) was

Tab. 3: Duration of copulation, occurrence of interruptions and period between termination of copulation and oviposition of selected pairs of *Elasmucha grisea*, observed in the field and in cages (n.a. = data not available).

| Pair | Duration of copulation | Copulation discontinued | Period between termination of copulation and oviposition |
|------|------------------------|-------------------------|--|
| 1 | > 8,5 h | n.a. | n.a. |
| 2 | > 7,0 h | n.a. | n.a. |
| 3 | > 24,0 h | n.a. | n.a. |
| 4 | > 24,0 h | n.a. | n.a. |
| 5 | > 13,0 h | n.a. | n.a. |
| 6 | 6 days | yes | < 12,0 h |
| 7 | 6 days | yes | < 6,0 h |
| 8 | 4 days | yes | < 12,0 h |
| 9 | 24,0 h | n.a. | < 4,0 h |
| 10 | 4 days | no | < 6,0 h |
| 11 | 3 days | n.a. | n.a. |
| 12 | 2,0 h | n.a. | n.a. |

checked in the spring of the following year. No significant differences in mortality rate between the sexes can be detected as 8 out of 17 males (47 %) and 9 out of 21 females (42.8 %) survived hibernation ($\chi^2=0.067$, $df=1$, $p=0.796$). Because all nymphs of one clutch hatch within a few days regardless of their sex, our results reflect real survival pattern of males and females and are not biased due to sex specific hatching times.

8. Female guarding behaviour of first instar nymphs

The guarding behaviour applied to the first instar nymphs is similar to the one performed in egg-guarding (see Figs 15, 17). Some first instar nymphs move around on the brood leaf, but females are eager to push them back under her body. In Figures 20-23, a female is shown pushing a first instar nymph back using her antenna as guidance. Note that the tarsi keep attached to the same position on the leaf, while the female stretches to reach the nymph. The same attaching of tarsi can also be observed in defence behaviour, when only the body is moved toward the direction of the disturbance (unpubl. observations).

Discussion

Selection of the oviposition site

In most insects, the mating site (rendezvous site) also functions as oviposition site. In the first generation of *E. grisea*, mating, oviposition and maternal guarding of eggs and nymphs take place on birch trees.



