Jihočeská univerzita v Českých Budějovicích

Přírodovědecká fakulta

Mgr. Petr Veselý

Newly emerged Batesian mimicry protects only unfamiliar prey

Rigorózní práce

2010

České Budějovice

Veselý, P. 2010: Newly emerged Batesian mimicry protects only unfamiliar prey. RNDr. Thesis, 11 pp., Faculty of Science, The University of South Bohemia, České Budějovice, Czech Republic.

Annotation

The present RNDr. thesis comprises an original research paper testing the efficacy of signal of the Batesian mimic under various familiarity of the predator with the ancestral species from which the mimic evolved.

Finanční podpora

Tato rigorózní práce vznikla za finanční podpory, Grantové agentury České Republiky (206/08/H044), Grantové agentury Akademie věd (IAA601410803) a Ministerstva školství, mládeže a tělovýchovy (MSM6007665801)

Poděkování

Na tomto místě bych rád poděkoval všem, kteří se jakýmkoli způsobem zasloužili o to, že tato disertační práce vznikla, především spoluautorovi a mému školiteli Romanu Fuchsovi, ale i dalším členům naší pracovní skupiny. Dále bych chtěl poděkovat Keithu Edwardsovi, Ph.D. za kontrolu anglického manuskriptu, jakož i anonymním recenzentům, za plodné a užitečné připomínky k manuskriptu. V neposlední řadě bych chtěl poděkovat své rodině za podporu.

Prohlašuji, že svoji rigorózní práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své rigorózní práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou; elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

V Českých Budějovicích 19. 7. 2010

....

Evol Ecol (2009) 23:919–929
DOI 10.1007/s10682-008-9281-1

ORIGINAL PAPER

Newly emerged Batesian mimicry protects only unfamiliar prey

Petr Veselý · Roman Fuchs

Received: 14 September 2006 / Accepted: 30 October 2007 / Published online: 14 November 2008

Abstract The evolution of Batesian mimicry was tested experimentally using avian predators. We investigated the effect of a search image on the protection effectiveness of a newly emerged Batesian mimic. The two groups of predators (adult great tits, *Parus major*) differed in prior experience with prey from which the mimic evolved. The Guyana spotted roach (*Blaptica dubia*) was used as a palatable prey from which the mimic emerged, and red firebug (*Pyrrhocoris apterus*) was used as a model. Optical signalization of the insect prey was modified by a paper sticker placed on its back. The cockroaches with the firebug pattern sticker were significantly better protected against tits with no prior experience with cockroaches. The protection of the firebug sticker was equally effective on cockroaches as it was on firebugs. The cockroaches with firebug stickers were not protected against attacks of tits, which were familiar with unmodified cockroaches better than cockroaches with a cockroach sticker. We suppose that pre-trained tits acquired the search image of a cockroach, which helped them to reveal the "fake" Batesian mimic. Such a constraint of Batesian mimicry effectiveness could substantially decrease the probability of evolution of pure Batesian mimic systems.

Keywords Evolution of Batesian mimicry · Warning signalization · Neophobia · Search image

Introduction

One of the striking phenomena connected with antipredatory signalization is mimicry. Two basic forms of mimicry have been distinguished (see Fisher 1930): Müllerian, in which two protected species are mutually protected by similar signalization; and Batesian when one unprotected species (mimic) parasites on the protected one (model) by imitating its signal.

P. Veselý (✉) · R. Fuchs
Department of Zoology, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31,
370 05 Èeské Budìjovice, Czech Republic
e-mail: petr-vesely@seznam.cz

The initial evolution of Batesian (as well as Müllerian) mimicry has always been considered trouble-free. The basic dilemma of evolving the warning colouration (predators unfamiliar with a novel conspicuous prey kill all emerged individuals and, thus, such a form cannot spread in the population; see e.g., Guilford 1990; Alatalo and Mappes 1996) is solved in this case, as the predator is familiar with a warning signal of the model species. Nonetheless, the low amount of evidence of pure Batesian systems in nature (see e.g., Turner and Speed 1999) indicates that there are some constraints in the evolution of Batesian mimicry.

