

Are gregarious red-black shieldbugs, *Graphosoma lineatum* (Hemiptera: Pentatomidae), really aposematic? An experimental approach

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ABSTRACT

Hypothesis: The coloration of the red-black shieldbug has a warning function. This quality can be lowered when the shieldbug is presented on a fragmented background.

Organism: We offered wild-coloured and artificially deaposematized (painted brown) red-black shieldbugs (*Graphosoma lineatum*) to avian predators (*Parus major*, *Parus caeruleus*).

Site of experiments: The experiments were conducted in a cage (0.7 m × 0.7 m × 0.7 m) fitted with a one-way mirror.

Methods: In succession, we offered five shieldbugs to each bird. We presented the shieldbugs on contrasting (white) and matching (imitating the shieldbug's habitat and imitating the striated shieldbug pattern) backgrounds.

Results: The blue tits avoided all shieldbugs offered to them regardless of their coloration. The great tits attacked both colour forms, but the brown one more frequently. The wild-coloured shieldbugs were significantly better protected against repeated attacks. Shieldbugs presented on any of the matching backgrounds were attacked less frequently than when presented on the white background.

Keywords: disruptive coloration, *Parus caeruleus*, *Parus major*, warning coloration.

INTRODUCTION

Warning (aposematic) colouration, which provides protection to a defended species against visually oriented predators (usually birds), is a controversial topic in evolutionary ecology. The initial evolution of aposematic anti-predator signalling is expected to increase predation risk before reaching a stage when local predators are able to learn to avoid the unpalatable prey (see Lindström *et al.*, 2001; Marples *et al.*, 2005). Fisher (1958) presented the idea of aggregation benefit through the survival of related individuals. However, Riipi *et al.* (2001) showed that grouping would have been highly beneficial for aposematic prey individuals, surrounded by naive predators, without requiring any kin selection. They proposed four possible non-kin selection mechanisms: non-linear growth of detectability

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risk/group size; low additional detectability costs due to conspicuous signals in the group-living prey; a 'dilution effect'; and rapid avoidance learning of the warning signal in groups. In contrast, Beatty *et al.* (2005) suggest that the common association between aggregation and distastefulness may primarily arise because of the significant vulnerability of aggregated palatable prey. However, they investigated responses of human 'predators' in computer 'novel world' experiments, not a realistic predator-prey system. The true influence of prey gregarious habit on aposematism efficiency has rarely been analysed experimentally [but see Reader and Hochuli (2003), who studied a caterpillar prey vs. hemipteran predator system; see also Nilsson and Forsman (2003) for application of phylogeny-based comparative analyses of evolutionary relationships of colouration, body size, and gregarious habit in the Lepidoptera].

The Palearctic red-black shieldbug, *Graphosoma lineatum* L. (Hemiptera: Pentatomidae), is a textbook example of the aposematic insect (for a review, see Komárek, 2000). Its contrasting colours form several longitudinal stripes on the dorsal side and a spotted pattern on the ventral side of its body (Fig. 1). As *G. lineatum* is a gregarious insect, it would be easy for an avian predator to learn its unpalatability because the bird is able to meet another prey item soon after encountering the first (Sillén-Tullberg and Leimar, 1988).

The shieldbugs in general (Pentatomidea) are known to be extremely distasteful for predators (e.g. Krall *et al.*, 1999) because they are able, when touched, to release a repellent secretion, predominantly from their thoracic scent glands. Though the pentatomoids usually do not combine their chemical defence with warning colouration, there are some obviously aposematic species, for example *Murgantia* and *Eurydema* spp. (Aldrich *et al.*, 1996; Aliabadi *et al.*, 2002), which are mostly black with yellow or red spots (or vice versa). The *G. lineatum*-like longitudinal striation is relatively common in pentatomoids (Tietz and Zrzavý, 1996), but their stripes have usually much less contrasting, presumably cryptic colours



Fig. 1. The shieldbug (*Graphosoma lineatum*).