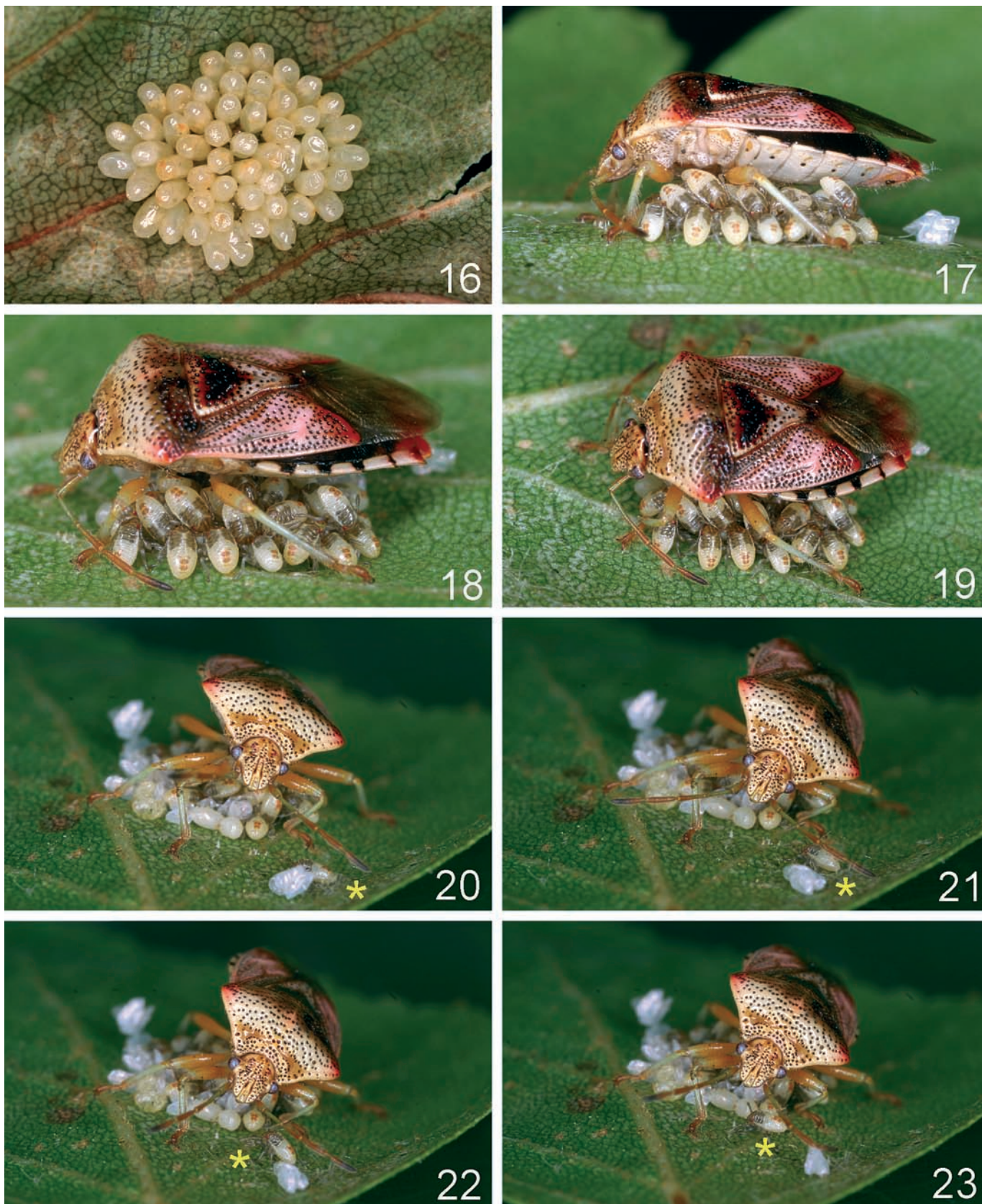
Figs 12-15: (12-14) A pair of *Elasmucha grisea* in tail-to-tail copulation position. While walking around on birch leaves and branches, male and female remain in copula up to 6 days. The bigger female is always leading with the male following. Here, the female is more vividly coloured, and the male appears duller overall. (15) Female guards her newly hatched first instar nymphs. First instar nymphs aggregate on empty eggshells. Female remains in the same guarding position while guarding her egg-clutch and first instar nymphs. Photos: Christian Fischer.

Males and females meet on birch and while in copula they walk around on leaves and branches until the female oviposits on a leaf. It has never been observed that pairs in copula change to a new tree. That means, we did not find any copulating pairs on the ground that would make a change to another birch tree likely. Flying to another tree while in tail-to-tail copula can be excluded. There is a short period between termination of copulation and oviposition. In the laboratory, females only move on the same branch. Usually, the male follows and attends the female. Therefore, we assume that the tree chosen as the mating site is also the one where oviposition eventually takes place and that the female chooses the oviposition site. Birch catkins provide the essential food resource for the offspring, which begin feeding on catkins as second instars nymphs. Evidently, birch trees play an important role in the reproductive biology of *E. grisea*, but do all aspects take place on the same tree? Our study reveals that egg-guarding females of *E. grisea* appear in clumps, i.e. some birch trees were preferred.

However, the factors of selecting a tree as oviposition site are not fully understood. As second instar nymphs feed on catkins, the female selects a tree that provides fresh catkins (JORDAN 1958; MELBER & SCHMIDT 1975b). In other studies it has been shown, that birch species (JORDAN 1958) affect host plant selection (MAPPES & KAITALA 1995).