First and foremost, the population of the model species must be bigger than the population of the mimic species (Fisher 1930) so that the predator has a higher probability to encounter the model and learn (or recall) the connection between signal and quality (unpalatability) than the connection between the signal and mimic (without quality). Experimental evidence for this precondition was provided by Lindström et al. (1997). Experimental predators (great tits) were confronted with models (warning signal and unpalatability) as well as mimics (warning signal without unpalatability) in a novel world design. This experimental approach uses artificial prey, which can be considered as being completely novel to the predators even in terms of evolutionary history (see Lindström 1999 for details). The experiments of Lindström et al. (1997) show that a higher proportion of mimics in the prey population reduced the protection of the models against predator attack. Moreover, this study tested the effect of the degree of model unpalatability on the effectiveness of Batesian mimicry. The more unpalatable is the model the better protected is the mimic.

Another parameter that could condition the effectiveness of Batesian mimicry is the accuracy of the mimic signal. The more perfect (similar) is the mimic signal, the higher should be the probability of its confusion with the model (Hetz and Slobodchikoff 1988; Johnstone 2002; Sherratt 2002). The novel world experimental design was used to test this parameter in experiments carried out by Mappes and Alatalo (1997). They showed that even an imperfect mimic signal may provide some protection. Similarly, Lindström et al. (2006) did not observe any increase of mimic mortality if their signal was imperfect (Müllerian mimics were tested in this case). On the contrary, Dittrich et al. (1993) found different results. Pigeons were trained to assess the similarity of presented items (so called same/different task). During the experiment, the pigeons were offered less or more perfect Batesian mimics (several dronefly species) together with their hymenopteran models. The pigeons were not able to distinguish a perfect mimic from the model, but the imperfect ones were distinguishable. The difference between this study and the novel world experiments studies can be explained by the different experimental approach. While Dittrich et al. (1993) were interested in the cognitive abilities of pigeons (they did not perceive the items as a prey), the novel world experiments observed bird reaction to a prey. The approach of a predator to any prey (including Batesian mimics) is affected not only by the quality of the warning signalization, but also by the predator cognitive abilities (Osorio et al. 1999) or psychology (Speed 2000).

Phobia is one of the perspectives of predator psychology that should be important in the study of Batesian mimicry; this is supposed to lower the willingness of the predator to attack encountered prey (Speed 2000). A specific case of phobia is fear of an unknown prey. This phenomenon was described as neophobia or dietary conservatism (see Marples and Kelly 1999). Both of these perspectives describe a wariness of new, unknown prey, but their principles are different. Neophobia is an immediate response that may subside rather fast, while dietary conservatism is a stable long-term phenomenon (see e.g., Greenberg and Mettke-Hoffman 2001). There are several experiments with various bird predators (zebra finch, domestic chick, robins or blackbird), which prove the neophobical reaction towards unknown warning colours or odours (Marples and Roper 1996; Marples et al. 1998; Kelly and Marples 2004, respectively). A computer simulation (Speed 2001) as well as an experimental study (Thomas et al. 2003) proved that neophobia (or/and dietary conservatism) induced the spreading of an unfamiliar conspicuous form in the population. The review of Marples et al. (2005) also emphasizes the key role of neophobia in the evolution of warning signalization.

The predator's reaction to a warning signalling prey could also affect another aspect of animal cognitive abilities caused by the limited rate of information processing in the animal brain. This constraint is called limited attention and it affects various components of animal behaviour (Dukas 2002, 2004). In foraging processes, limited attention results in selective attention to a specific (e.g., most abundant or most profitable) prey; this is more effective than spreading the search for various prey types (Bond and Kamil 1999; Dukas and Kamil 2001). This selective attending to the desired prey is called a search image (Dukas 2002). The existence and principles of a search image have been experimentally tested with several avian species (Great tits—Tinbergen 1960; chicks—Dawkins 1971 and blue jays—Pietrewicz and Kamil 1979; Bond and Kamil 1999; Dukas and Kamil 2001).

Neophobia and search image work together, because the former causes the refusal of an unfamiliar prey and the latter a preference for a desired (and familiar) prey. Therefore, if a Batesian mimic arises in a population of unprotected palatable prey; Both the search image and neophobia of a predator should lower the willingness to attack it. Lindström et al. (2004) found that predators were more likely to refuse an unfamiliar warning coloured and unpalatable prey as well as its Batesian mimics if an alternative cryptic and palatable prey was more available. We suppose that the predators form a search image of the cryptic prey, resulting in a lack of interest to other potential prey.

