Avoidance of aposematic prey in European tits (Paridae): learned or innate?

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Predators may either learn to avoid aposematic prey or may avoid it because of an innate bias. Learned as well as innate avoidance has been observed in birds, but the existing evidence is based on experiments with rather few unrelated model species. We compared the origin of avoidance in European species of tits (Paridae). First, we tested whether wild-caught birds (blue tits, great tits, crested tits, coal tits, willow tits, and marsh tits) avoid aposematic (red and black) adult firebugs *Pyrrhocoris apterus* (Heteroptera) more than nonaposematic (brown painted) ones. Larger proportion of birds avoided aposematic than brown-painted firebugs in majority of species (except coal tits). Second, we tested whether naive hand-reared birds of 4 species (blue tits, great tits, crested tits, and coal tits) attack or avoid aposematic and nonaposematic firebugs, both novel for them. Behavior of the naive blue tits and coal tits was similar to that of the wild-caught birds; majority of them did not attack the firebugs. Contrastingly, the naive great tits and crested tits behaved differently than the wild-caught conspecific adults; majority of the wild-caught birds avoided the aposematic firebugs, whereas the naive birds usually did not show any initial avoidance and had to learn to avoid the aposematic prey. Our results show that the origin of avoidance may be different even in closely related species. Because blue tits and coal tits avoided not only aposematic firebugs but also their brown-painted form, we interpret their behavior as innate neophobia rather than innate bias against the warning coloration. *Key words:* aposematism, European Paridae, innate avoidance, learning, neophobia, *Pyrrhocoris apterus*. *[Behav Ecol 18:148–156 (2007)]*

A posematism is a type of antipredatory strategy, when the prey signals its unprofitability by a signal understandable to predators (Ruxton et al. 2004). Birds, mainly visual predators, are widely used as model predators of aposematic prey (e.g., Sillén-Tullberg 1985; Marples et al. 1994; Alatalo and Mappes 1996; Gamberale and Tullberg 1996; Rowe and Guilford 1996; Lindström et al. 1999; Thomas et al. 2003). Studies taking into account various specific traits of different bird predators are still scarce (Endler and Mappes 2004). In our previous study (Exnerová, Landová et al. 2003), we found substantial differences in attitudes of 9 passerine species toward a model heteropteran prey—the firebug *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). However, the interspecific variation in an acquirement of avoidance of aposematic prey has not been investigated comparatively.

Predators may either learn to avoid aposematic prey or may avoid the prey because of an innate bias against a particular trait of the prey (Lindström et al. 1999). Many studies have demonstrated importance of associative learning of predators. Color (Sillén-Tullberg 1985), taste (Marples et al. 1994), smell (Roper and Marples 1997), gregariousness of prey (Gamberale and Tulberg 1998; Riipi et al. 2001), and its contrast with the background (Roper 1994) may facilitate avoidance learning of noxious prey in birds.

The evidence that some bird species may have an innate ability to avoid aposematic prey exists for venomous snakes, which are potentially lethal to predators (Pough 1988). Smith

(1975, 1977) found that naive hand-reared turquoise-browed motmots (*Eumomota superciliosa*) and great kiskadees (*Pitangus sulphuratus*) avoided the coral snake pattern on an artificial prey (wooden sticks). However, naive house sparrows (*Passer domesticus*), red-winged blackbirds (*Agelaius phoeniceus),* and blue jays (*Cyanocitta cristata*) coming from areas situated outside the range of coral snakes did not avoid that pattern (Smith 1980).

Other studies showed that innate avoidance is not limited to cases of extremely dangerous prey. Naive domestic chicks (*Gallus gallus domesticus*) avoided red-painted larvae of *Tenebrio molitor* (Roper 1990) and those with black-and-yellow stripes as well (Schuler and Hesse 1985); naive northern bobwhites (*Colinus virginianus*) avoided red and yellow pinheads (Mastrota and Mensch 1995); and naive great tits (*Parus major*) avoided black-and-yellow–striped mealworms (Lindström et al. 1999). Moreover, innate biases against warning colors may be hidden and manifest themselves when at least 2 components of multimodal warning signals are present at the same time (Rowe and Guilford 1996; Rowe and Guilford 1999; Lindström, Rowe et al. 2001). Because most aposematic insects are provided with multimodal antipredatory defense systems, the experiments with living aposematic prey are necessary.

