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Behaviour of the central European Acanthosomatidae (Hemiptera: Heteroptera: Pentatomoidea) during oviposition and parental care

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HANELOVÁ J. & VILÍMOVÁ J. 2013: Behaviour of the central European Acanthosomatidae (Hemiptera: Heteroptera: Pentatomoidea) during oviposition and parental care. In: KMENT P., MALENOVSKÝ I. & KOLIBÁČ J. (eds.): Studies in Hemiptera in honour of Pavel Lauterer and Jaroslav L. Stehlík. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **98(2):** 433–457. – Six central European Acanthosomatidae: Acanthosomatinae species were studied with particular reference to the behaviour of females during and after oviposition. *Acanthosoma haemorrhoidale* (Linnaeus, 1758), *Cyphostethus tristriatus* (Fabricius, 1758), and *Elasmostethus interstinctus* (Linnaeus, 1758) females do not exhibit maternal care. Eggs are deposited in many small batches as a strategic adaptation against predators and parasitoids. In contrast, *Elasmucha ferrugata* (Fabricius, 1787), *Elasmucha fieberi* Jakovlev, 1864, and *Elasmucha grisea* (Linnaeus, 1758) do exhibit maternal care. The defensive behaviour of the *Elasmucha* species is almost identical. Reactions to a potential aggressor graduate from fine to strong intensity. If the female leaves her eggs while feeding, she cannot distinguish her own eggs upon return, only the eggs of her own species.

Keywords. Pentatomomorpha, Acanthosomatidae, true bugs, *Acanthosoma haemorrhoidale, Cyphostethus tristriatus*, *Elasmostethus interstinctus*, *Elasmucha ferrugata*, *Elasmucha fieberi*, *Elasmucha grisea*, behaviour, maternal care

Introduction

Parental care of offspring is a subsocial behaviour occurring quite often within the Arthropoda, including Hexapoda. Members of 13 insect orders tend and defend their immature stages, including eggs (TALLAMY & WOOD 1986, TALLAMY 2001). Heteroptera have been the focus of numerous studies, because some of them show maternal care, also – if rarely – paternal care (e.g. SMITH 1997, Belostomatidae summary; TALLAMY & SCHAEFER 1997). Parental care is distributed across several recent heteropteran taxa. In addition to Belostomatidae, paternal care has been mentioned in Coreidae and Gerridae (e.g. KAITALA *et al.* 2001, TALLAMY 2001), and maternal care is known in a total of 15 families (HANELOVÁ 2005). The generally accepted hypothesis is that parental care is an advanced mode of behaviour. However, TALLAMY & SCHAEFER (1997) have suggested quite the opposite: that the care may be a surviving ancestral pattern of reproductive behaviour.

Parental care provides effective protection of the offspring against the predators, parasites, and parasitoids that regularly increase mortality in the species. Important comprehensive studies of parental care in the Heteroptera include, for example, COBBEN (1968), RIDLEY (1978), TALLAMY & WOOD (1986), TALLAMY & SCHAEFER (1997), and TALLAMY (2000, 2001). TALLAMY & WOOD (1986) distinguished three basic patterns of care behaviour: (i) physical protection of egg batches and young larvae by an adult (many studies); (ii) protection of food resources or providing food for larvae in Cydnidae and Parastrachiidae (e.g. SITES & MCPHERSON 1982, FILIPPI *et al.* 2000, NOMAKUCHI *et al.* 1998); (iii) female feeding the larvae in Phloeidae (e.g. BEQUAERT 1935, TSUKAMOTO & TOJO 1992, GUILBERT 2003).

Maternal care occurs within the heteropteran superfamily Pentatomoidea, particularly in members of the families Acanthosomatidae (see below), Cydnidae (e.g. KIGHT 1996, FILIPPI-TSUKAMOTO *et al.* 1995), and Tessaratomidae (e.g., GOGALA *et al.* 1998, MONTEITH 2006).

This subsocial pattern of behaviour in the Acanthosomatidae has been known for 250 years or more, first recorded in the 18th century. It was first studied in detail in a few European species, and later in Japanese ones (TALLAMY 1999). Maternal care is known in eleven species from four acanthosomatid genera, *Anaxandra* Stål, 1876, *Elasmucha* Stål, 1864, *Sastragala* Amyot & Serville, 1843, and *Sinopla* Signoret, 1863 (Table 1). Most species with parental care (seven) are of the genus *Elasmucha*. All three central European *Elasmucha* species (*E. ferrugata* (Fabricius, 1787), *E. fieberi* Jakovlev, 1864, and *E. grisea* (Linnaeus, 1758)) exhibit parental care. The first published note on parental care in Acanthosomatidae was an observation on *E. grisea* (MODEER 1764, after TALLAMY 1999), also the most studied acanthosomatid species in recent years (e.g. MELBER *et al.* 1980, KAITALA & MAPPES 1997; Table 1). In contrast, *E. fieberi* and *E. ferrugata* have been studied far less (e.g. KAITALA & MAPPES 1997). No detailed recent data, except a study by FISCHER (2006), mention possible care in other central European acanthosomatids.

The behaviour of an *Elasmucha grisea* female while she cared for her brood was studied in detail, including experiments designed to elicit defence reactions (MELBER & SCHMIDT 1975a, MAPPES & KAITALA 1994). MELBER & SCHMIDT (1975a) and later MELBER *et al.* (1980) classified defence behaviour into five stages. More studies have been dedicated to defence behaviour in *Elasmucha dorsalis* (Jakovlev, 1876) and *Elasmucha signoreti* Scott, 1874 (e.g. KUDO *et al.* 1989, KUDO & NAKAHIRA 1993).

A detailed account of the behaviour of the female *E. ferrugata* in the course of parental care is the central aim of this paper. However, other central European Acanthosomatidae were also observed in terms of care for offspring including eggs.

Material and methods

Material. All the Acanthosomatidae material for this study was collected in central Bohemia, in the wider surroundings of Vlašim (map grid 6255, after PRUNER & MÍKA 1996) (see HANEL & HANELOVÁ 2007). Two species, *Elasmucha ferrugata* (Fabricius, 1787) and *Elasmucha grisea* (Linnaeus, 1758), were observed in detail and used in experiments. Four species, *Acanthosoma haemorrhoidale* (Linnaeus, 1758), *Cyphostethus tristriatus* (Fabricius, 1758), *Elasmostethus interstinctus* (Linnaeus, 1758) and *Elasmucha fieberi* Jakovlev, 1864, were studied only partially, for oviposition mode and parental care (Table 2). The numbers of specimens of particular Acanthosomatidae species are summarized in Table 2.

Breeding. Acanthosomatids were bred in small plastic containers or in larger cylindrical containers made of gauze, both covered with very fine netting (Figs 1, 2). The host plants (Table 3) were placed in glass containers with water. The containers were kept in normal room conditions (approximate temperature 18o–30oC).

Observations and experiments. Records of the experiments were kept with a Nikon D 70 camera, and the plates were prepared with the aid of Adobe PhotoShop software.