Nevertheless, if the predator prefers the ancestor prey and possesses its search image, its reaction to a newly emerged Batesian mimic could be quite different. Forming a search image may employ several prey features, such as conspicuousness (Blough 1989a; Dukas and Ellner 1993), size (Blough 1989b) or shape (Blough 1985; Blough and Franklin 1985). The colour is undoubtedly the most conspicuous characteristic of a prey, but other features can be used for prey recognition as well. For example, insects provide several characteristics like body shape, length of legs or antennae, way of movement (e.g., Yamawaki 2000, 2003) or absence of repugnant odour (Roper and Marples 1997; Rowe and Guilford 1999; Lindström et al. 2001). If a search image includes such features of a prey, a predator can reveal the signal fake of a Batesian mimic and attack it. The newly emerged warning coloured form will not spread in the population in such a case.

In the present study, we experimentally simulated the emergence of a warning coloured Batesian mimic in the population of an edible prey. We used a real insect prey species, which provides several signals to the predator (Guyana spotted roach—*Blaptica dubia*). It was provided with a perfect colour pattern of a well protected model insect species, the red firebug (*Pyrrhocoris apterus*; see e.g., Exnerová et al. 2003). Adult great tits (*Parus major*) were used. These were caught in the wild as predators supposedly being familiar with the model from nature (Exnerová et al. 2003).

We tested the following hypotheses:

H1 The cockroach mimicking red firebug is protected against predators unfamiliar with the cockroach.

H2 The cockroach mimicking red firebug is less protected against predators familiar with the cockroach (possessing a search image of it) than against unfamiliar ones.

Materials and methods

Experimental prey

The red firebug, *Pyrrhocoris apterus* (L., 1758), has a red and black colouration that has been proved to be a warning signal (Wiklund and Järvi 1982; Exnerová et al. 2003, 2007). It also possesses a chemical defence based on short-chained alkanes and their derivatives, produced by the repugnatory metathoracic glands (Farine et al. 1992). Firebugs for the experiments were collected in the surroundings of České Budějovice (South Bohemia, Czech Republic) during 2004 and 2005. Groups of about 50 individuals were kept in the laboratory in glass jars (15 cm in diameter). Dry linden tree seeds (*Tilia cordata*) and water were supplied *ad libitum*.

The Guyana spotted roach, *Blaptica dubia* (Audinet-Serville, 1838), is used as a common feed for insectivorous animals. Similarly as with other cockroach species, it uses chemical protection when endangered; it empties its stomach and stains the predator with its contents. Cockroaches in our experiments used this strategy when trying to avoid attacks of experimental great tits, but as they were fed mostly with carrots, the titmice were not repelled by these excretions and considered Guyana spotted roaches palatable. In our experiments, we used the second and third larval instar (8–14 mm in length equalling firebug length), which are brownish with dark and pale spots. They were kept in a glass terrarium (40 × 30 × 20 cm) at high densities. Fresh vegetables (carrot, beet root, and potatoes), dry cat and dog foods and water were supplied *ad libitum*.

Both insect species were reared at 25°C under long-day (18 h light, 6 h dark) conditions. These two insect species are of comparable appearance, with similar body shapes and movements. The main differences between the species are in the shape of the antennae and legs, and in body posture.

The natural colouration of the experimental prey was changed using paper stickers placed on its back, thus covering the body of the insect from above and partially from the sides. Stickers are very useful in modifying the colouration of insects and do not influence the insect's behaviour. There were four experimental prey types (Fig. 1), as each of the tested prey species could "wear" two types of stickers, either a cockroach or a firebug pattern. The sticker patterns were made from printed photographs of both insect species.

Experimental predators

Adult great tits (*Parus major* L., 1758), caught with mist nets in the vicinity of České Budějovice (South Bohemia, Czech Republic), were used as experimental predators. Captures were conducted during 2004–2006, except during the breeding seasons

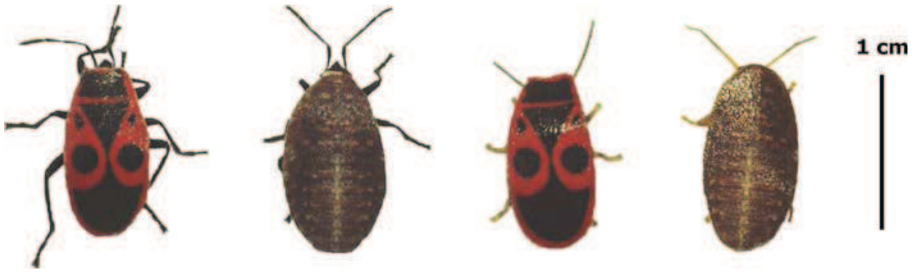

Fig. 1 Experimental prey types. From the *left* firebug with firebug sticker, firebug with cockroach sticker, cockroach with firebug sticker, cockroach with cockroach sticker

(May–July). Birds were kept in standard birdcages at lowered indoor temperature and under outdoor photoperiod conditions. Birds were acclimatized to laboratory conditions and food (sunflower seeds and mealworms or cockroaches, see "Trials") for one to 2 days prior to the experiments. They were ringed and released immediately after the experiments.