In addition, several characteristics of the host plants, birches and alder, should influence the choice of a female *E. grisea* for oviposition: exposition and weather exposure of the plant, occurrence of catkins as food resource for nymphs, nutrient/physiological condition of the host plant, distance to the neighbouring host plant, intraguild competition, and predation risks. For example, in Thuringia egg clutches were found frequently exposed to sunny parts of a birch tree.

With regard to the host plant shift of the second generation (see MELBER et al. 1981), our results indicate that the parents of this generation mate and oviposit regardless of the occurrence of the host plant. Note, that our experiment was performed in late summer and the result is in agreement with



Figs 16-23: Female guarding behaviour of *Elasmucha grisea* (**16**) egg-clutch with 53 eggs (**17-19**) Different angles of view of a female guarding freshly hatched first instar nymphs. Note that the female remains in the same guarding position as the tarsi of all six legs remain in the same position. In case of disturbance, the female only tilts and shifts her body (**20-23**) A first instar nymph left the aggregation in front of the female. The female tilts her body, stretches with her left antenna to reach the nymph and pushes the nymph back to the aggregation (see yellow asterisk). Photos: Christian Fischer.

MELBER et al. (1981), who reported a higher attractiveness of alder not before September. We and others (MELBER & SCHMIDT 1975b) observed a surprising outcome that the females both in the field and in cage experiments deposited their egg-clutches on dry leaves, although fresh leaves and catkins were close by. In our study, the mortality of the first instar nymphs on dry leaves was very high (>90%), indicating that nymphs need fresh leaves for at least water supply (see also MELBER & SCHMIDT 1975b). These results give rise to future investigations, why females occasionally oviposit on a dry leaf.

Mating system of *E. grisea*

JORDAN (1958) mentioned acoustic signals of males and discussed their role in intersexual interactions but in general, the mating behaviour of *E. grisea* has not been studied in detail yet. This is in contrast to comprehensive knowledge about the morphology of the reproduction tract (e.g. FISCHER 1994). In theory, males can increase their reproductive success (fitness) if they copulate with numerous females. In most insect species females lay their eggs in batch and eggs mature continuously, consequently, fertile females should be available over a long period.

However, the conditions in *E. grisea* differ from these requirements. Most females of *E. grisea* only produce a single egg-clutch during their whole lifetime (KAITALA & MAPPEL 1997) regardless how many mates she has. Preliminary field observations suggest that all females of a population mate within a period of two weeks. Male mate guarding may ensure males to be the father all of the offspring of a female if they copulate with a virgin female. Therefore, males should 1) copulate as soon as females appear in spring or early summer, 2) try to mate with numerous females, 3) prevent remating of female, and 4) in addition, take part in the parental care both of egg clutch and nymphs. The latter two aspects could lead to male territoriality.

In fact, Kaitala (in litt.) found in about 20% of all egg guarding females a male very close by, and, assumed a kind of male territoriality. However, we found no evidence for male territoriality in our study. In the early

beginning of the season (May 10-12) all four males thus observed left their sites within 1-3 hours. In the later season, we observed that pairs in copula stay for several hours (20-24h) on the same leaf. After copulation was determined, both partners disappeared from the leaf. Few males tend to stay in areas with aggregated females, but no longer than 24-36 hours. Moreover, males supporting single or joint brood guarding females have never been observed. Observations both in the field and in the laboratory reveal that males mostly die before the nymphs hatch from the eggs.

As in some other heteropteran species (e.g. ANDERSON 1962) males have a shorter lifetime than females in *E. grisea* (Fig. 3). Most males of *E. grisea* live long enough to be able to join and to support the female in guarding the eggs, but only few males even live until hatching of the nymphs. However, males guarding eggs or nymphs have not been observed in this study. Again, very few males seem to survive until the second generation is mature. A simultaneous occurrence of females of the first and second generation may happen for several days in the field. At least in theory, a mating with a female of the first generation and a further one with a female of the second generation should be possible for some males.