Naive predators may avoid aposematic prey not only because of specific biases against certain signals but also because of neophobia (Coppinger 1970; Lindström, Alatalo et al. 2001) and dietary conservatism. Marples and Kelly (1999) distinguished neophobia as a short-lasting avoidance response (minutes to days), whereas dietary conservatism was defined as a long-lasting process (weeks, months) of refusing a novel prey. Neophobia may be deactivated by experience with diverse food items (Jones 1986). Although there is a considerable individual variation in both the processes (Marples et al. 1998; Marples and Kelly 1999), those adult birds (e.g., the

wild-caught blue jay *C. cristata*) that have had a previous experience with a novel unpalatable prey often subsequently avoid a novel, differently looking prey (Schlenoff 1984). On the contrary, initial neophobia of naive birds may in some cases decay with age (Langham 2006). Both neophobia and dietary conservatism increase avoidance of aposematic prey; this may be important when a new aposematic form appears (Rowe and Guilford 1999; Thomas et al. 2003; Marples et al. 2005).

Several authors have shown that wild-caught individuals of different bird species may react differently toward a warning signal of the same prey species (Evans and Waldbauer 1982; Exnerová, Landová et al. 2003). Even closely related species of predators may have considerably different impact on population of aposematic prey because of species-specific foraging strategies (Fink and Brower 1981; Brower 1988). These facts have important implications for the theory of evolution of warning signals (Endler and Mappes 2004). A distinction between innate and learned nature of predator's avoidance of the warning signal of an aposematic prey is important for the prey as well. Each generation of young individuals of those predator species, which have no innate biases against warning signals, would regularly kill certain number of individuals of the aposematic prey. Such predators exert a considerable selection pressure on the populations of aposematic preys, the final effect depending on predator's cognitive, learning, and generalization abilities. On the other hand, predators with an innate avoidance of a certain warning signal will produce none or negligible selection pressure on the signal-bearing prey.

We have investigated interspecific differences in the origin of avoidance in closely related species of Paridae. First, we tested, whether wild-caught birds of 6 species (blue tit, great tit, crested tit, coal tit, marsh tit, and willow tit) do avoid the aposematic red-and-black firebug *P. apterus*. We compared their reactions with reactions of birds tested with the conspecific but artificially nonaposematic (brown painted) prey. By painting the firebugs, we could assess the importance of their warning coloration within their multiple defenses involving also olfactory and gustatory cues.

Second, we tested whether avoidance of aposematic prey in 4 tit species (blue tit, great tit, crested tit, and coal tit) has the same origin, that is, whether naive (hand reared) birds of these species learn to avoid the aposematic prey or whether they have an unlearned bias against aposematic coloration. To distinguish the specific bias against aposematic coloration from a novelty effect, we compared the reactions of naive birds tested with aposematic firebugs with the reactions of naive birds tested with brown-painted bugs.

MATERIAL AND METHODS

Characteristics of species studied

European tits are small arboreal passerine birds; their weight ranges from 8–12 g in coal tits and blue tits to 14–22 g in great tits (Cramp and Perrins 1993; Harrap and Quinn 1996). They inhabit a variety of woodlands, where they find suitable holes for nesting. Individual species differ in their habitat preferences: the crested tit and coal tit inhabit coniferous forests; the marsh tit prefers deciduous woodland; the willow tit lives in damp deciduous, mixed, and coniferous forests; the blue tit inhabits deciduous and mixed forests and gardens; and the great tit is nearly ubiquitous (Cramp and Perrins 1993). Tits are sedentary throughout the year or vagrant around small areas. Diet of tits consists mainly of insects, spiders, and other invertebrates as well as of nuts and seeds, especially in winter; the great tit and blue tit nestlings are fed mainly with caterpillars and spiders, the nestling diet of other species is more diverse (Gibb and Betts 1963; Török and Tóth 1988; Krištín 1992;