Experimental equipment

The experimental cages were made from wooden cubic frames (0.7 m × 0.7 m × 0.7 m) covered with wire mesh (2 × 2 mm) and with a one-way mirror as a front wall (see Exnerová et al. 2003 for details). The cages were equipped with one perch, a bowl with water, and a rotating circular feeding tray, containing six small cups (only one cup contained a prey item during each trial). The distance between the perch and the tray was approximately 25 cm. The bottom of the cups was white. Standard illumination was generated by a light source (LUMILUX COMBI 18 W, OSRAM) that simulates full daylight spectrum (including UV radiation).

Trials

The 120 tested great tits were divided into two groups. The first group (80 individuals) was fed mealworms during acclimatization in the laboratory. The other 40 individuals were fed cockroaches. The food was supplied *ad libitum* in both groups, so that several tens of prey items were eaten during the pre-experimental period. Subsequently, the birds from the first group were divided into four groups of 20 individuals each. The first group was offered cockroaches with cockroach pattern stickers. The second group was given cockroaches with firebug pattern stickers. The third group was offered firebugs with cockroach stickers and the fourth group was presented with firebugs with firebug stickers. The birds that were fed cockroaches were divided into two groups of 20 individuals. The first was offered cockroaches with cockroach stickers and the other group was presented with cockroaches with firebug stickers. To avoid pseudo-replication, each individual bird was used for a single series of trials only.

Each bird was placed into the experimental cage before the experiment in order to adapt itself to the new conditions, and was provided with food (mealworms or cockroaches according to the experimental group) and water. Each bird was deprived of food for 1.5–2.5 h prior to the experiment to enhance its motivation.

The bird was assumed to be ready for the experiment as soon as it attacked the offered prey immediately after introduction. Each experiment with an individual bird consisted of a series of four trials, in which two control preys (mealworm or cockroach without any sticker) and two experimental preys (stickered cockroach or firebug) were offered alternately, starting with the control prey (sequence control/experimental/control/experimental). The control prey was used to check the bird's motivation to forage, and the trial ended after the prey was eaten. The trials with experimental prey always lasted 5 min.

We distinguished three possible results of each trial: (1) the experimental prey was neither handled nor killed during the 5 min trial, (2) the prey was handled (touched, pecked or seized) but not killed; (3) the prey was killed.

Statistical analyses

The numbers of birds that handled or killed at least one of the two offered experimental prey were used to compare the experimental groups of predators (all tests were performed

Table 1 Fisher exact test statistics comparing the frequencies of handled or killed insects between the first and second group

First group			Second group			Fisher exact test *P* value	
Predator search image	Prey species	Sticker pattern	Predator search image	Prey species	Sticker pattern	Handling	Killing
Mealworm	Cockroach	Cockroach	Mealworm	Cockroach	Firebug	0.0003	0.0012
Mealworm	Cockroach	Firebug	Mealworm	Firebug	Firebug	0.4075	0.3416
Mealworm	Firebug	Cockroach	Mealworm	Firebug	Firebug	1	1
Mealworm	Cockroach	Firebug	Cockroach	Cockroach	Firebug	<0.0001	<0.0001
Mealworm	Cockroach	Cockroach	Cockroach	Cockroach	Cockroach	0.2308	0.0471

in Statistica 5.5, 1984–1999, ©StatSoft, Inc.). A Fisher exact test was used to compare the proportions of birds handling or killing the offered prey (Fisher 1922). The compared groups are described in Table 1.

Results

All control mealworms or cockroaches were killed and eaten during the 5 min trials.

Warning function of the firebug pattern placed on unfamiliar palatable prey (experiments with predators used to being fed mealworms)

Cockroaches were well protected from attacks of predators inexperienced with cockroaches (as a prey) when disguised by the firebug pattern stickers. A significantly smaller number of great tits handled and killed cockroaches with firebug stickers than those with cockroach stickers (Table 1, row 1; Fig. 2). Cockroaches with the firebug stickers were protected against being handled or killed equally as firebugs with the firebug stickers (Table 1, row 2; Fig. 2). On the other hand, the cockroach stickers did not lower the protection of firebugs from predator's attack. The firebugs with the cockroach stickers were not handled nor killed more often than the firebugs with the firebug stickers (Table 1, row 3; Fig. 2).