(mostly brownish and yellowish). The combination of longitudinal striation with contrasting colouration is an evident evolutionary novelty of *G. lineatum* and a few closely related species, which suggests that *G. lineatum* is a suitable model species for studies of the evolution of warning colouration (Zrzavý, 1994). However, the functional aposematism of *G. lineatum* is not evident, although Schlee (1986) showed that *G. lineatum* is attacked less frequently than other hemipteran species. The possible warning pattern in *G. lineatum* is limited to adult bugs, since the enlarged longitudinally striated shield (mesoscutellum), covering the whole abdomen dorsally, is not present in the juvenile stages. Only the longitudinal striation on the head and pronotum (a trapezoid shield just behind the head) is sequentially developed in the juvenile stages (Tietz and Zrzavý, 1996). The juveniles are yellowish to brownish and hence not aposematic. This ontogenetic change in the colouration display is interesting for an understanding of possible shieldbug aposematism, because shieldbugs are hemimetabolous insects with juveniles morphologically and ecologically similar to the adults (they live on the same plants, later juvenile and adult instars are of comparable sizes and shapes). As there is no sexual dichroism in *G. lineatum*, infraspecific colour signalling is unlikely.

Naturally, the striped pattern of *G. lineatum* could have a different anti-predatory function. Stripes are often used by animals to disrupt their body outline or to mask vulnerable or important parts of their bodies (e.g. eyes). The shieldbugs feed on umbelliferous plants (*Apiaceae*) (Popov, 1971), whose inflorescences (umbels) consist of numerous short twigs with very small white flowers. Against the background of brown or brown-red dried umbel twigs, the colouration of the adult shieldbug could be rather cryptic (breaking up the outline of its body), just like the colouration of juveniles. As most European pentatomoids (including *G. lineatum*) hibernate as adults, they are often encountered on dried and rotten plant remains. The 'aposematic' red-black shieldbugs are indeed surprisingly difficult to find in nature unless they are sitting on a spread of white umbels (Musolin and Saulich, 1995).

In the present study, we examined the warning function of shieldbug colouration experimentally, using two species of wild-caught passerine predators. We examined whether the colouration of a shieldbug presented on a white background acts as a warning signal, by comparing the attack rates against wild-coloured and artificially 'non-aposematic' (brown-painted) shieldbugs (for methodological details, see Exnerová *et al.*, 2003a, 2006). Furthermore, we examined whether the colouration of a shieldbug presented on variously patterned backgrounds still acts as a warning, by comparing the attack rates against the wild-coloured form presented on white and patterned backgrounds. In each experiment, several trials were performed with several shieldbugs, thus simulating the gregarious habit of the species. Instead of presenting a group of shieldbugs to an individual predator, we presented them sequentially to simulate natural circumstances more closely. In addition, the sequential design of the experiments had the aims of minimizing a predator's neophobia and determining the stability of a bird's foraging motivation.

MATERIALS AND METHODS

Experimental prey

The experimental shieldbug individuals were collected around České Budějovice (South Bohemia, Czech Republic) during spring 2002 and 2003. Groups of about 50 individuals were kept in the laboratory in transparent plastic boxes (16 × 13 × 7 cm). Dry seeds of carrot (*Daucus carota sativa*), cow parsley (*Anthriscus sylvestris*), and wild angelica

(*Angelica sylvestris*) together with water were supplied *ad libitum*. The insects were reared at 25°C and in long-day (18 h light, 6 h dark) conditions.

We eliminated the aposematic colouration of bugs using brown watercolour (burned sienna) spread all over its dorsal side (pronotum and mesoscutellum). The dye is odourless and non-toxic and the treatment did not affect the locomotion or secretion of the bugs (see Exnerová *et al.* 2003a, 2006).

Experimental predators

Adult birds of two tit species (blue tit *Parus caeruleus* L. and great tit *Parus major* L), caught with mist nets in the vicinity of České Budějovice, were used as experimental predators. Captures were conducted from 2002 to 2003 except in the breeding seasons (May to July). We have licenses to catch and ring birds (Bird Ringing Centre Praha #975 and #1004) and conduct experiments with animals (Czech Animal Welfare Commission #489/01). Birds were kept in standard bird cages at a lowered indoor temperature and under outdoor photoperiod conditions. Birds were acclimated to the laboratory conditions and food (sunflower seeds and mealworms) for 1–3 days before the experiments. They were ringed and released immediately after the end of the trials.