Cramp and Perrins 1993). All species are known to consume occasionally true bugs, mainly the Miridae and Pentatomidae (Krištín 1992; Cramp and Perrins 1993; Exnerová, Štys et al. 2003). Tits forage mainly on trees and partly also on the ground, the species differing in their preference of various parts of the tree (Suhonen et al. 1994). The great tit and the blue tit do not store food, whereas other species do, namely seeds (Cramp and Perrins 1993; Harrap and Quinn 1996).

Phylogeny and classification of the Paridae

The best-corroborated phylogenetic hypothesis of Paridae is that by Gill et al. (2005) based on nucleotide sequences of mitochondrial cytochrome *b* gene of 42 parid species. It is congruent with cytochrome *b* data and consistent with osteological characters by James et al. (2003), a study based on 12 species. We accept it because the global sample studied is extensive, and the trees produced by both maximum parsimony and maximum likelihood methods are congruent. The hypothesis is shown in Figure 1A, pruned to the 6 species studied. The splitting generic classification, suggested by Gill et al. (2005) and Slikas et al. (1996) is accepted as well. Formerly, all species studied were included in *Parus* sensu lato but the broadly defined *Parus* is paraphyletic (James et al. 2003; Gill et al. 2005). Out of the species studied, only the 2 *Poecile* species are immediate sister species, and the other species examined, particularly, *Cyanistes caeruleus* and *P. major*, are separated by branches of many extralimital clades.

The competing hypotheses (e.g., Kvist et al. 1996; Garamszegi and Eens 2004; references therein) are either based on taxonomically and regionally incomplete samples or result from purely phenetic methods, and are, therefore, rejected. They differ mainly by regarding *C. caeruleus* and *P. major* as sister species and these as sisters to the rest.

Wild-caught birds

Fifty-four blue tits *C. caeruleus*, 50 great tits *P. major*, 33 crested tits *Lophophanes cristatus*, 50 coal tits *Periparus ater*, 58 willow tits *Poecile montanus*, and 50 marsh tits *Poecile palustris* (see Table 1) were studied. Birds were caught in the mist nets over the year except the breeding season (May–August) at localities around Prague (50.05 N, 14.25 E), Velemín (50.32 N, 13.59 E), Tábor (49.25 N, 14.41 E), and České Budějovice (49.00 N, 14.30 E), the Czech Republic. The sample included mainly adults (2 or more years old) and a smaller number of yearlings. Birds were habituated 1–7 days prior to the experiment. Housing light conditions were set according to outdoor photoperiod. The birds were offered a varied diet: sunflower seeds, mealworms (larvae of *T. molitor*), house crickets (*Acheta domestica*), and commercial food for insectivorous birds (Vitacraft Soft Mix).