Warning function of the firebug pattern placed on familiar palatable prey (experiments with predators used to being fed cockroaches)

Firebug pattern did not protect cockroaches from attack of predators experienced with cockroaches as prey. The Great Tits used in these experiments handled and killed cockroaches more often when familiar with the cockroach (Table 1, row 4; Fig. 2). Since some great tits inexperienced with cockroaches did not attack cockroaches with the cockroach sticker, there was a significant difference in the killing, but not on handling, of this prey between experienced and inexperienced great tits (Table 1, row 5; Fig. 2).

Discussion

Our experiments with predators used to the mealworms proved the protective function of the firebug pattern placed on palatable as well as unpalatable insect prey. The edible prey

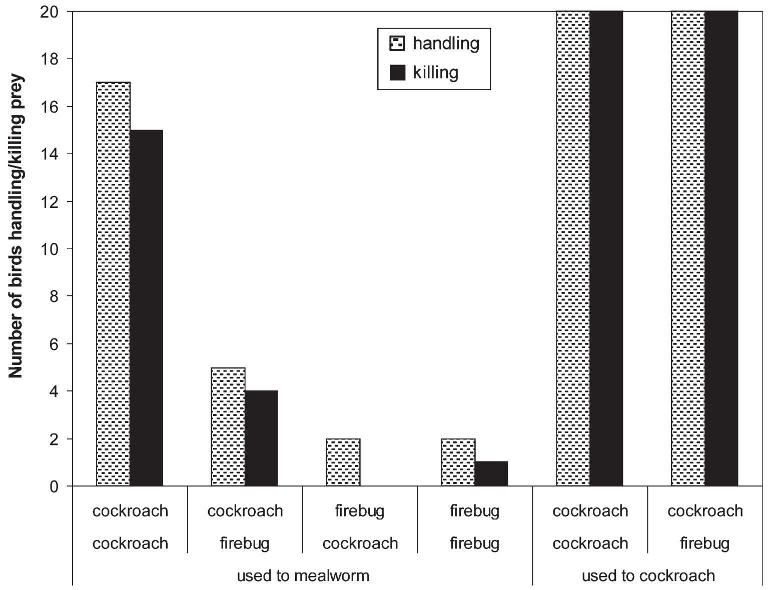

Fig. 2 Number of great tits that handled or killed at least one of two offered prey. Under each column there is (from above down): **a** prey species, **b** sticker type, **c** experience of predator

was protected equally from predator attack as the inedible one. These results support the traditional theory of evolution of Batesian mimicry formulated in the nineteenth century (Bates 1862 and Poulton 1890 ex. Komárek 2003). We have shown that prey protected by no chemical defence or other defensive mechanism profits from mimicking other protected species. This result is in concordance with conclusions of most experimental studies testing the efficacy of Batesian mimics' signalling using real unmodified prey and real predators (Prudic et al. 2002; Kauppinen and Mappes 2003; Taniguchi et al. 2005; Nelson et al. 2006a, b or Sherbrooke and Westphal 2006).

On the other hand, our experiments showed that the unpalatable prey was protected regardless of its colouration; the predators were able to identify the firebug even when covered with a cockroach sticker. This result suggests that the red firebug's warning signalization comprises not only conspicuous coloration. It is possible that birds can detect the scent of firebugs upon closer inspection, but a significant proportion of the experimental birds avoided attacking a cockroach stickered firebug without even approaching it. Moreover, firebugs actively release a noxious substance only when disturbed (Socha 1993). We can presume that other optical firebug signals, such as body posture, shape and length of antennae and legs or whole body shape, could help the predator to recognize a firebug. Our finding, that the protection of unpalatable prey remains even when warning colouration is artificially removed, is not unique. Exnerová et al. (2003, 2007) reached similar conclusions with the red firebug and some passerine predators (e.g., marsh tits). Similarly, in experiments with dragonflies as predators, wasps (as prey) lost a significant part of their protection when deprived of their natural warning colouration (Kauppinen and Mappes 2003).

In contrast to great tits fed with mealworms, the birds used to being fed with cockroaches were not repelled by the warning colouration of cockroaches with firebug stickers. None of the tested birds was misled by the colouration of the sticker.

It is probable that the compared groups of birds possessed different prey search images in their minds. The mealworm-diet birds were ready to attack prey of a worm-like appearance. Therefore, they were not able to distinguish an edible cockroach under the warning colour sticker. Birds used to the cockroach diet searched for a prey of cockroach-like appearance, since they were able to identify a cockroach under the sticker.