Experimental apparatus

The experimental cages were made from wooden frames (0.7 × 0.7 × 0.7 m) covered with wire mesh (2 mm²) with the front wall incorporating a one-way mirror (for details, see Exnerová *et al.*, 2003a). The cages were equipped with one perch, a bowl with water, and a rotating circular feeding tray, containing six small cups (a single cup contained a prey item during a trial). The distance between the perch and the tray was approximately 25 cm. The colour of the bottom of the cups was either white or patterned. The UMBEL patterned background was a brown (burned sienna) pattern consisting of crossed lines in the shape of a schematized umbel seen from above (Fig. 2). The STRIPES patterned background consisted of a shieldbug-like pattern (Fig. 3), the colouration and size of which were obtained by scanning the shieldbug. Standard illumination was generated by a light source (Lumilux Combi 18 W, Osram) that simulates the full daylight spectrum.

Trials

The 40 blue tits were divided into two groups of 20 individuals. The first group was offered the wild-coloured form of the shieldbug, the second group the brown one, in both cases on the white background. The 80 great tits were divided into four groups of 20 individuals. As with the blue tits, the first group was offered the wild-coloured shieldbugs, the second group the brown ones, in both cases on the white background. The third and fourth groups, however, were offered the wild-coloured shieldbugs presented on two different backgrounds (UMBEL and STRIPES, see above). To avoid pseudoreplication, each individual bird was used for a single series of trials only.

Each bird was placed into the experimental cage before the experiment to allow it to adapt to the new conditions, and was provided with food (mealworms) and water. The bird was deprived of food for 1.5–2.5 h before the experiment. The bird was assumed to be ready for the experiment as soon as it attacked the mealworm immediately after being offered it.

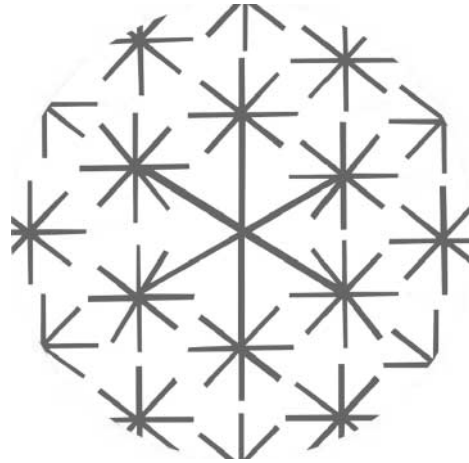


Fig. 2. The UMBEL background.

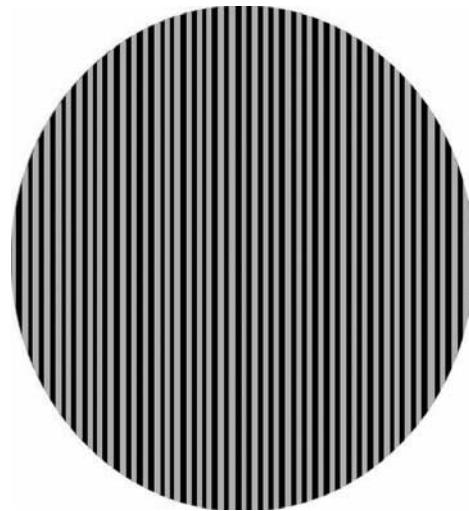


Fig. 3. The STRIPES background.

Each experiment with an individual bird consisted of a series of 10 successive trials, in which five mealworms and five test bugs were offered alternately, starting with a mealworm. Repetition of several trials within a single experiment was used to eliminate the effects of individual differences in predators' neophobia. The trials with mealworms were used to check a bird's motivation to forage, and they ended after the mealworm had been eaten. The trials with shieldbugs always lasted 5 min.

A continuous description of a bird's behaviour was recorded in the program Observer version 3 (1989–1992, ©Noldus). We distinguished three possible results of each trial: (1) the bug was neither handled nor killed during the 5-min trial; (2) the bug was handled (touched, pecked or taken by the bird's bill) but not killed; or (3) the bug was killed.

Statistical analysis

We used two sets of data for the statistical analyses (all tests were performed in Statistica 5.5, 1984–1999, © StatSoft, Inc.):

1. The numbers of birds in each experimental group that handled/killed at least one of the five bugs offered to it. Fisher's exact test was used for this analysis.
2. The numbers of bugs handled/killed by individual birds in each experimental group. The distribution of these data was not different from a Poisson distribution (Kolmogorov-Smirnov test, $P > 0.05$). They were normalized using square root transformation. An analysis of variance (F -test) with *post hoc* comparison among particular groups (Tukey HSD test) was used to analyse these data.