Hand-reared birds

We hand-reared juvenile tits of 4 species: 54 blue tits, 50 great tits, 20 crested tits, and 50 coal tits (Table 1). The nestlings were taken from nest-boxes at the age of 12–15 days. At this age, they were 3–6 days before fledging and had no visual experience with prey. The nest-boxes were placed in the mixed wood near the towns of Hradec Králové (50.13 N, 15.50 E) and České Budějovice. Not more than 4 chicks were taken from one brood. Nestlings from the same brood were kept together in artificial nests and then, after fledging, in cages (50 × 30 × 30 cm). We fed them by forceps every hour from 5 AM to 9 PM for several days, until they were able to feed themselves. Their diet consisted of boiled eggs, commercial pellets for insectivorous birds (Vitacraft), mealworms (larvae of *T. molitor*), house crickets (*A. domestica*), and insects
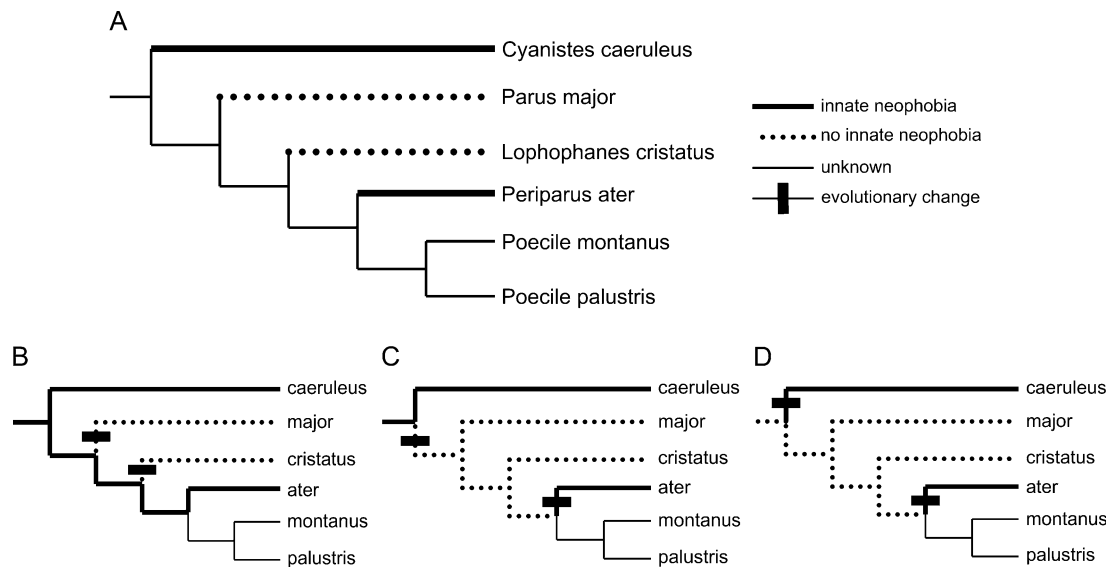
Figure 1
(A) Phylogenetic hypothesis on relationships of European tits and their classification based on Gill et al. (2005), but pruned to the species studied, and showing the occurrence/absence of innate neophobia. Figures B, C, and D show 3 equally parsimonious explanations of evolution of the trait (2 steps each), assuming that neophobia is primitive (B and C) or derived (D).

swept in the field (mainly caterpillars, grasshoppers, and beetles) with vitamins (Vitacraft) and calcium added. Birds were tested when they were fully independent (age 35–40 days).

Prey

Adult firebugs (*P. apterus*) reared on linden seeds (*Tilia cordata*) were used as a prey. Firebugs are widespread in various habitats of Central Europe, mainly in deciduous woodlands, parks and gardens, and also in open landscape, where their host plants (*Tilia, Robinia*, and mallows) are frequent. For other bionomical details, see Socha (1993) and Exnerová et al. (2006). We used the wild-type form (aposematic, with red-and-black color pattern) and the artificial nonaposematic (brown painted) form. Dark brown watercolor—burned sienna—and chalks (improving covering properties) were used for painting; the dye is odorless and nontoxic. We did not cover the metapleural

orifices of scent glands; hence, both color forms could release the same defensive secretion, which makes them largely unpalatable for small passerines (Exnerová, Landová et al. 2003).

Experimental setup

The experiments were carried out in the cage equipped with one-way glass, a perch, and a rotating feeding tray with 6 cups. Both color forms of the firebug appeared conspicuous on the beige background of the cups. Bird's behavior was scored as a continuous record in Observer Video-Pro (13 behavioral elements) and recorded by videocamera, following Exnerová, Landová et al. (2003). A bird was released into the experimental cage 3–5 h before the experiment to become accustomed to the allocation of prey and water and was deprived of food approximately 2 h before starting the experiment. Each experiment consisted of a sequence of 10 consecutive 5-min

Table 1

Numbers of hand-reared and wild-caught individuals of the tit species (blue tit, *Cyanistes caeruleus*; great tit, *Parus major*; crested tit, *Lophophanes cristatus*; coal tit, *Periparus ater*; willow tit, *Poecile montanus*; and marsh tit, *Poecile palustris*) tested with aposematic (red and black) or artificially nonaposematic (brown painted) firebug *Pyrrhocoris apterus*