This result is unique in the context of current studies which test Batesian mimic efficacy experimentally. The cause of this incoherence lies doubtlessly in the different design of our experiments. In other studies, pre-trained predators had been used, but they were always familiarised only with model species (Ritland 1991; Taniguchi et al. 2005; Darst and Cummings 2006), not with the species from which the Batesian mimic evolved.

The most important conclusion of our experiments is the possibility that Batesian mimics are less protected against predators possessing a search image of the unprotected prey from which the Batesian mimics evolved. Such a limitation of Batesian mimicry effectiveness should significantly decrease the profitability (and thereby the probability) of the emergence of Batesian mimics. Most species have their more or less specialized predator(s), which possesses its search image at a high probability. Restricting the protection of Batesian mimics could significantly help to clarify the low occurrence of pure Batesian systems in nature.

Predators form a search image of frequently encountered (and therefore common) prey (see e.g., Dukas and Kamil 2001). A Batesian mimic originating in a population of rare (in space as well as in time) prey should be protected better than a mimic that emerges from an at least locally common population. Fisher (1930) proposed the necessity of a low abundance of mimic species as a basic precondition for the function of Batesian mimicry. Our results suggest that, for the evolution of a Batesian mimic, a low abundance of ancestral species per se is necessary, regardless of the abundance of the model species.

Our results show that, in some circumstances, the warning colouration itself is not sufficient for the protection of Batesian mimics. The search image of a prey is a multi-modal phenomenon perceived by different senses (e.g., optical and olfactory—Chiszar et al. 1985 or Gazit et al. 2005). Evolution should favour Batesian mimics differing from their unprotected ancestors and resembling the model in as many features as possible. Some observations from nature, describing behavioural Batesian mimicry (e.g., similar way of movement in droneflies and hymenopterans—Golding and Edmunds 2000; Golding et al. 2001; Srygley 2004 or the evidence of compound mimicry in ants and their spider mimic—Nelson and Jackson 2006), are in concordance with this prediction.

Droneflies (Diptera, Syrphidae) are a group where pure Batesian mimics very often occur; see Howarth et al. (2004). This can be explained by the theory of search image as well. These flies are well known for their unusually high flight speed (see e.g., Nachtigall 2003). A predator possessing a search image of a fly (e.g., spotted flycatcher *Muscicapa striata* searching for prey using the “sit and wait” foraging technique, see e.g., Davies 1977) then has only a minor opportunity to examine a mimicking dronefly elaborately and thus confuses it easily with a wasp. However, a predator searching for prey using the gleaning foraging technique (e.g., great tit in our experiments) could easily reveal a fake behind the mimicking, because it has enough time for prey observation.

Acknowledgments We thank Dr. Keith Edwards for the language improvement. We thank the Academy of Sciences of the Czech Republic (IAA601410803), Ministry of Education, Youth and Sport of the Czech Republic (MSM 6007665801) and the Grant Agency of the Czech Republic (206/08/H044) for financial support. Authors are licensed for catching and ringing birds (Bird Ringing Centre Prague No. 1004) and for animal experimentation (Czech Animal Welfare Commission No. 489/01).

References

Alatalo RV, Mappes J (1996) Tracking the evolution of warning signals. Nature 382(6593):708–710

Audinet-Serville JG (1838) Suites à buffon. Paris

Bates HW (1862) Contributions to an insect fauna of the Amazon Valley. Trans Linn Soc Zool 23:495–566

Blough DS (1985) Discrimination of letters and random dot patterns by pigeons and humans. J Exp Psychol Anim B 11(2):261–280

Blough DS (1989a) Contrast as seen in visual-search reaction-times. J Exp Anal Behav 52(3):199–211

Blough DS (1989b) Odd-item search in pigeons—display size and transfer effects. J Exp Psychol Anim B 15(1):14–22

Blough DS, Franklin JJ (1985) Pigeon discrimination of letters and other forms in texture displays. Percept Psychophys 38(6):523–532

Bond AB, Kamil AC (1999) Searching image in blue jays: facilitation and interference in sequential priming. Anim Learn Behav 27(4):461–471

Chiszar D, Radcliffe CW, Overstreet R et al (1985) Duration of strike-induced chemosensory searching in cottonmouths (*Agkistrodon piscivorus*) and a test of the hypothesis that striking prey creates a specific search image. Can J Zool 63(5):1057–1061