Direct observation of the behaviour of the bugs, either in their breeding containers or natural conditions, was carried out several times a day, on average five. Experiments were performed in subject bugs in breeding containers as well as in natural conditions. A range of animals and equipment was used to elicit defensive reactions: Chelicerata: Acarina: *Ixodes* sp. (Ixodidae), body length 2 mm; Hexapoda: Coleoptera: *Chrysomela populi* Linnaeus, 1758 (Chrysomelidae), body length 10 mm; *Phyllopertha horticola* (Linnaeus, 1758) (Scarabaeidae), body length 10 mm; *Rhagonycha fulva* (Scopoli, 1763) (Cantharidae), body length 9 mm; Hymenoptera: *Formica polyctena* Förster, 1850 (Formicidae), body length 7 mm; Diptera: Asilidae gen. sp., body length 17 mm; other stages of the same *Elasmucha* species, body length 7 mm; other *Elasmucha* species, body length 7 mm; tips of soft tweezers; and a magnifying glass 13 cm in diameter. The arthropod species represented possible natural enemies that *Elasmucha* species might encounter in nature. MELBER *et al.* (1980) used similar insect taxa in their experiments with *E. grisea*.

The experiment of intensity of care involved eleven females of *E. ferrugata* and their hatched eggs; they took care of eggs and also of young larvae. Within a period of 120 minutes every day, the female was intruded upon from the side with soft tweezers (15 cm long, 2 mm wide at the tip) every five minutes (Fig. 3). The females reacted in repeatedly recognisable fashion. There was a body shift that turned the female to face the threat every time. After reaction and retraction of threat, the female returned to her default position, i.e. parallel to the surface of the leaf with the egg batch.

Slight intensity reactions

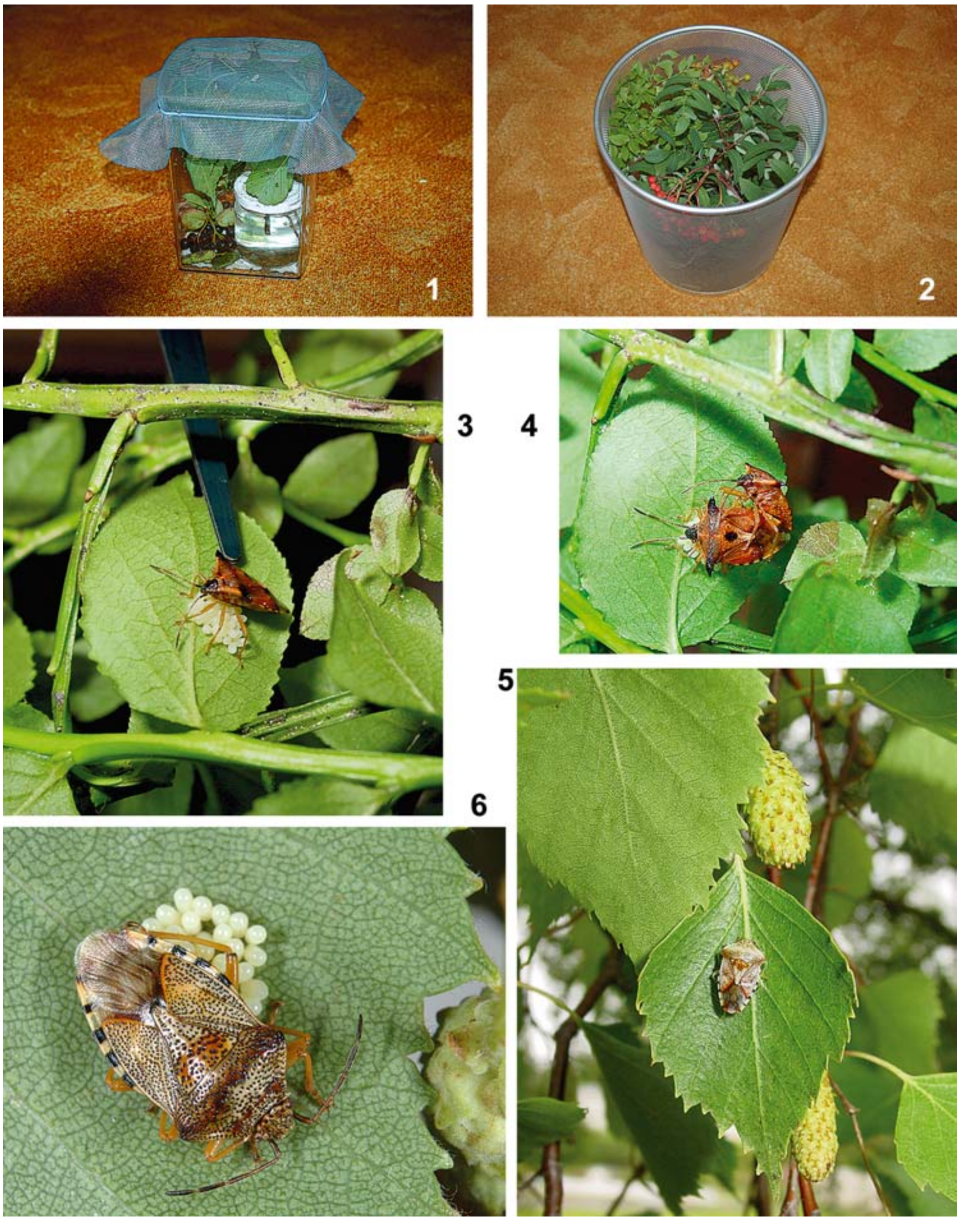
- Movements of the antennae – quick changes of antennal position, such as straightening, lifting, and jerking.