RESULTS

Wild-coloured ('aposematic') vs. brown-painted ('non-aposematic') form of the shieldbug on a white background (great tits and blue tits as predators)

The great tits tended to avoid the wild-coloured form of the shieldbug slightly more than the brown-painted one; however, the difference was not significant. There was a trend for handling ($P = 0.111$) and killing ($P = 0.092$) to occur more readily if brown-painted shieldbugs were offered (Tables 1, 3). In contrast, the numbers of wild-coloured and brown-painted shieldbugs that were handled/killed by a single bird during the series of trials differed significantly (Fig. 4; Tables 2, 3). Even the birds that were ready to handle a red-black shieldbug usually did not re-attack (on average, they handled 1.33 of 5 shieldbugs). The attacks on the brown-painted shieldbugs were repeated more frequently (on average, the birds handled 2.69 of 5 shieldbugs). The blue tits did not distinguish the two colour forms of the shieldbugs and avoided both (the wild form strictly so; see Tables 1, 2).

Wild-coloured ('aposematic') shieldbug on patterned vs. white backgrounds (great tits as predators)

Great tits handled and killed wild-coloured shieldbugs on both patterned backgrounds slightly more willingly than the same shieldbugs on a white background, but the differences were not significant (Fig. 4; Tables 1, 2, 3).

DISCUSSION

The anti-predatory function of the red and black colouration of various bugs (Lygaeidae, Rhopalidae, Pyrrhocoridae) has been proved experimentally (Gamberale-Stille and Sillén-Tullberg, 1999; Aliabadi *et al.*, 2002; Exnerová *et al.*, 2003a, 2006). However, the ecological function of the conspicuous longitudinal pattern has rarely been analysed, in contrast to transversally striped prey (Järvi *et al.*, 1981; Evans and Waldbauer, 1982; Wiklund and Järvi, 1982; Howarth and Edmunds, 2000; Kauppinen and Mappes, 2003). Schlee (1986) offered blackbirds (*Turdus merula*) adult shieldbugs that were reared in captivity as well as wild-caught ones, and showed that *G. lineatum* is attacked less frequently than three non-aposematic pentatomoid species. However, this approach was unable to separate effects of colouration *per se* from other biological characteristics of the species in question (e.g. body size and shape, amount and composition of the defensive gland secretions, behaviour).

Table 1. Reaction of the great tit (*Parus major*) and the blue tit (*Parus caeruleus*) to different forms of the shieldbug (*Graphosoma lineatum*)

| Tit species | Shieldbug colour | Background | Numbers of birds that handled at least one shieldbug | Numbers of birds that killed at least one shieldbug |
|---------------------------------|------------------|------------|--|---|
| <i>Parus major</i> (n = 20) | wild | white | 6 | 1 |
| <i>Parus major</i> (n = 20) | brown painted | white | 12 | 6 |
| <i>Parus major</i> (n = 20) | wild | UMBEL | 8 | 4 |
| <i>Parus major</i> (n = 20) | wild | STRIPES | 8 | 4 |
| <i>Parus caeruleus</i> (n = 20) | wild | white | 1 | 0 |
| <i>Parus caeruleus</i> (n = 20) | brown painted | white | 3 | 1 |

Table 2. Median, mean, minimum, and maximum numbers of shieldbugs handled and killed by individual birds (*Parus major* and *Parus caeruleus*)

| Tit species | Shieldbug colour | Background | Handled | | | Killed | | |
|---------------------------------|------------------|------------|---------|--------|-------|---------|--------|-------|
| | | | min-max | median | mean* | min-max | median | mean* |
| <i>Parus major</i> (n = 20) | wild | white | 0-2 | 0 | 1.33 | 0-1 | 0 | 1.0 |
| <i>Parus major</i> (n = 20) | brown | white | 0-5 | 1 | 2.69 | 0-5 | 0 | 3.71 |
| <i>Parus major</i> (n = 20) | wild | UMBEL | 0-2 | 0 | 1.5 | 0-2 | 0 | 1.5 |
| <i>Parus major</i> (n = 20) | wild | STRIPES | 0-5 | 0 | 2.5 | 0-4 | 0 | 3.25 |
| <i>Parus caeruleus</i> (n = 20) | wild | white | 0-1 | 0 | 1.0 | 0-0 | 0 | 0 |
| <i>Parus caeruleus</i> (n = 20) | brown | white | 0-2 | 0 | 1.67 | 0-1 | 0 | 1.0 |

* The mean was computed only from data for birds that handled or killed shieldbugs.