Bird species	Age category	Number of birds tested with		Number of birds that handled at least one		Number of birds that killed/consumed at least one	
		Aposematic firebugs	Nonaposematic firebugs	Aposematic firebugs	Nonaposematic firebugs	Aposematic firebugs	Nonaposematic firebugs
Blue tit	Hand reared	27	27	7	12	1/1	2/1
	Wild caught	27	27	6	15	0	1/0
Great tit	Hand reared	25	25	25	25	24/20	23/20
	Wild caught	25	25	7	19	1/0	17/17
Crested tit	Hand reared	10	10	6	7	3/3	5/5
	Wild caught	17	16	4	9	4/4	9/9
Coal tit	Hand reared	25	25	9	7	2/2	4/4
	Wild caught	25	25	10	14	5/3	6/6
Willow tit	—	—	—	—	—	—	—
	Wild caught	30	28	5	11	2/2	7/7
Marsh tit	—	—	—	—	—	—	—
	Wild caught	25	25	0	4	0	0

trials. The bird was alternatively offered one specimen of a mealworm and one specimen of a firebug; each bird was thus successively presented with 5 mealworms and 5 firebugs. The mealworms (familiar to birds) were used to check foraging motivation of the bird; all mealworms were eaten during the experiments. Birds of the same species and age category were subdivided into 2 groups: one offered aposematic wild-type form of the firebug and the other artificially nonaposematic (brown painted) form (see Table 1). Each bird was subjected only to one experiment. In the hand-reared birds not more than 2 individuals from the same brood were tested with the same color form of the firebug.

Ethical note

Czech Animal Welfare Commission gave its permission (No. 17537/2003-30/300) to carry out the experiments. We are endowed with licenses allowing us to catch and ring birds by Bird Ringing Center Prague (No. 876 and 975) and to experiment with animals by Czech Animal Welfare Commission (No. 18847/2003-1020). The experiments were performed from 1997 to 2004. After the experiment, all the birds were ringed and released back to the site of their origin.

Statistical analysis and the statistical tests

Interspecific comparison of wild-caught tits and interspecific comparison of hand-reared tits
Data were analyzed by logistic regression in GLIM v. 4 (Francis et al. 1994), separately for the aposematic and nonaposematic firebugs and separately for the wild-caught and hand-reared tits. Presence/absence of either handling or killing was the binary response variable, whereas tit species was the explanatory variable. Significance of the overall difference among species was evaluated by G^2 test (e.g., Quinn and Keough 2002, p. 363–365) and differences among the means of individual species by a priori least significant difference (LSD) test (e.g., Sokal and Rohlf 1995, p. 243).

Intraspecific comparison—importance of firebug coloration and predator's age category (hand reared and wild caught)
Counts of firebugs handled by each bird were the response variable and age category of bird (hand reared vs. wild caught) and prey coloration (aposematic vs. nonaposematic) the explanatory variables. The data were analyzed in GLIM v. 4 (Francis et al. 1994) by fixed effect 2-way ANOVAs with interactions, using Poisson distribution of errors (GLM ANOVAs). Overdispersion of errors was treated by dividing Pearson's chi square by the residual degrees of freedom (df) (McCullagh and Nelder 1989). Data on crested tits had unequal sample sizes and were analyzed by a fixed effect factorial ANOVA with disproportional and unequal sample sizes, using an iterative approximate estimation technique in SPSS v. 12. The appropriateness of the models was checked by plotting standardized residuals against fitted values and by normal probability plots (Crawley 1993). Counts of birds that handled/killed at least one aposematic firebug were compared with counts of birds that handled/killed at least one nonaposematic firebug by chi-square tests. Because of limited numbers of tested birds (especially in case of crested tits) we have decided to take into account all marginally significant results to avoid a large type II error.

