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European birds and aposematic Heteroptera: review of comparative experiments

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Abstract

The efficiency of defensive mechanisms in 11 European aposematic species of Heteroptera against various passerine predators was analysed. Bird species differed in their reactions to aposematic preys: small insectivorous birds generally avoided aposematic bugs, but granivorous birds as well as large insectivorous birds frequently attacked them. The ability to overcome heteropteran chemical defences appears to be connected with the larger body size of birds and with their food-storing behaviour. From the bird's point of view, various red-and-black aposematic species of Heteroptera form a mimetic complex. However, antipredatory defence properties of individual species differ substantially in their efficiency against bird predators, and the nature of the mimetic complex is rather quasi-Batesian than Müllerian.

Key words: antipredatory defences, warning signals, Heteroptera Pentatomomorpha, Passeriformes.

Introduction

Aposematism is a type of antipredatory strategy, when the prey signals its own unprofitability by a signal understandable to predators (Ruxton *et al.*, 2004). There is considerable evidence that prey defences as well as warning signals may be multimodal, i.e. may consist of visual, behavioural, acoustic, olfactory and gustatory components. Two or more warning signals either reinforce themselves or act synergistically, and the effect may lead to predator's unlearned avoidance or phobia, may accelerate avoidance learning, or enhance memorability of the warning signal (Rowe and Guilford, 1999; Ruxton *et al.*, 2004). With few exceptions (Marples *et al.*, 1994) the evidence is based mainly on experiments with artificial prey items and model predator species (usually domestic chicks). Therefore, the function of multimodal warning signals and defences of real prey species against a variety of their natural predators remains largely unknown.

The Heteroptera possess multimodal antipredatory defences whose main components are (a) visual signals (warning coloration or cryptic coloration), (b) acoustic signals (warning stridulation), and (c) allelochemicals (signalling the unpalatability, or directly repellent to toxic; synthesized by exocrine glands or taken over from hostplants and sequestered). This complex array of antipredatory defences makes the Heteroptera an excellent model group for studying aposematism and mimicry. Our studies were focused mainly on following problems (1) universality of warning function of aposematic signals against different avian predators, (2) abilities of predators to overcome bug defence system, (3) comparison of the efficiency of defensive mechanisms of various heteropteran species, (4) role of individual species in the potential mimetic complex of red-and-black pentatomomorphan true bugs, (5) importance of various components of heteropteran warning signals for learning and discrimination in bird predators.

Materials and methods

Heteroptera

We tested the reactions of birds to adults of the following species: *Pyrrhocoris apterus* (L.), its white, yellow, and orange mutants, and brown-painted individuals; *Pyrrhocoris marginatus* (Kolenati); *Scantius aegyptius* (L.); *Lygaeus equestris* (L.)*/simulans* Deckert; *Spilostethus saxatilis* (Scopoli); *Tropidothorax leucopterus* (Goeze); *Horvathiolus superbus* (Pollich); *Corizus hyoscyami* (L.); *Graphosoma lineatum* (L.); *Eurydema oleraceum* (L.); *Eurydema ornatum* (L.). We included ladybirds *Coccinella septempunctata* L. and *Propylaea quatuordecimpunctata* (L.), and froghopper *Cercopis vulnerata* Rossi as possible non-heteropteran members of mimetic complexes.

Birds

Wild-caught passerine birds of the following species were tested: (1) mainly insectivorous species - *Turdus merula* L., *Erithacus rubecula* (L.), *Phoenicurus ochruros* (S. G. Gmelin), *Parus major* L., *Cyanistes caeruleus* (L.), *Periparus ater* (L.), *Lophophanes cristatus* (L.), *Poecile montanus* (Conrad), *Poecile palustris* (L.), *Aegithalos caudatus* (L.), *Sitta europaea* L., *Sylvia atricapilla* (L.); (2) partly granivorous species - *Passer montanus* (L.), *Passer domesticus* (L.), *Fringilla coelebs* L., *Carduelis chloris* (L.), and *Emberiza citrinella* L.. Hand-raised great tits (*P. major*) were used as naive predators in learning, memory, and discrimination experiments.

Experimental set-up

Experiments were carried out in the cage equipped with one-way glass, perch, and rotating feeding tray. Cage illumination simulated the full daylight spectrum. Bird's behaviour was scored as a continuous record in Observer Video-Pro (Noldus) and recorded by

videocamera. Each bird was deprived of food about two hours before starting the experiment. Experiment consisted of a sequence of several consecutive five-minute trials, during which the birds were offered individual bugs. The trials followed one after another and alternated with presentations of a standard prey, *Tenebrio molitor* L. larvae, to check bird's foraging motivation.