Medium intensity reactions

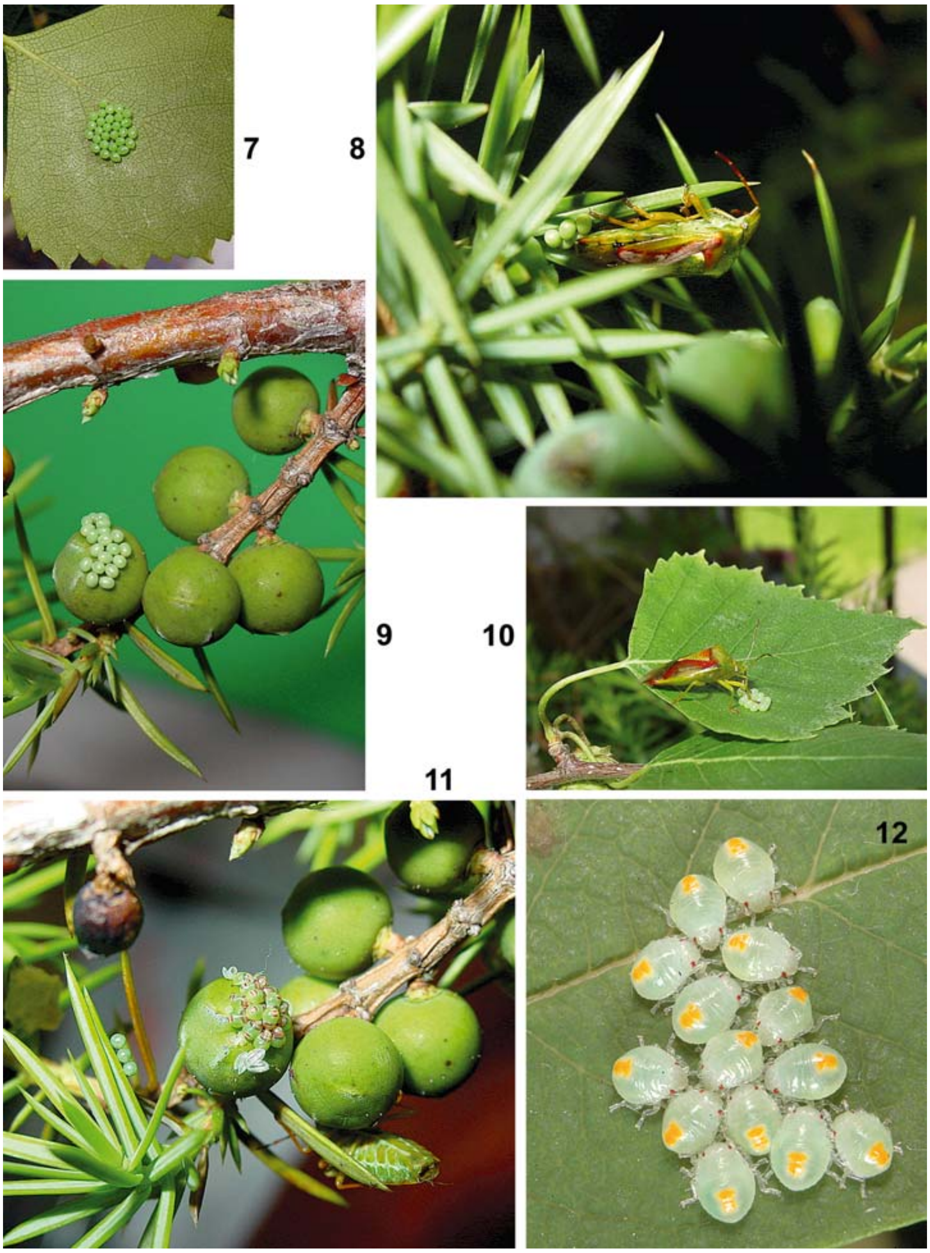
- Covering the egg batch with the female's body, partially or completely.
- Body tilting, facing the threat.

Strong intensity reactions

- Body jerking – quick side-to-side movements of the body (= short changes of horizontal position of entire body).
- Body swinging – slower changes of body position from left to right and back again.
- Wing-fanning – short, quick, spinning movements of the partly-outspread wings, both pairs.



Figs 1–6. 1 – small breeding container; 2 – large breeding container; 3 – *Elasmucha ferrugata* (Fabricius, 1787) female intruded upon with soft tweezers; 4 – *Elasmucha ferrugata* male attempting to copulate with female over an egg batch; 5 – *Elasmucha grisea* (Linnaeus, 1758) female with clutch on the dorsal surface of a birch leaf; 6 – *Elasmucha fieberi* Jakovlev, 1864 female with clutch on a birch leaf.



Figs 7–12. 7 – egg batch of *Elasmostethus interstinctus* (Linnaeus, 1758); 8 – ovipositing female of *Cyphostethus tristriatus* (Fabricius, 1758); 9 – egg batch of *Cyphostethus tristriatus* on *Juniperus communis* L. berry; 10 – *Elasmostethus interstinctus* sucking on conspecific eggs; 11 – larvae of *Cyphostethus tristriatus* aggregated on *Juniperus communis* berry; 12 – first instar larvae of *Acanthosoma haemorrhoidale* (Linnaeus, 1758) on a rowan leaf.

Results

If no information is available for a given species, it is not mentioned. The numbers of specimens used in the experiments are listed in Table 2.

Copulation

Acanthosoma haemorrhoidale, Cyphostethus tristriatus, *Elasmostethus interstinctus*, *Elasmucha ferrugata*, and *E. grisea*: Pairs of all species in copula assumed a tandem position. In two pairs of *E. ferrugata*, the male tried to copulate with a female over an egg batch. The male was on the female's back, adequate for the first stage of copulation, but the pairing was not successfully completed (Fig. 4).

Oviposition and size of egg batch (Table 4)

Females lay their eggs only after feeding on host plants with fruit, during the night in *E. ferrugata* and *E. grisea* but during the day in *Acanthosoma haemorrhoidale* and *Cyphostethus tristriatus.*

Females of *Elasmucha ferrugata* (n = 25) laid 33–39 eggs, without exception on the ventral surface of host plant leaves, in containers as well as in natural conditions. Females of *Elasmucha grisea* (n = 20) laid 35–45 eggs on either surface of leaves; of 70 batches, 30 were on a dorsal surface, 40 on a ventral surface (Fig. 5). A female of *Elasmucha fieberi* laid 34 whitish eggs (Fig. 6). The eggs of all *Elasmucha* species are whitish. Females of *Elasmostethus interstinctus* laid smaller egg batches, 4–30 (Fig. 7), on either surface of the host plant leaves. The eggs are green. *Cyphostethus tristriatus* deposited similarly small egg batches, with 3–20 eggs in each eggs in each batch (Figs 8–9), on needles and berries of the host plant. One female of *C. tristriatus* did not deposit an egg batch all at once, but did so by stages. The eggs are pale green.

Females of *E. ferrugata* can deposit a second egg batch (32 % = 16 observed specimens) and eventually a third batch (8 % = 4 specimens), particularly when the first egg batch or larvae have been destroyed. This species occurred and oviposited first on bilberry (*Vaccinium myrtillus*), often moving on to fly honeysuckle (*Lonicera xylosteum*), where it (potentially) deposited a second egg batch. Four females in breeding containers continued their care even after all the larvae of the first instar had died. They stood over them for 4–6 days; this behaviour was not observed in *E. grisea*.