In concurring with previous studies (e.g. JORDAN 1958; MELBER & SCHMIDT 1975a), we assume that mating in spring is the most frequent scenario in *E. grisea*, but might not be obligate. Before hibernation mating may occur and lead to oviposition of fertile eggs.

In our laboratory experiments we found both prolonged copulation time (from several hours up to 6 days) (see also JORDAN 1958) and rematings. Interruptions occurred frequently with following postcopulatory behaviour, i.e. male stays near the female and finally try to get in copula again. It is not known when sperm is transferred during such long copulation time. In the field, we did not observe females mating with another male but remating occurred frequently in laboratory. We assume that there is a high selection pressure on the males to perform mate guarding until the female deposited her eggs. In fact, males do remain close to the female after copulation and within 12 hours at

maximum, the female lays her eggs (Tab. 4). JORDAN (1958) mentioned that eggs have to mature 5-7 days before oviposition but he did not relate this period to copulation.

Frequency of joint brood guarding in European *E. grisea* populations

There are marked differences of joint brood guarding females among European populations. MAPPES et al. (1995) found frequencies of 20-30% of females in joint brood in most Northern parts of Europe (latitude >60°) but not in more southern study sites in Finland. In our study of 2001, we found joint brood guarding of *E. grisea* only in one of three investigated locations in Germany, and then, less than 5% of the found brood guarding females. There is more evidence that this phenomenon occurs to be rare in central European populations. In several years of study on *E. grisea* no joint guarding females were found, neither in Lower Franconia (Bavaria), in Hannover (Lower Saxony) (Melber, pers. comm.) or Austria (Rabitsch, pers. comm.). JORDAN (1958) published his detailed observations on *E. grisea* after a five-year period of study without mentioning joint brood guarding. Apart from MAPPES et al. (1995) only a few reports of joint brood guarding females in the literature are known. MELBER et al. (1980, p. 36-37) report on a field observation that two egg-clutches of *E. grisea* were found on the same leaf, but the single present female only guarded her own clutch. In 2000, Fischer (unpubl. observation) found several joint brood guarding females of *E. grisea* in the Schorffheide (near Berlin, Germany). Even three females were breeding on the same leaf. The same tree was checked again in 2001, but no females of *E. grisea* with egg-clutches or nymphs were found.

Different proportions in joint brood guarding behaviour in European *E. grisea* populations may be related to different predation risks among European regions. MELBER & SCHMIDT (1975b) found that the defence behaviour of single guarding females is very effective and assumed that almost 100% of the eggs can be defended against entomophagous arthropods. In contrast, single guarding females lost about 60-70% of their eggs due to predation in Finland (MAPPES et al. 1995). The reason for this

difference is unknown. However, defence may be difficult against the most common predators in Scandinavia, ants, (MAPPES & KAITALA 1995). In Germany, the most important egg predators are *Kleidocerys resedae* (Lygaeidae, Heteroptera), next being Cantharidae and Coccinellidae species (Coleoptera), whereas ants are less frequent predators (MELBER et al. 1980). *Elasmucha grisea* is able to defend successfully their eggs against *Kleidocerys resedae*, even with high densities of this predator species (MELBER et al. 1980, pers. observations).

To our knowledge, joint brood guarding of non-European *Elasmucha* species has not been particularly mentioned but as it obvious from a photograph in KUDO et al. (1989, Fig. 1a), two females of *E. dorsalis* are breeding on the same leaf.

Joint brood guarding females attending mixed groups of nymphs („kindergarten“)

MAPPES & KAITALA (1995) first studied joint brood guarding behaviour in Scandinavian populations of *E. grisea*. However, this study only covers the egg-guarding period. For the first time, our study investigates the whole guarding period from egg guarding until the female finally leaves the nymph aggregation.

After deposition of egg on the brood leaf the female sits on the clutch, shielding and defending the eggs with her body, whereby the female neither moves nor feeds while egg guarding (JORDAN 1958; MELBER & SCHMIDT 1975b; MELBER et al. 1980). The first instar nymphs aggregate on the eggshells and are protected by the female in the very same position as she guarded the eggs.