Darst CR, Cummings ME (2006) Predator learning favours mimicry of a less-toxic model in poison frogs. Nature 440(7081):208–211

Davies NB (1977) Prey selection and search strategy of spotted flycatcher (*Muscicapa striata*)—field study on optimal foraging. Anim Behav 25:1016–1024

Dawkins M (1971) Perceptual changes in chicks: another look at the ‘search image’ concept. Anim Behav 19:566–574

Dittrich W, Gilbert F, Green P et al (1993) Imperfect mimicry—a pigeons perspective. P R Soc B-Biol Sci 251(1332):195–201

Dukas R (2002) Behavioural and ecological consequences of limited attention. Philos T R Soc B 357(1427):1539–1547

Dukas R (2004) Causes and consequences of limited attention. Brain Behav Evol 63(4):197–210

Dukas R, Ellner S (1993) Information processing and prey detection. Ecology 74:1337–1346

Dukas R, Kamil AC (2001) Limited attention: the constraint underlying search image. Behav Ecol 12:192–199

Exnerová A, Landová E, Štys P et al (2003) Reactions of passerine birds to aposematic and non-aposematic bugs (*Pyrrhocoris apterus*; Heteroptera). Biol J Linn Soc 78:517–525

Exnerová A, Štys P, Fučíková E et al (2007) Avoidance of aposematic prey in European Tits (Paridae): Learned or innate? Behav Ecol 18(1):148–156

Farine JP, Bombard O, Brossut R et al (1992) Chemistry of defensive secretions in nymphs and adults of fire bug, *Pyrrhocoris apterus* L. (Heteroptera, Pyrrhocoridae). J Chem Ecol 18(10):1673–1682

Fisher RA (1922) On the interpretation of χ^2 from contingency tables, and the calculation of P. J R Stat Soc 85(1):87–94

Fisher RA (1930) The genetical theory of natural selection. Mimicry, 2nd edn. Dover, New York

Gazit I, Goldblatt A, Terkel J (2005) Formation of an olfactory search image for explosives odours in sniffer dogs. Ethology 111(7):669–680

Golding YC, Edmunds M (2000) Behavioural mimicry of honeybees (*Apis mellifera*) by droneflies (Diptera:Syrphidae:Eristalis spp.). P R Soc B-Biol Sci 267(1446):903–909

Golding YC, Nenos AR, Edmunds M (2001) Similarity in flight behaviour between the honeybee *Apis mellifera* (Hymenoptera:Apidae) and its presumed mimic, the dronefly Eristalis tenax (Diptera:Syrphidae). J Exp Biol 204(1):139–145

Greenberg R, Mettke-Hoffman C (2001) Ecological aspects of neophobia and exploration in birds. Cur Ornit 16:119–169

Guilford T (1990) Evolutionary pathways to Aposematism. Int J Ecol 11(6):835–841

Hetz M, Slobodchikoff CN (1988) Predation pressure on an imperfect Batesian Mimicry Complex in the presence of alternative prey. Oecologia 76(4):570–573

Howarth B, Edmunds M, Gilbert F (2004) Does the abundance of hoverfly (syrphidae) mimics depend on the numbers of their hymenopteran models? Evolution 58(2):367–375

Johnstone RA (2002) The evolution of inaccurate mimics. Nature 418(6897):524–526

Kauppinen J, Mappes J (2003) Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeshna grandis*). Anim Behav 66:505–511

Kelly DJ, Marples NM (2004) The effects of novel odour and colour cues on food acceptance by the zebra finch, *Taeniopygia guttata*. Anim Behav 68:1049–1054

Komárek S (2003) Mimicry, Aposematism and related phenomena—Mimetism in nature and the history of its study. LINCOM, München

Lindström L (1999) Experimental approaches to studying the initial evolution of conspicuous aposematic signalling. Evol Ecol 13(7–8):605–618

Lindström L, Alatalo RV, Mappes J (1997) Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. P R Soc B-Biol Sci 264(1379):149–153

Lindström L, Rowe C, Guilford T (2001) Pyrazine odour makes visually conspicuous prey aversive. P R Soc B-Biol Sci 268(1463):159–162

Lindström L, Alatalo RV, Lyytinen A et al (2004) The effect of alternative prey on the dynamics of imperfect Batesian and Mullerian mimicries. Evolution 58(6):1294–1302

Lindström L, Lyytinen A, Mappes J et al (2006) Relative importance of taste and visual appearance for predator education in Mullerian mimicry. Anim Behav 72:323–333