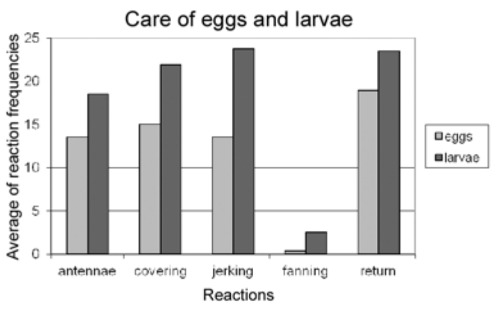
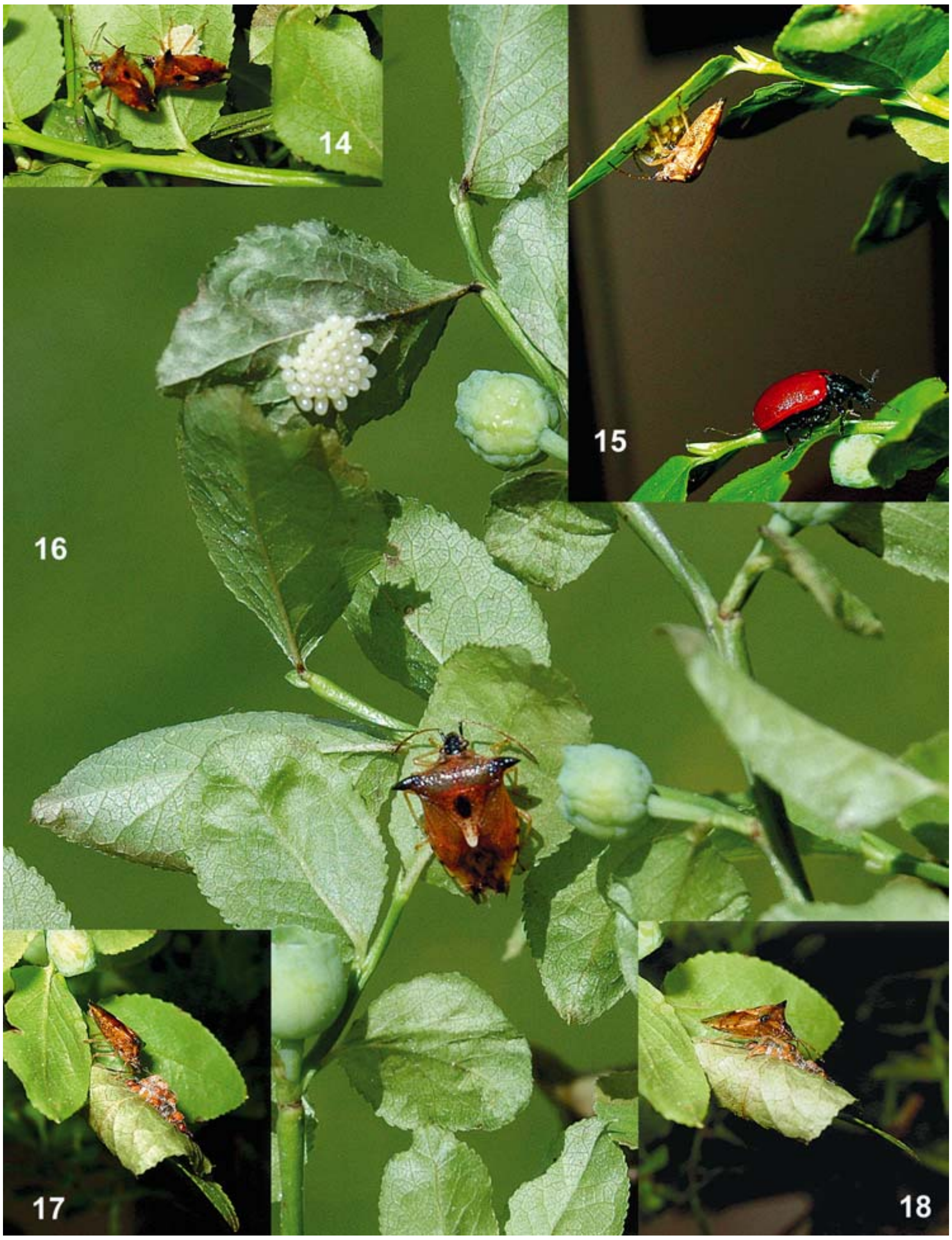
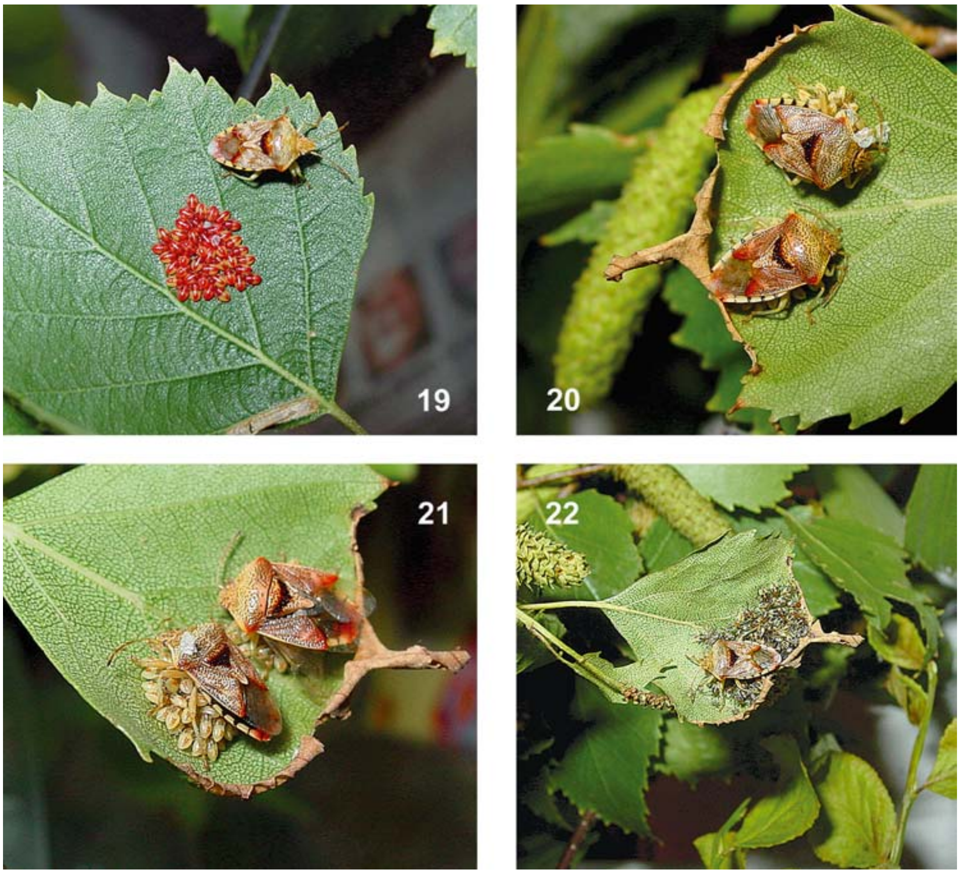


Fig. 13. Intensity of defence of eggs and larvae in *Elasmucha ferrugata* (Fabricius, 1787) females.

Elasmostethus interstinctus and *Cyphostethus tristriatus* deposited larger numbers of egg batches, for which they showed no inclination to care at all: the females simply left the egg batch immediately after oviposition. Cannibalism, feeding on



Figs 14–18. 14 – *Elasmucha ferrugata* (Fabricius, 1787) female responds to the presence of a conspecific male; 15 – *E. ferrugata* female responds to the presence of *Chrysomela populi* (Linnaeus, 1758); 16 – *E. ferrugata* female feeding on the host plant, away from eggs; 17–18 – *E. ferrugata* female adopting conspecific first-instar larvae.



Figs 19–22. Female of *Elasmucha grisea* (Linnaeus, 1758). 19 – female shows no interest in larvae of *Elasmostethus interstinctus* (Linnaeus, 1758); 20 – two females with egg batches on one leaf; 21 – two females with hatched larvae on one leaf; the female on the right wing-jerking at the other; 22 – the stronger female adopts the larvae of the weaker one.

the eggs of their own species, was observed in *E. interstinctus* (Fig. 10). *Acanthosoma haemorrhoidale* laid 2–28 whitish eggs, always located on the ventral side of a rowan (*Sorbus aucuparia*) leaf. This species also lays her eggs in several batches, as do other species that lack care (HANEL & HANELOVÁ 2008).