In *E. grisea*, second instar nymphs initiate to the move to new feeding sites. This aggregation of nymphs is followed by her mother, which attends and defends them against disturbers, usually sitting near the base of a branch. After feeding, the nymphs return to the brood leaf. Single breeding females usually join the nymphs on their way back to the brood leaf. The behaviour of both investigated pairs of joint brood guarding females revealed a striking similarity. Whenever one female left, the other female

remained on the brood leaf. Smaller and younger nymphs stayed with one female on the brood leaf, while older nymphs move to new sites on the tree with the other one. It is obvious from our studies that nymphs of joint guarding females form mixed groups. Mixing of nymphs from different females occurred frequently, and even a total exchange of nymphs happened during our investigations. Even single guarding females of *E. grisea* frequently loose their nymphs, or will exchange some or all of her nymphs with another female during walking around. This is consistent with results of previous studies that *Elasmucha* spp. females do not discriminate between their own offspring and that of other conspecific females (MELBER & SCHMIDT 1975b). Females of *E. grisea* cannot recognise their own egg-clutch, and even defend egg-clutches of *Elasmucha fieberi*, where females had been experimentally removed before (MELBER & SCHMIDT 1975b). The lack of kin-recognition is also reported from the Japanese *Elasmucha dorsalis* (KUDO et al. 1989).

The guarding of mixed aggregations of nymphs from different females is one of the most interesting results of this study and gives rise to further investigations. Obviously, a female performs guarding behaviour without respect to nymphs being hers or not. A variety of phenomena of subsocial offspring care are reviewed for Heteroptera in MELBER & SCHMIDT (1984), in TALLAMY & SCHAEFER (1997), and in LOEB & BELL (2006). However, providing maternal care for offsprings from other females („kindergarten“) has been published mainly for vertebrates (CLUTTON-BROCK 1991).

Benefits of joint brood guarding behaviour

At first sight, the lack of kin-recognition in *E. grisea* is surprising. One would expect that a female could increase her fitness if she restricts her maternal care behaviour exclusively to her own offspring. There is no benefit for a female being able to recognise her own offspring, as she continuously keeps the closest contact to her eggs and first instar nymphs as possible. Therefore, there has been no selective pressure on kin-recognition during this period of guarding behaviour.

There is a dramatic change when second instar nymphs begin to move and feed at new sites of the host tree. Depending on nymphal instars females show a special guarding posture (KUDO 2000), but do not rule movement, aggregation and foraging behaviour of nymphs (MELBER & SCHMIDT 1975b). Keeping a close contact to her moving nymphs, the female ensures that she guards and defends her own offspring. The defence behaviour of females is triggered by visual and tactile stimuli, or alarm pheromones released by injured nymphs (MELBER & SCHMIDT 1975b; MASCHWITZ & GUTMANN 1979).

If the mother dies or loses contact to her nymphs, nymphs will join other females and receive maternal care from another female. This kind of interactions seems to be a general pattern in *E. grisea* and is definitely not restricted to joint breeding females. It has to be kept in mind, that the distribution of females and their clutches within a tree and among trees are significantly clumped. Consequently, nymphs will meet other females frequently, and changes of nymphs to other females are very likely. MELBER & SCHMIDT (1975b) reported that females are not able to distinguish between own nymphs and those of other females. However, it is not known whether nymphs are able to recognise each other or their mother.