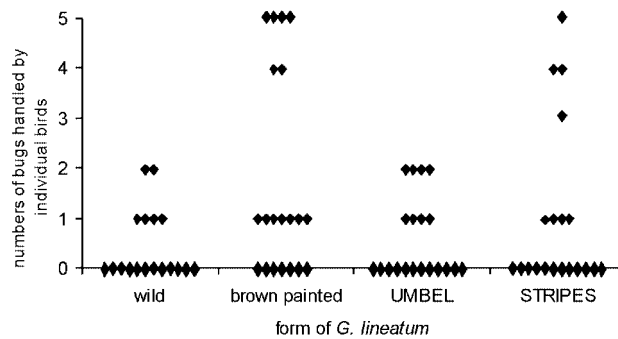


Fig. 4. Numbers of bugs handled by individual great tits (*Parus major*). Each point is an individual bird.

Table 3. Results of statistical analyses for *Parus major*

| Comparison | Data type | Test result (<i>P</i> -value) | |
|----------------------|-----------|--------------------------------|-----------------|
| | | Handling | Killing |
| WT on Wh vs. B on Wh | 1 | 0.111 | 0.092 |
| | 2 | <0.05 | <0.05 |
| WT on U vs. WT on Wh | 1 | 0.741 | 1.0 |
| | 2 | 0.945 | 0.990 |
| WT on S vs. WT on Wh | 1 | 0.507 | 0.152 |
| | 2 | 0.606 | 0.407 |

Note: Multiple comparisons in ANOVA: handling, $F_{76,80} = 3.22$, $P = 0.027$; killing, $F_{76,80} = 3.51$, $P = 0.02$.

Abbreviations: WT, wild-type bug; B, brown-painted bug; Wh, white background; U, UMBEL background; S, STRIPES background.

Data type: 1, Number of birds that handled/killed at least one bug offered to them (Fisher exact test). 2, Number of bugs handled/killed by individual birds (Tukey HSD test of ANOVA).

Although there is no significant difference in the great tits' readiness to attack any colour form of a shieldbug, the birds usually do not repeat their attacks on the aposematic wild-coloured shieldbugs. The great tits seem to have to learn that this species is unsuitable as a prey, and they are able to learn it more accurately if the negative stimulus is associated with conspicuous colouration. We used wild-caught birds of unknown individual histories, but they were most probably not familiar with *G. lineatum* in the field, as great tits do not forage frequently in the shieldbugs' microhabitat (Harrap and Quinn, 1996). Exnerová *et al.* (2003a) studied the reaction of several passerine species (including the blue and great tits) to another aposematic bug, the red firebug (*Pyrrhocoris apterus* L.), using the same experimental equipment and 'artificially non-aposematic' insects as in the present paper. Both great and blue tits were shown to reject the wild-coloured form of the firebug. This is in line with the reaction of the blue tits to shieldbugs, but the great tits were more ready to attack wild-coloured shieldbugs (30% of tested birds) than wild-coloured firebugs (16% of tested birds). In contrast, the mean numbers of the insects handled by an individual bird in our single trial series was 1.33 for shieldbugs versus 1.80 for firebugs in the experiments of Exnerová *et al.* (2003a). These results might suggest that shieldbug colouration is ecologically important, especially in cases of the repeated encounter of an individual predator with *G. lineatum* (see Sillén-Tullberg and Leimar, 1988). Hence, the gregarious habit could be beneficial for the aposematic insect.