Mappes J, Alatalo RV (1997) Batesian mimicry and signal accuracy. Evolution 51:2050–2053

Marples NM, Kelly DJ (1999) Neophobia and dietary conservatism: two distinct processes? Evol Ecol 13:641–653

Marples NM, Roper TJ (1996) Effects of novel colour and smell on the response of naive chicks towards food and water. Anim Behav 51:1417–1424

Marples NM, Roper TJ, Harper DGC (1998) Responses of wild birds to novel prey: evidence of dietary conservatism. Oikos 83(1):161–165

Marples NM, Kelly DJ, Thomas RJ (2005) Perspective: the evolution of warning coloration is not paradoxical. Evolution 59(5):933–940

Nachtigall W (2003) High flight speeds in subalpine diptera. Entomol Gen 26(4):235–239

Nelson XJ, Jackson RR (2006) Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics. P R Soc B-Biol Sci 273(1584):367–372

Nelson XJ, Jackson RR, Li DQ et al (2006a) Innate aversion to ants (Hymenoptera:Formicidae) and ant mimics: experimental findings from mantises (Mantodea). Biol J Linn Soc 88(1):23–32

Nelson XJ, Li DQ, Jackson RR (2006b) Out of the frying pan and into the fire: a novel trade-off for batesian mimics. Ethology 112(3):270–277

Osorio D, Miklosi A, Gonda Z (1999) Visual ecology and perception of coloration patterns by domestic chicks. Evol Ecol 13(7–8):673–689

Pietrewicz A, Kamil AC (1979) Search image formation in the blue jay (*Cyanocitta cristata*). Science 204:1332–1333

Poulton EB (1890) The colours of animals. Int Sci Ser 68:360–395

Prudic KL, Shapiro AM, Clayton NS (2002) Evaluating a putative mimetic relationship between two butterflies, *Adelpha bredowii* and *Limenitis lorquini*. Ecol Entomol 27(1):68–75

Ritland DB (1991) Revising a classic butterfly mimicry scenario-demonstration of Mullerian mimicry between Florida viceroys (*Limenitis-Archippus-Floridensis*) and queens (*Danaus-Gilippus-Berenice*). Evolution 45(4):918–934

Roper TJ, Marples NM (1997) Odour and colour as cues for taste-avoidance learning in domestic chicks. Anim Behav 53:1241–1250

Rowe C, Guilford T (1999) The evolution of multimodal warning displays. Evol Ecol 13(7–8):655–671

Sherbrooke WC, Westphal MF (2006) Responses of greater roadrunners during attacks on sympatric venomous and nonvenomous snakes. Southwest Nat 51(1):41–47

Sherratt TN (2002) The evolution of imperfect mimicry. Behav Ecol 13(6):821–826

Socha R (1993) *Pyrrhocoris apterus* (Heteroptera)—an experimental model species: a review. Eur J Entomol 90(3):241–286

Speed MP (2000) Warning signals, receiver psychology and predator memory. Anim Behav 60:269–278

Speed MP (2001) Can receiver psychology explain the evolution of aposematism? Anim Behav 61:205–216

Srygley RB (2004) The aerodynamic costs of warning signals in palatable mimetic butterflies and their distasteful models. P R Soc B-Biol Sci 271(1539):589–594

Taniguchi K, Maruyama M, Ichikawa T et al (2005) A case of Batesian mimicry between a myrmecophilous staphylinid beetle, *Pella comes*, and its host ant, *Lasius (Dendrolasius) spathepus*: an experiment using the Japanese treefrog, *Hyla japonica* as a real predator. Ins Soc 52(4):320–322

Thomas RJ, Marples NM, Cuthill IC et al (2003) Dietary conservatism may facilitate the initial evolution of aposematism. Oikos 101(3):458–466

Tinbergen N (1960) The natural control of insects in pine woods: Vol. I. Factors influencing the intensity of predation by songbirds. Arch Neeland Zool 13:265–343

Turner JRG, Speed MP (1999) How weird can mimicry get? Evol Ecol 13(7–8):807–827

Wiklund C, Järvi T (1982) Survival of distasteful insects after being attacked by naive birds: reappraisal of the theory of aposematic coloration evolving through individual selection. Evolution 36:998–1002

Yamawaki Y (2000) Effects of luminance, size, and angular velocity on the recognition of nonlocomotive prey models by the praying mantis. J Ethol 18(2):85–90

Yamawaki Y (2003) Responses to worm-like-wriggling models by the praying mantis: effects of amount of motion on prey recognition. J Ethol 21(2):123–129