If females breed in close neighbourhood to each other, mixing of nymphs occurs more often. Breeding on the same leaf is the closest neighbourhood. Therefore, the maternal care behaviour of joint brood guarding females is of special interest. The benefits for nymphs of joint brood guarding females are obvious from our results. In case of joint guarding females, nymphs stay or leave according to their developmental conditions and therefore a nymph can optimise its individual development independent from the developmental conditions of its brothers and sisters (siblings). Eggs laid at the periphery are facing a higher predation risk. Therefore, females allocate their investment and eggs laid on the edge of the cluster are smaller (KUDO 2001). Since, egg size is correlated with physiological and developmental traits (MAPPES et al. 1996 and references in KUDO 2001), ontogenetic differences among nymphs of one clutch should occur

regularly. Competition among nymphs and/or varying food quality near the brood leaf may have an effect on different development among offspring. A female having first and second instar nymphs at the same time faces a trade-off between defend nymphs on the brood leaf or guard walking nymphs („should I stay or should I go“). Recent studies in Heteroptera revealed the role of chemical signals (e.g. solicitation pheromones) in such parent-offspring conflicts (KÖLLIKER et al. 2006), and we believe that chemical communication between mother and nymphs in *Elasmucha* species deserves more attention in further studies.

In case of disappearing or dead mothers, all nymphs will benefit in those flexible female-nymph interactions. It has to be considered that the mortality rate of females might be high because of high rates of up to 40 % of the adults being parasitized (MELBER et al. 1980) and death of such females with nymphs might occur frequently. Flexible female-nymph interactions may be an advantage to maintain the guarding care of females to nymphs under a high mortality pressure of parasitism.

To summarize, we assume that low distances between egg guarding females has three advantages for females and their offspring: 1) success of defending offspring against some predators is increased (e.g. ants) 2) it optimizes the guarding behaviour with respect to the different nymphs development and 3) especially in case of a parasitized mother, her offspring can be guarded by other females. The latter can be considered as a kind of brood parasitism, whereby the former may be considered as kin-selection or reciprocal altruism.

MAPPES et al. (1995) discuss the costs and risks of joint brood guarding. In theory, joint brood guarding is a trade-off. While joint brood guarding is advantageous with regard to defend predators, it also increases the competition on food resources among the nymphs. Moreover, predators and parasitoids can detect two joint breeding females more easily. Here we briefly discuss some evolutionary aspects of the guarding behaviour of *E. grisea*. Kin-selection can be a driving force for the evolution of joint brood guarding if 1) joining guarding females are

close relatives (see LOEB et al. 2000) or 2) nymphs are relatives because both females have mated with the same male. The first case has not been tested yet and can therefore not be ruled out. We performed a simple experiment in which two females were mated to the same male. This experiment was repeated three times with different individuals. In all experiments, the females did not join each other and laid eggs on a separate leaf (unpubl. data). The role of kin-selection clearly requires and deserves further study about the relationship among females and offspring in joint brood situations. Is there any evidence for brood parasitism in joint brood guarding in *E. grisea*? Brood parasitism will be the case if one female dumps her eggs close to another female, which will guard the other female's eggs as well. On the same leaf, a guarded egg-clutch and an unguarded egg-clutch should be found. However, there is only a single (published) observation reported (MELBER et al. 1980) of one female with two egg clutches at one leaf but circumstances were not observed and predation of the second female is not unlikely (see for unguarded clutches in MELBER & SCHMIDT 1975a).

As females of *E. grisea* not only guard their egg-clutch but their nymphs too, another case of brood parasitism might occur. One of the joint brood guarding females can leave her clutch after the nymphs hatched and her nymphs will then crawl under the other guarding female. Our observations showed that at least some nymphs might crawl under the other guarding female. According conclusions can be drawn from pictures published in SEDLAG (1979, p.77) and FISCHER (1994, Fig. 7). However, there is no evidence so far, that females produce a second egg clutch after dumping her first clutch to another female. In *E. grisea*, we assume that selection aims towards producing a single egg-clutch and optimizing clutch size in within a female's lifetime (MAPPES & KAITALA 1994; KAITALA & MAPPES 1997).

The presence and density of specific predator species may have an effect on the occurrence of joint brood guarding. In regions without high predatory pressure, single females can defend their eggs successfully by themselves and no joint breeding behaviour will be performed.