The profound difference between the two tested species of tits is quite surprising, although Exnerová *et al.* (2003a) also showed that blue tits were more careful than great tits (especially to the brown painted form). In our experiments, the blue tits did not handle shieldbugs at all, regardless of their colour form. The shieldbug-like insects (body size, solidity) are probably more suitable for more robust predators, as are the great tits. However, in the parallel study on two juvenile and adult instars of *Pyrrhocoris apterus*, the predator/prey body size ratio does not explain the different behaviour of blue and great tits to the firebug developmental stages (M. Prokopová, R. Fuchs and J. Zrzavý, in preparation). Another possible explanation is the different foraging ecology and behaviour of both species. The great tits seem to be more experimental predators, while the blue tits show a higher degree of

neophobia. Neophobia was shown to be an important factor in the reaction of bird predators to aposematic prey (for details, see Marples and Kelly, 1999).

Presenting shieldbugs on variously patterned backgrounds appears to slightly decrease the strength of the aposematic signal, although not significantly so. The behaviour of a predator towards aposematic and non-aposematic prey on contrasting and matching backgrounds was examined by Sillén-Tullberg (1985). She examined the reactions of naive zebra finches (*Poephilla guttata*) to wild-type red individuals and grey mutants of *Lygaeus equestris* (Heteroptera: Lygaeidae) on red and grey backgrounds and showed that the warning signal of the red form was not weakened on the matching background.

Although the morphology and chemical defence of the pentatomoids do not prevent attacks by birds in general [17 pentatomoid species were present in the diet of 14 Central European bird species (Exnerová *et al.*, 2003b)], *G. lineatum* has never been found in the birds' diet (Creutz 1953; Exnerová *et al.*, 2003b). The aposematism of *G. lineatum* appears to be supported by a combination of conspicuous colouration, defensive chemicals, gregarious habit, living and feeding on the upper parts of herbs (where they are visible to possible avian predators), and their absence in the bird diet. Nonetheless, the warning signal of the shieldbug colouration does not work unequivocally. It does not prevent the attack but, after handling the first prey item, the bird learns its unpalatability and does not repeat its attack. Moreover, it is possible that the shieldbug colouration, when presented on patterned backgrounds, loses its warning power and becomes more or less disruptive. The effect of the aposematic signalling of *G. lineatum* may thus be context-dependent and function in accordance with other defensive devices.

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REFERENCES

- Aldrich, J.R., Avery, J.W., Lee, C.J., Graf, J.C., Harrison, D.J. and Bin, F. 1996. Semiochemistry of cabbage bugs (Heteroptera: Pentatomidae: *Eurydema* and *Murgantia*). *J. Entomol. Sci.*, **31**: 172–182.
- Aliabadi, A., Renwick, J.A.A. and Whitman, D.W. 2002. Sequestration of glucosinolates by harlequin bug *Murgantia histrionica*. *J. Chem. Ecol.*, **28**: 1749–1762.
- Beatty, C.D., Bain, R.S. and Sherratt, T.N. 2005. The evolution of aggregation in profitable and unprofitable prey. *Anim. Behav.*, **70**: 199–208.
- Creutz, G. 1953. Heteropteren als Vogelnahrung. *Beitrage zur Entomologie*, **3**: 411–419.
- Evans, D.L. and Waldbauer, G.P. 1982. Behavior of adult and naive birds when presented with a bumblebee and its mimic. *Zeitschrift für Tierpsychologie*, **59**: 247–259.
- Exnerová, A., Landová, E., Štys, P., Fuchs, R., Prokopová, M. and Cehláriková, P. 2003a. Reactions of passerine birds to aposematic and non-aposematic bugs (*Pyrrhocoris apterus*; Heteroptera). *Biol. J. Linn. Soc.*, **78**: 517–525.
- Exnerová, A., Štys, P., Křištín, A., Volf, O. and Pudil, M. 2003b. Birds as predators of true bugs (Heteroptera) in different habitats. *Biologia*, **58**: 253–264.
- Exnerová, A., Svádová, K., Štys, P., Barcalová, S., Landová, E., Prokopová, M. *et al.* 2006. Importance of colour in the reaction of passerine predators to aposematic prey: experiments with mutants of *Pyrrhocoris apterus* (Heteroptera). *Biol. J. Linn. Soc.*, **88**: 143–153.