Parental care

Acanthosoma haemorrhoidale, *Cyphostethus tristriatus,* and *Elasmostethus interstinctus*. Females of all these species left the egg batches immediately after oviposition and never returned. Parental care does not appear to occur in these species. First and second instars aggregated on, or close to, food resources (Figs 11, 12).

Elasmucha ferrugata, *E. fieberi*, and *E. grisea*. Females of all three species exhibit maternal care of the egg batch and young larvae. Behaviour was studied in detail only for *E. ferrugata* and *E. grisea*. The female stood over the egg batch throughout egg development. First instars barely moved after hatching, keeping in a compact group with the female, just sucking on their empty egg shells. The second instar moved towards food – berries or catkins – with the female in close attendance. She checked the larvae constantly and managed them with touches of her antennae.

Elasmucha ferrugata cared for the larvae until the second instar. Care was the most intensive for the first instar. The female did not stay with the second instar all the time, but remained close to where it was feeding. The female returned to the larvae for the night.

Females of *E. grisea* cared for the larvae until the third instar. The female stood over the eggs and first instar aggregated on empty egg shells. The second instar was similarly gregarious and the female remained with it. During the third instar, larvae moved towards food and back to the leaf and the female guarded them. Larvae split into smaller groups and dispersed at the end of the third instar, at which point the female left them.

Behaviour of the females with eggs and larvae. The female in repose over the egg batch keeps her antennae directed backwards along the body. If stimulated, she straightens them and directs them forwards. Other types of reaction follow, not necessarily in the same order every time (Table 5). A hundred responses to "attack" with soft tweezers were recorded in 20 *E. ferrugata* females. Defensive behaviour began when the tweezers were about 10 cm from them. A total of 12 combinations of reaction were recognized. The most frequent sequence (37 %) was: straightening the antennae – body tilting against the attack – body jerking. All possible reactions were recorded in 6 % of cases. Body jerking and wing-fanning occurred as strongly intensive reactions; they might be repeated several times. Similar experiments were carried out on an *E. grisea* female; these served only as a control, since the behaviour of that species is well known.

Ten *E. ferrugata* females were "attacked" by an approaching magnifying glass. All of them responded with combinations of antenna-straightening – body-jerking – wing-fanning. They also reacted to the movements of a relatively huge intruder, i.e. a person, usually by pressing themselves more strongly against the egg batch when the threat was about one metre away.

The females defended larvae at a markedly higher level of intensity than they showed for the eggs (Fig. 13). In an experiment that lasted two hours, significantly higher frequencies of antennal movement, covering of the egg batch with the body, body-jerking, and wing-fanning were recorded when the larvae were being defended in comparison with the eggs.

Experimental attack by other arthropods. The females of *E. ferrugata* reacted to the presence of other arthropods with: slight intensity of reaction towards *Ixodes* sp.; and medium intensity to other specimens of *E. ferrugata* (Fig. 14), *Chrysomela populi* (Fig. 15), *Phyllopertha horticola*, *Rhagonycha fulva*, and Asilidae gen., sp. An ant, *Formica polyctena*, attacked an *E. ferrugata* female with eggs. She promptly left the clutch and only returned to it after the ant had been removed. Similarly, *E. grisea* females reacted only slightly to the presence of a conspecific male but strongly to *Rhagonycha fulva*. A female of *E. grisea* with eggs actively attacked larvae of *E. ferrugata* occurring close to her.

Female feeding during care. Females of both *Elasmucha* species were observed to feed during their care of egg batches. Five females of *E. ferrugata* left the egg batch for various time periods, from 30 minutes to six hours, and sucked from fresh parts of the host plant (Fig. 16). Two of these females were minding a second egg batch. The females of *E. grisea* exhibited identical behaviour.

Egg batch adoption. In the course of the experiments, all 25 *E. ferrugata* females adopted a conspecific egg batch that was not their own, for various periods of time from 39 to133 minutes. An *E. ferrugata* female bred in the container took over care of whatever batch she found first, regardless of any parental relationship. On finding a clutch, the female checked it with her antennae and rostrum for 9–16 minutes, and then took up position over it. Larvae could also be adopted; an *E. ferrugata* female took over the larvae of other females (Figs 17, 18), whether actively or if new larvae became mixed in with her own. Egg batches of different but congeneric species, i.e. *E. grisea*, were not adopted by *E. ferrugata*. The latter touched the batch with the antennae and rostrum for a couple of minutes, then left.

Females of *E. grisea* exhibited identical behaviour in terms of adoption of other clutches of conspecific eggs or eggs of other congeneric species, i.e. *E. ferrugata*. The females of *E. grisea* did not adopt larvae of *Elasmostethus interstinctus* (Fig. 19); they left after only very short contact with them.

In only one case, two *E. grisea* females with egg batches were found on one leaf in natural conditions. After transfer to the container, they did not react to one another until the larvae hatched. They then showed defensive behaviour of medium intensity, turning to face one another. The more vigorously the larvae moved, the stronger the females' reaction, with bodies jerking and wings fanning. In the end, one of the females left her larvae and the second female adopted them (Figs 20–22).

Discussion and conclusions

Copulation and oviposition. The pattern of copulation observed in the acanthosomatids studied is typical of most of the Pentatomoidea. JORDAN (1958) and FISCHER (2006) described copulation options in Acanthosomatidae in some detail. A female carrying eggs may well be unwilling to copulate.

The females of all acanthosomatid species chose oviposition sites as near as possible to fruit of the host plant, facilitating the larvae's finding food. Much of the literature indicates that *E. grisea* egg batches are almost exclusively deposited on the lower surface of leaves (JORDAN 1958, MELBER & SCHMIDT 1975a, MAPPES 1994, MAPPES & KAITALA 1994), but our observations found only 57 % (40 out of 70) of batches deposited on the lower surface. ROTH *et al.* (2006) also mentioned oviposition on the upper side of leaves in *E. grisea*. Birch leaves move easily in the breeze, switching upper and lower sides and thus exposure to the sun, rain, and predators, a fact that goes some way towards explaining oviposition on either leaf surface. An identical situation was also found in *E. interstinctus*.

Elasmucha ferrugata deposited all its egg batches on the lower sides of bilberry leaves, which do not change position at all. KOBAYASHI (1953) also described oviposition by this species on the lower side of host plant leaves. However, females of *Cyphostethus tristriatus* deposited the eggs in all possible positions on *Juniperus communis*. FISCHER (2006) described the needles of the host plant as the most obvious place for a *C. tristriatus* clutch.

The literature generally appears to indicate that females that care for the eggs deposit fewer of them than females that take no care of their offspring (e.g. TALLAMY & SCHAEFER 1997). In species that stand over their brood, the size of the batch is limited by the body size of the female covering it (MAPPES 1994). Eggs in the centre of the batch are larger than those at the margins in *E. ferrugata* (MAPPES *et al.* 1997). In our specimens, the number of eggs in *E. ferrugata* batches ranged from 33 to 39 (usually 34, 35, and 36, rarely 38 and 39). However, STRAWIŃSKI (1951) gave a broader range for this species, at 17–52, and KOBAYASHI (1953), with the females on *Hydrangea paniculata* (Sieb.) (Hydrangeaceae), a narrower one, at 20–25. The differences in numbers may depend on the size of the eggs. Similarly, in *E. grisea*, from 35 to 45 eggs were laid, most often 38, 39, and 40, rarely 35, 36, 42, and 45, while ROTH *et al.* (2006) counted from 40 to 50 eggs per batch. The body sizes of both *Elasmucha* species are comparable; the size of the egg batch is therefore similar.