In the experiments with wild-caught birds, the sequence consisted of 5 trials with heteropterans. In experiments focused on learning in naive hand-reared birds, the sequence of five-minute trials continued until the birds reached the learning criterion. Memory or discrimination tests were performed next day after the learning session. The birds were subjected either to the sequence of trials with the same prey they learned to avoid, or with another prey, or to the preference test with several different types of prey.

Results and discussion

Universality of warning function of aposematic signals against different predators

Warning coloration of a certain species of Heteroptera does not have a universal function among passerine predators (Exnerová *et al.*, 2003). Smaller and insectivorous birds (chats, warblers and tits) generally avoided aposematic bugs, but granivorous birds (finches and buntings) as well as larger insectivorous birds (blackbirds and nuthatches) frequently attacked them. Even closely related bird species (family Paridae) can differ in the way they acquire the avoidance; it appears to be innate in some species and learned in others (Exnerová *et al.*, 2007). Surprisingly, firebugs (*P. apterus*) were avoided also by tree sparrows (*P. montanus*), which readily attacked and consumed unpalatable and poisonous ladybirds (*C. septempunctata*) during the experiments.

Abilities of predators to overcome bug defence system

Generally, it appears that body size (weight) of the bird affects its cautiousness in encounters with potentially noxious aposematic bugs. Out of nine passerine species tested with *P. apterus*, the smallest species (*A. caudatus* and *C. caeruleus*) were most cautious and the largest species (*T. merula*) most prone to attacking and consuming the firebugs (Exnerová *et al.*, 2003). Similar trend was observed in the experiments with *L. equestris/simulans*, *S. saxatilis*, and *G. lineatum*. Some predators may possess physiological or behavioural adaptations to overcome the prey defences (Yosef and Whitman, 1992). Nuthatches (*S. europaea*) and crested tits (*L. cristatus*) frequently used slits in the experimental cage for storing the bugs (*P. apterus*), then checked them time from time, and eventually consumed them, after the repellent secretion vanished. Both species store the food regularly; food-storing behaviour seems to be a general exaptation for consuming noxious prey.

Importance of heteropteran visual warning signals for learning and discrimination in bird predators

The colour is especially important cue for passerine predators among the various components of the visual warning signal of the true bugs. Majority of wild-caught birds (*P. major, C. caeruleus, E. rubecula, S. atricapilla*) experienced with red-and-black wild type of *P. apterus*, did not recognize its yellow and white colour mutants as the same prey, even though they had the same shape, size, and black pattern (Exnerová *et al.*, 2006). Similarly, naive great tits (*P. major*) primarily attended to colour and not pattern, when they learned to avoid *P. apterus* and its colour mutants. Moreover, their ability to generalize among various aposematic colours seems to be limited – birds generalized their experience with yellow form to the red one but not in the opposite direction. On the contrary, typical warning coloration (red-and-black) did not accelerate the avoidance learning when compared with the non-aposematic (uniformly brown) coloration. However, great tits remembered their experience with red-and-black *P. apterus* even after three months, while their memory for brown-painted form vanished.

Comparison of the efficiency of defensive mechanisms of various species of Heteroptera

Effectiveness of defensive mechanisms was assessed in the experiments with naive great tits (*P. major*), in which the rate of avoidance learning and memory for the experience with various species of Heteroptera was measured. *L. equestris/simulans* and *S. saxatilis* were strongly defended, the birds usually avoided them after one or two encounters, and even the attacked bugs usually survived. *G. lineatum* appeared similarly well defended, and was protected also by its strongly sclerotised cuticle. *P. apterus* was rather weakly defended; the birds usually took several encounters to develop the avoidance reaction and the encounters were usually lethal for the bug. *Eurydema* species seemed to be weakly defended, and they are probably quasi-Batesian mimics of other heteropterans and ladybirds; this hypothesis may explain their otherwise surprising colour polymorphism.

Role of individual species in the potential mimetic complex of red-and-black pentatomomorphan true bugs

Majority of red-and-black Pentatomomorpha from Central Europe form a mimetic complex. Wild-caught great tits (with a few exceptions) avoided all the heteropterans studied. Similarly, naive great tits generalized their experience with one of the red-and-black species to any other one, even if it was of quite different appearance. Nevertheless, protection of the individual species does not fit the simple Müllerian concept of all the species sharing the costs and benefits equally. Individual species play rather different roles in the complex: *L. eguestris/simulans* and *S. saxatilis* being effective models, and *P. apterus* rather quasi-Batesian mimic. The complex includes also non-heteropteran members – *C. septempunctata* and *C. vulnerata*, which both can play a role of models.

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