- Fisher, R.A. 1958. *The Genetical Theory of Natural Selection*, 2nd edn. New York: Dover.
- Gamberale-Stille, G. and Sillén-Tullberg, B. 1999. Experienced chicks show biased avoidance of stronger signals: an experiment with natural color variation in live aposematic prey. *Evol. Ecol.*, **13**: 579–589.
- Harrap, S. and Quinn, D. 1996. *Tits, Nuthatches and Treecreepers*. London: Christopher Helm.
- Howarth, B. and Edmunds, M. 2000. The phenology of Syrphidae (Diptera): are they Batesian mimics of Hymenoptera? *Biol. J. Linn. Soc.*, **71**: 437–457.
- Järvi, T., Sillén-Tullberg, B. and Wiklund, C. 1981. The cost of being aposematic – an experimental study of predation on larvae of *Papilio machaon* by the Great Tit *Parus major*. *Oikos*, **36**: 267–272.
- Kauppinen, J. and Mappes, J. 2003. Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeshna grandis*). *Anim. Behav.*, **66**: 505–511.
- Komárek, S. 2000. *Mimicry, Aposematism and Related Phenomena – Mimetism in Nature and the History of Its Study*. Munich: LINCOM.
- Krall, B.S., Bartelt, R.J., Lewis, C.J. and Whitman, D.W. 1999. Chemical defense in the Stink Bug *Cosmopepla bimaculata*. *J. Chem. Ecol.*, **25**: 2477–2494.
- Lindström, L., Alatalo, R.V., Lyytinen, A. and Mappes, J. 2001. Predator experience on cryptic prey affects the survival of conspicuous aposematic prey. *Proc. R. Soc. Lond. B*, **268**: 357–361.
- Marples, N.M. and Kelly, D.J. 1999. Neophobia and dietary conservatism: two distinct processes? *Evol. Ecol.*, **13**: 641–653.
- Marples, N.M., Kelly, D.J. and Thomas, R.J. 2005. The evolution of warning coloration is not paradoxical. *Evolution*, **59**: 933–940.
- Musolin, D.L. and Saulich, A.H. 1995. Factorial regulation of the seasonal cycle of the Stink Bug *Graphosoma lineatum* L. (Heteroptera: Pentatomidae). I. Temperate and photoperiodic responses. *Entomologicheskoe Obozrenie*, **74**: 736–743 (in Russian).
- Nilsson, M. and Forsman, A. 2003. Evolution of conspicuous coloration, body size and gregariousness: a comparative analysis of lepidopteran larvae. *Evol. Ecol.*, **17**: 51–66.
- Popov, G.A. 1971. Rearing of bugs (Hemiptera, Pentatomidae) for the cultures of egg parasites of *Eurygaster integriceps*. *Byulleten' Vsesoyuznogo Nauchno-Issledovatel'skogo Instituta Zashchity Rastenii*, **19**: 3–10 (in Russian).
- Reader, T. and Hochuli, D.F. 2003. Understanding gregariousness in a larval lepidopteran: the roles of host plant, predation, and microclimate. *Ecol. Entomol.*, **28**: 729–737.
- Riipi, M., Alatalo, R.V., Lindström, L. and Mappes, J. 2001. Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. *Nature*, **413**: 512–514.
- Schlee, M.A. 1986. Avian predation on Heteroptera: experiments on the European Blackbird *Turdus m. merula* L. *Ethology*, **73**: 1–18.
- Sillén-Tullberg, B. 1985. The significance of coloration *per se*, independent background, for predator avoidance of aposematic prey. *Anim. Behav.*, **33**: 1382–1384.
- Sillén-Tullberg, B. and Leimar, O. 1988. The evolution of gregariousness in distasteful insects as a defense against predators. *Am. Nat.*, **132**: 723–734.
- Tietz, D. and Zrzavý, J. 1996. Dorsoventral pattern formation: morphogenesis of longitudinal coloration in *Graphosoma lineatum* (Heteroptera: Pentatomidae). *Eur. J. Entomol.*, **93**: 15–22.
- Wiklund, C. and Järvi, T. 1982. Survival of distasteful insects after being attacked by naive birds – a reappraisal of the theory of aposematic coloration evolving through individual selection. *Evolution*, **36**: 998–1002.
- Zrzavý, J. 1994. Red bugs and the origin of mimetic complexes (Heteroptera: Pyrrhocoridae: Neotropical *Dysdercus* spp.). *Oikos*, **69**: 346–352.