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 as 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 pentatomomorph 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); Scinticus 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 Cercois vulgaris 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. Mgelin), 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
trend was observed in the experiments with L. eques-
tions to overcome the prey defences (Yosef and Whit-
tually noxious aposematic bugs. Out of nine passerine
s with several different types of prey.

Results and discussion

Universality of warning function of aposematic sig-
_against different predators

Warning coloration of a certain species of Heteroptera
does not have a universal function among passerine
ners, and buntings) as well as larger insectivorous birds
the experiments with wild-caught birds, the se-
sequence consisted of 5 trials with heteropterans. In ex-
iments focused on learning in naive hand-reared
birds, the sequence of five-minute trials continued until
the birds reached the learning criterion. Memory or dis-
motion. The birds were 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 in-
dividual 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.

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Results and discussion

Universality of warning function of aposematic sig-

Warning coloration of a certain species of Heteroptera
does not have a universal function among passerine
predators (Exnerová et al., 2003). Smaller and insect-
vorous 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 (Ex-
nerová 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 ex-
periments.

Abilities of predators to overcome bug defence system

Generally, it appears that body size (weight) of the
bird affects its cautiousness in encounters with poten-
tially 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. equest-
ris/simulans, S. saxatilis, and G. lineatum. Some preda-
tors may possess physiological or behavioural adapta-
tions to overcome the prey defences (Yosef and Whit-
man, 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

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
tended 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 learn-
ing 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 mecha-
nisms 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 ex-
perience with various species of Heteroptera was meas-
ured. 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 sur-
vived. 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 re-
tion 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 heter-
opterans 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 heter-
opterans 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 appear-
ance. Nevertheless, protection of the individual species
does not fit the simple Müllerian concept of all the spe-
cies sharing the costs and benefits equally. Individual
species play rather different roles in the complex: L.
equestris/simulans and S. saxatilis being effective mod-
els, and P. apterus rather quasi-Batesian mimic. The

164
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References


YOSEF R., WHITMAN D. W., 1992.- Predator exaptations and defensive adaptations in evolutionary balance: No defence is perfect.- Evolutionary Ecology, 6: 527-536.

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