In general, the species that do not indulge in parental care deposit more eggs. In Acanthosomatidae, *Elasmostethus humeralis* Jakovlev, 1883 lays clutches of more than 200 eggs (KUDO 2001) and *Elasmostethus atricornis* (Van Duzee, 1904) deposits several batches of around 25 eggs each (CARTER & HOEBEKE 2003). The number of batches laid by species with no parental care varies widely. *Elasmostethus interstinctus* and *C. tristriatus* deposited a large number of batches with a lower number of eggs, possibly a strategy against egg predators, which either cannot find all the small batches or are replete with several batches and thus leave the remainder untouched. Moreover, *Cyphostethus tristriatus* has only the limited surface of narrow needles or fruit of *Juniperus* for its egg batch, and is forced by sheer physical area to divide the eggs into small groups. The highest number of eggs in one batch for *C. tristriatus* is 14, according to FISCHER (2006) because the females have paired ovaria with seven ovarioles each. However, we also found batches with 20 and 19 eggs.

The eggs of both species that leave the eggs without care show a further adaptation to unassisted survival; shortly after deposition, the colour of the eggs turns green, merging with the colour of the background. The eggs of the species in which females care for the eggs are white; they do not change colour, which contrasts with the background. However, these eggs are not visible in the natural “caring” position with the female over the clutch. *Acanthosoma haemorrhoidale* is an exception; its eggs are whitish even though the species is without maternal care. However, greenish pigmentation is hardly necessary as the batches are always located on the ventral side of a rowan leaf, which is significantly lighter that the dorsal side. The first instar in *A. haemorrhoidale* and

Cyphostethus tristriatus is inconspicuously greenish, whereas in *Elasmosthetus interstinctus* it is red, perhaps as a warning coloration.

It has been generally assumed that a female with care invests her time and energy in only one clutch and the care of it (TALLAMY & SCHAEFER 1997). However, more egg batches have also been mentioned in several species, e.g. *Sehirus cinctus* (Palisot, 1811) from Cydnidae (KIGHT 1998). A second, or even a third, batch can compensate for a decayed batch or provide an increased number of offspring to make the most of optimal conditions (STRAWIŃSKI 1951). KAITALA & MAPPES (1997) recognized that *E. ferrugata* regularly deposits a second egg batch (the only European *Elasmucha* species to do so). Our results confirmed this pattern. *Elasmucha grisea* laid only one batch in central European conditions (also pointed out by FISCHER (2006)). No clear explanation exists as to why oviposition behaviour varies between these species. KAITALA & MAPPES (1997) suggested that parental care lasts a shorter time when eggs are larger and in lower numbers, as the female can deposit further batches. *Elasmucha ferrugata* admittedly shows a lower number of eggs in its batches than does *E. grisea,* but only insignificantly so.

Parental care. Eight members of the family Acanthosomatidae occur in central Europe. An absence of the parental care has been confirmed in three of them.

Elasmostethus interstinctus. Although TEYROVSKÝ (1920) maintained that parental care had not been recognized in central European populations of *E. interstinctus*, STEHLÍK (1984) mentioned parental care. Other authors who studied the biology of this species found no parental care either (e.g., BUTLER 1923, MACGILL 1942, MAPPES *et al.* 1996, FISCHER 2006). Our study also recorded an absence of parental care in *E. interstinctus*. All the egg batches were abandoned by the females, both in the wild and under laboratory conditions. Egg cannibalism was observed. The eggs are green, almost indistinguishable from the background to the human eye, almost certainly representing a defensive adaptation. The absence of parental care is probably a feature of the genus *Elasmostethus*, as it is not mentioned in other species (e.g. JONES & MCPHERSON 1980; KUDO 1990, 2001; CARTER & HOEBEKE 2003).

Cyphostethus tristriatus. BUTLER (1923) and STEHLÍK (1984) recorded that *C. tristriatus* lacks parental care. FISCHER (2006) described the reproductive behaviour of *C. tristriatus* in detail for the first time. Like the previous species, *C. tristriatus* has developed its own strategy. Females deposit larger numbers of egg batches consisting of a lower numbers of eggs. Moreover, females are limited by the space available on the narrow needles and small berries of the host plant conifer, *Juniperus communis*. *Cyphostethus tristriatus* also shows adaptation in egg coloration; they are pale green.

Acanthosoma haemorrhoidale does not exhibit parental care, as briefly noted by FISCHER (2006). Details of its biology are presented in HANEL & HANELOVÁ (2008).

Elasmucha species. All three European *Elasmucha* species exhibit maternal care. More is known about *E. grisea*, less about *E. ferrugata* and *E. fieberi*. The biology of *E. fieberi* and *E. grisea* is similar (MELBER & SCHMIDT 1975a, ROTH *et al.* 2006, HANEL & HANELOVÁ 2011). Maternal care is one of the features of the entire genus, and is mentioned in all species for which the biology is known. However, the duration of care varies between *Elasmucha* species.

We confirmed that *E. grisea* protects its larvae until the third instar, although MELBER & SCHMIDT (1975a) and MAPPES (1994) extend this to the fourth instar as well, while ROTH *et al.* (2006) limit it to just the first instar. The explanation of this wide range of data about care in *E. grisea* is not known.

Elasmucha ferrugata continues care until the second instar. A shorter period of care, just for the first instar in *E. ferrugata*, was recorded by SOUTHWOOD & LESTON (1959), KAITALA & MAPPES (1997) and MAPPES *et al.* (1997). Care of the first instar was significantly more intensive than that for the second instar in *E. ferrugata*, which may indicate a trend. However, larvae of the second instar still fed close to the female and spent the night with her. Females of *E. fieberi* left their larvae during the second instar (MELBER & SCHMIDT 1975a).

Wide variability exists in the duration of maternal care within Acanthosomatidae. Only the first instar comes under the protection of *Anaxandra gigantea* (Matsumura, 1913) after HAYASHI (1987) and *Elasmucha grisea*, after ROTH *et al.* (2006). Larvae are protected until the second instar by some females of *Anaxandra gigantea* and of *Sastragala esakii* Hasegawa, 1959 after HASEGAWA (1967). *Elasmucha signoreti* (KUDO & NAKAHIRA 1993), *Elasmucha ferrugata* (present paper) and *Elasmucha fieberi* (MELBER & SCHMIDT 1975a) also protect larvae until the second instar. Females of *Elasmucha putoni* Scott, 1874 (HONBO & NAKAMURA 1985, KUDO 1990, TACHIKAWA 1971), and according to the observations in hand, *Elasmucha grisea* as well, continue care until the third instar, while those of *Elasmucha dorsalis* (KUDO *et al.* 1989, KUDO 1990) and some of the females of *Elasmucha grisea* according to MELBER & SCHMIDT (1975a) carry on until the fourth instar. Some *E. dorsalis* females are still exhibiting care routines even during the fifth instar (KUDO *et al.* 1989, KUDO 1990).