One can speculate if a high selection pressure to perform joint defence behaviour against predators as found in Northern Europe will lead from a clumped, close range breeding to joint brood guarding. In that case joint brood guarding could be considered as a very special case of the clumped distribution pattern of breeding females and their interactions after hatching.

Our study adds a new aspect and view to the joint brood guarding behaviour of *E. grisea*. Nymphs benefit in terms of optimising their individual development by choosing a female's guarding behaviour according to their developmental status and physiological conditions. Females of *E. grisea* are not able to discriminate her offspring from conspecific, or intraspecific egg batches or nymphs, nor even dummies (MELBER & SCHMIDT 1975b). We assume that this aspect, already present in the female's behaviour of *E. grisea*, is a prerequisite for maintaining a „kindergarten“, i.e. a female guarding a mixed group of nymphs.

Acknowledgements

We like to thank Arja Kaitala (University of Oulu, Finland) for stimulating ideas and discussions. The study was funded by the Academy of Finland, project no. 42 587 to SR. We are grateful to Albrecht Manegold (Naturmuseum Senckenberg, Frankfurt, Germany), Wolfgang Rabitsch (Wien) and Klaus Reinhardt (University of Sheffield) for comments on an early draft of the manuscript. Albert Melber (Tierärztliche Hochschule Hannover) provided helpful information about his field and behavioural studies in *E. grisea*. Jürgen Deckert (Museum für Naturkunde Berlin) kindly provided photographs of joint guarding females.

Zusammenfassung

Weibchen von *Elasmucha grisea* bewachen und schützen sowohl ihr Gelege als auch die ersten Nymphenstadien. In mehreren Populationen in Deutschland haben wir dieses Verhalten untersucht. Während in skandinavischen Populationen der Anteil gemeinsam auf einem Blatt Brutfürsorge betreibender Weibchen sehr groß ist, ist dieser in Deutschland mit 5 % (n=114) geringer.

Zum ersten Mal werden Interaktionen zwischen Weibchen, die „joint guarding“ betreiben, und auch deren Nymphen beschrieben. Beobachtungen im Freiland und im Labor ergänzen bisherige Untersuchungen zum Verbreitungsmuster Brutfürsorge betreibender Weibchen, zur Auswahl des Eiablageplatzes, zum Wirtspflanzenwechsel, zum Fortpflanzungsverhalten und zur Überlebensrate von Männchen und Weibchen. Wir haben Hinweise gefunden, dass die synchrone Entwicklung in den frühen Nymphenstadien verloren gehen kann. Während einige Nymphen sich noch im ersten Stadium befinden, haben sich andere bereits zum zweiten Stadium gehäutet und verlassen das Blatt, auf dem sich das Gelege befindet. Das Weibchen ist dann nicht länger in der Lage allen Nymphen einen effektiven Schutz zu bieten. Nymphen verschiedener Weibchen nehmen Kontakt zu einander auf und aggregieren. In diesen Fällen schützen sowohl „joint guarding“ als auch „non-joint guarding“ Weibchen ebenso Nachkommen anderer Weibchen. Bisher wurde das „joint guarding“ Verhalten nur unter dem Gesichtspunkt eines Schutzes vor Räubern untersucht. Wir nehmen allerdings an, dass Weibchen, die eine gemischte Gruppe von Nymphen bewachen, eine Art „Kindergarten“ betreiben. Insbesondere Nachkommen, deren Mütter sterben oder sich vom Gelege oder ihren Nymphen entfernen, profitieren von diesem Verhalten.

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Zeitschrift/Journal: [Denisia](#)

Jahr/Year: 2006

Band/Volume: [0019](#)

Autor(en)/Author(s): Roth Steffen, Adaschkiewitz Wolfgang, Fischer Christian

Artikel/Article: [Notes on the bionomics of Elasmucha grisea \(LINNAEUS 1758\) \(Heteroptera, Acanthosomatidae\) with special regard to joint brood guarding 1153-1167](#)