Female feeding. Reviewing the literature on whether acanthosomatid females feed or not during their care of offspring gives ambiguous results. Many authors have maintained that the females of a number of species probably fast, e.g. *Elasmucha signoreti* (KUDO & NAKAHIRA 1993), *E. fieberi* (MELBER & SCHMIDT 1975a), and *E. grisea* (MELBER & SCHMIDT 1975a). KAITALA & MAPPES (1997) cited DOLLING (1991) that females of *E. ferrugata* did not leave the egg batch and only sucked from the mesophyllum. However, KUDO *et al.* (1989) found that some *Elasmucha dorsalis* females with eggs and first instars probably fed during their care.

We established that *E. ferrugata* and *E. grisea* females took nourishment in the period during which they were caring for eggs. They left the clutch and sucked close to it, then returned immediately after feeding. The hypothesis that females fast was offered, by BEQUAERT (1935) among others, but this was not based on exact, direct studies. If a fasting female were to perish, her clutch would be left defenceless. It appears that risking a little time and energy to feed represents a far better investment than leaving the clutch entirely vulnerable to predator or parasitoid should the parent succumb to starvation.

Discrimination between broods and adoption. Females of *Elasmucha* species very probably employ chemical sensitivity when they are search for an egg batch. The acceptance threshold appears to lie at species, rather than individual, level. In all cases, a seeking female adopted the first conspecific clutch that she came upon. It may also be important how long a female has already stayed with her clutch and how long she has been away from it. It is generally suggested that subsocial hemipterans cannot distinguish their eggs from other conspecific eggs. That situation had previously been confirmed in *Elasmucha dorsalis*, *E. grisea,* and *E. putoni*, and now in *E. ferrugata* (e.g., Melber & Schmidt 1975a, Honbo & Nakamura 1985, Faeth 1989).

Tsukamoto & Tojo (1992) and Filippi-Tsukamoto *et al.* (1995) compared the situation in *Elasmucha* species with the behaviour of *Parastrachia japonensis* (Scott, 1880) (Parastrachiidae) with reference to maternal care. A *P. japonensis* female exhibits "evasive guarding behaviour"; she may remove the eggs from a dangerous location and provide the larvae with berries from the host tree. The female may thus distinguish her own larvae by the "smell" of berries brought to the nest with larvae. In contrast, *Elasmucha* species glue the egg batch tightly to the surface of the host plant. The female thus defends the place with clutch and food, and her defensive behaviour is more aggressive. In natural conditions, a female does not leave the eggs, thus never coming under any pressure to distinguish her own clutch from any other.

Female behaviour. The defensive behaviour of *E. grisea* females with an egg batch was first mentioned by Modeer (1764). The greatest intensity of defence is triggered by a secretion from the nymphal dorso-abdominal scent glands (e.g. Maschwitz & Gutmann 1979, Kudo *et al.* 1989, Kudo 1990). The results of our experiments categorised the five types of defensive behaviour already described and classified by Melber & Schmidt (1975a) and complemented by Mappes *et al.* (1995), depending on the perceived intensity of attack. The sequence in which these types occur is not always identical, and not all must necessarily be performed. We confirm the results of Teyrovský (1920), that defensive behaviour differs with the size of aggressor and intensity of the threat.

The defensive reaction of an *E. ferrugata* female with larvae is more intensive than that of one with only eggs. It appears that the female has already made a larger investment in larvae that have hatched than in "merely" the egg batch. One of the intensive reactions is the fanning the wings, which has several possible explanations. The female may be conveying a visual impression of increased body size, or she may be trying, quite literally, to blow away both intruder and unwanted males (Tallamy & Wood 1986, Tingidae). However, a female may also be releasing a secretion from the dorso-abdominal glands, more quickly distributed and directed against potential danger by wing-fanning (Podoubský 1997).

This defensive behaviour of the *E. ferrugata* female is very similar to that of other *Elasmucha* species. Kudo *et al.* (1989) recorded the reaction of an *E. dorsalis* female visually stimulated by shaking forceps in front of it; Kudo (1990) noted that an *E. putoni* behaved similarly, as did an *E. signoreti* female, stimulated by shaking a small black ball at it (Kudo & Nakahira 1993).

Comparison with other Pentatomoidea with parental care. Data on parental care of offspring within the Pentatomoidea are sparse. In the temperate zone, females of only two families, Acanthosomatidae and Cydnidae, are known to exhibit this behaviour. Maternal care is known from more taxa in the latter family; it runs in two possible patterns. The female of *Cydnus aterrimus* (Forster, 1771) cares for the egg batch and feeds the larvae with a special secretion, probably from the rectum (Schorr 1957). In the second pattern, the female defends the eggs and provides the larvae with seeds for food; this is more widespread within the Cydnidae, e.g. in *Adrisa* species (summary in Filippi *et al.* 2001), in *Sehirus* species (e.g., Sites & McPherson 1982, Kight 2000), in *Tritomegas* species (Southwood & Leston 1959, Tallamy & Wood 1986), and others.

The pattern described in Cydnidae is very similar to that of *Parastrachia japonensis,* in the Palaearctic region, the female of which deposits the eggs in a hole she digs in the ground. The female guards the eggs passively, and she may translocate them in the event of threat. After the larvae hatch, the female provides them with food in the form of seeds or berries. The similarity between maternal care in Cydnidae and Parastrachiidae is clear. They live under vegetation, on or in the substratum, assumed to be an ancestral type of biotope for a hypothetical ancestor of the Pentatomoidea (Schaefer 1972). Paternal/maternal care could in this light be considered a plesiomorphic feature within Pentatomoidea, at the least. The defensive behaviour of pentatomoids should thus have a similar pattern, as may be observed in the very similar reactions of females to threat in both *Elasmucha ferrugata*, and *Parasrachia japonensis*. This pattern may represent an ancestral mode of female behaviour within Pentatomoidea.

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Table 1. Maternal care in the family Acanthosomatidae. (Continued on pages 453–454.)

TAXON	STUDY	DATA
Acanthosomatidae	Teyrovský (1920)	parental care, behaviour of female with egg batch
	Butler (1923)	biology, habitat, life cycle, maternal care
	Bequaert (1935)	summary of maternal care in Heteroptera
	Aldrich (1988)	secretion of pheromones in connection with parental care
	Kudo (2001)	maternal care, investment to the egg size
***Anaxandra gigantea* (Matsumara, 1978)**	Hayashi (1987)	parental care
	Kudo et al. (1989)	parental care
***Elasmucha* Stål, 1864**	Southwood (1956)	brief note about parental care
	Tachikawa (1971)	maternal care
	Thomas (1991)	brief note about parental care
	Filippi-Tsukamoto et al. (1995)	comparison with *Parastrachia*
***E. dorsalis* (Jakovlev, 1876)**	Kudo et al. (1989)	experiments with maternal care
	Kudo (1990)	female defense behaviour in details
	Kudo (2000)	effect of maternal care against predators
***E. ferrugata* (Fabricius, 1787)**	Teyrovský (1918)	maternal care
	Strawiński (1951)	fertility, size of the egg batch
	Kobayashi (1953)	maternal care, description of larvae, size of the egg batch
	Southwood & Leston (1959)	development of larvae, length of the parental care
	Kaitala & Mappes (1992)	parental care in Finland
	Kaitala & Mappes (1997)	size of egg batches
	Mappes (1994)	defensive behaviour of female with eggs
	Mappes et al. (1997)	maternal care, defense behaviour
***E. fieberi* Jakovlev, 1864**	Melber & Schmidt (1975a)	parental care, comparison with *E. grisea*
	Melber & Schmidt (1975b)	defense of eggs, comparison of defended batch with batch without female
	Melber et al. (1980)	parental care
	Stehlík (1984)	parental care
	Kaitala & Mappes (1992)	parental care
	Kaitala & Mappes (1997)	parental care, size of an egg batch

TAXON	STUDY	DATA
***E. grisea* (Linnaeus, 1758)**	Modeer (1764)	maternal care, defense behaviour
	Hellins (1870)	care of larvae
	Hellins (1872)	maternal care, study of female with larvae
	Hellins (1874)	maternal care, description of an egg batch
	Duda (1879)	parental care
	Pierre (1903)	maternal care, scent of female and larvae
	Kirkaldy (1904)	maternal care
	Rossum (1904)	parental care
	Boselli (1932)	maternal care
	Hussey (1934)	parental care
	Couturier (1946)	parental care
	Schorr (1957)	maternal care, comparison with Cydnidae
	Jordan (1958)	maternal care, location of the egg batch
	Southwood & Leston (1959)	parental care
	Odhiambo (1960)	summary of knowledge on maternal care
	Melber & Schmidt (1975a)	comparison with other *Elasmucha* species, defense behaviour
	Melber & Schmidt (1975b)	biology of female with egg batch
	Maschwitz & Gutmann (1979)	maternal care, alarm pheromones
	Melber et al. (1980)	parental care, parasitism, defense behaviour
	Faeth (1989)	comparison with Tingidae
	Kaitala & Mappes (1992)	parental care (in Finland)
	Kaitala & Mappes (1994)	defensive behaviour, experiments with females
	Mappes (1994)	maternal care, female behaviour in connection with size of a batch
	Hawkins (1995)	maternal care, food
	Mappes et al. (1995)	experiments with females, solitary and in a group, defense behaviour
	Kaitala & Mappes (1997)	parental care, size of egg batches
	Tallamy & Schaefer (1997)	defensive behavior, parental care
	Gogala et al. (1998)	comparison with Tessaratomidae
	Tallamy (1999)	parental care
	Parr et al. (2002)	parental care, comparison with Tingidae
	Ogorzałek & Trochimczuk (2009)	ovary study, 2 generations

TAXON	STUDY	DATA
E. lateralis **(Say, 1831)**	Drake (1922)	parental care
	Frost & Haber (1944)	description of larvae
	Odhiambo (1960)	observation of female with eggs and larvae
	Jones & McPherson (1980)	parental care
E. putoni **Scott, 1874**	Tachikawa (1971)	parental care of *Elasmucha* species
	Honbo & Nakamura (1985)	maternal care
	Kudo (1988)	defensive behaviour, oviposition
	Kudo (1990)	detailed study of defensive behaviour
	Kudo (1996)	parental care and parasitism
	Kudo (2001)	parental care and predators
E. signoreti **(Scott, 1874)**	Kudo & Nakahira (1993)	models of maternal care
	Kudo (2006)	size of eggs within clutch
Sastragala esakii **Hasegawa, 1959**	Kudo (2001)	subsocial
S. scutellata **(Scott, 1874)**	Kudo (2001)	subsocial, care the following instars
Sinopla perpunctatus **Signoret, 1864**	Faúndez & Osorio (2010)	oviposition, care of larvae

Table 2. Number of studied Acanthosomatidae specimens used in the behavioral experiments.

SPECIES	**Experiments in containers**	**Experiments in natural conditions**	**Reared from egg to adult**
Acanthosoma haemorrhoidale (Linnaeus, 1758)	2 adults	20 larvae	4 specimens
Cyphostethus tristriatus (Fabricius, 1758)	7 adults	20 larvae	10 specimens
Elasmostethus interstinctus (Linnaeus, 1758)	25 adults, 10 larvae	30 adults	15 specimens
Elasmucha ferrugata (Fabricius, 1787)	50 adults	120 larvae + adults	10 specimens
Elasmucha fieberi Jakovlev, 1864	2 adults	8 larvae	2 specimens
Elasmucha grisea (Linnaeus, 1758)	55 adults, 15 larvae	150 larvae + adults	20 specimens

Table 3. Host plants of studied Central European Acanthosomatidae.

Bug species	**Host plant species**
Acanthosoma haemorrhoidale (Linnaeus, 1758)	*Sorbus aucuparia* L.
Cyphostethus tristriatus (Fabricius, 1758)	*Juniperus communis* L.
Elasmostethus interstinctus (Linnaeus, 1758)	*Betula pendula* Roth *Alnus glutinosa* (L.) Gaertn.
Elasmucha ferrugata (Fabricius, 1787)	*Vaccinium myrtilus* L. *Lonicera xylosteum* L.
Elasmucha fieberi Jakovlev, 1864	*Betula pendula* Roth
Elasmucha grisea (Linnaeus, 1758)	*Betula pendula* Roth *Alnus glutinosa* (L.) Gaertn. *Crataegus* sp.

Table 4. Number of eggs in the individual batches of Acanthosomatidae.

SPECIES	Number of eggs	Number of batches
Acanthosoma haemorrhoidale	23	1
(Linnaeus, 1758) (N = 6)	28	1
	14	1
	27	1
	16	1
	2	1
Cyphostethus tristriatus	20	1
(Fabricius, 1758) (N = 4)	19	1
	3	1
	7	1
Elasmostethus interstinctus	4	1
(Linnaeus, 1758) (N = 16)	5	1
	6	1
	7	2
	9	1
	11	1
	12	2
	13	1
	18	1
	20	1
	26	1
	27	1
	29	1
	30	1
Elasmucha ferrugata	33	3
(Fabricius, 1787) (N = 25)	34	5
	35	6
	36	5
	37	3
	38	2
	39	1
Elasmucha fieberi	34	1
Jakovlev, 1864		
Elasmucha grisea	35	1
(Linnaeus, 1758) (N = 20)	36	1
	37	2
	38	3
	39	4
	40	3
	41	2
	42	1
	43	2
	45	1

Table 5. Reaction of *Elasmucha ferrugata* (Fabricius, 1787) female to the attack by soft tweezer. A = antennae straightening; B = antennae jerking; C = body tilting; D = body jerking; E = body swinging; F = wings fanning. 0 = no reaction of female on the convoluted leaf. N = 100 attacks of 20 females.

Combination of reactions	**Number of answers**
A	2
A + B	2
A + B + C	17
A + B + C + D	20
A + B + C + D + E	5
A + B + C + D + E + F	6
A + C + D	37
A + C + D + E	3
A + C + D + F	2
A + C + F	1
A + C + D + F + D	4
0	1