RESULTS

Summarized results from all tit species

Only a minority of wild-caught individuals in all the tested tit species attacked the aposematic firebugs (21% of all wild-

caught tits). Much larger proportions of wild-caught individuals in all the tit species attacked nonaposematic firebugs (49% overall wild-caught tits). The firebugs have often survived the attacks of birds. The proportions of wild-caught birds that killed the aposematic firebugs were smaller (8% overall wild-caught tits) than the proportion of birds that killed the non-aposematic firebugs (27% overall wild-caught tits).

In hand-reared tits (great tits, blue tits, coal tits, and crested tits), we found higher proportion of birds that attacked/killed at least one aposematic firebug (54% attacked/34% killed), comparing to wild-caught tits of the same 4 species (29% attacked/11% killed). No differences are between these 2 age categories in proportion of birds that attacked/killed at least one nonaposematic firebug (59%/39% of hand-reared birds and 61%/35% of wild-caught birds). Proportions of the hand-reared tits that attacked aposematic and nonaposematic firebugs did not differ (54% and 59% of all hand-reared tits, respectively). The same is true for killing (34% and 39%, respectively).

Interspecific comparison of wild-caught tits

Reaction to aposematic firebugs
None of the marsh tits ever handled an aposematic firebug. Some individuals of other 5 species—coal tit, great tit, crested tit, blue tit, and willow tit—handled the aposematic firebugs (Table 1, Figure 2A); the proportion of handling birds did not differ among the species ($G^2 = 4.127$; df = 4; $P = 0.39$).

Individuals of 2 species—the marsh tit and blue tit—did not kill any aposematic firebugs. Small proportion of individuals in other tit species (crested tit, coal tit, willow tit, and great tit) killed the firebugs during the handling (Table 1, Figure 2A). However, killing was equal in all species ($G^2 = 5.942$; df = 3; $P = 0.11$).
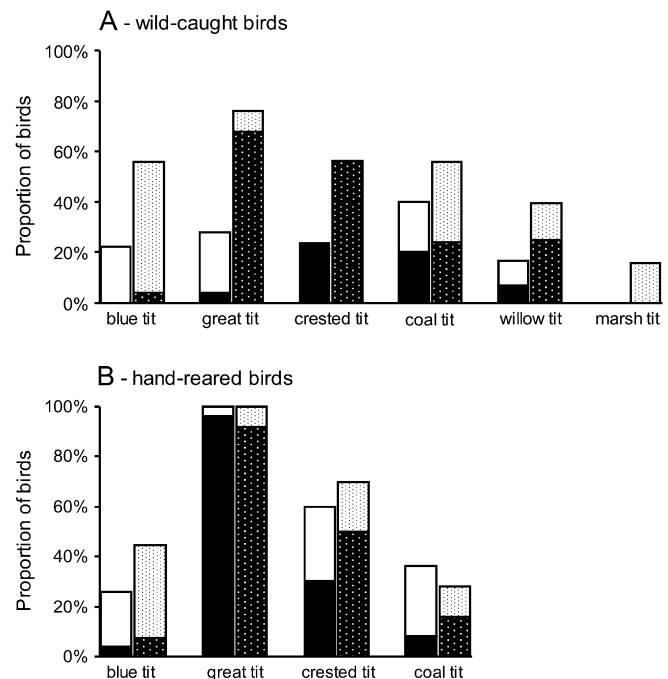

Figure 2
Proportions of wild-caught (A) and hand-reared (B) tits that handled aposematic (plane bars) or nonaposematic (dotted bars) firebugs (*Pyrrhocoris apterus*). Black parts of the columns indicate the proportion of birds that killed the prey.

Reaction to nonaposematic firebugs
In all tit species, the proportions of birds that handled non-
aposematic firebugs (Figure 2A) were generally higher than
proportions of birds that handled aposematic firebugs (Table
1, Figure 2A). The proportion of handling birds differed sig-
nificantly among the species ($G^2 = 21.99$; df = 5; $P < 0.001$).
In all, 5 species (great tit, crested tit, coal tit, blue tit, and
willow tit) formed a homogenous group with high proportion
of handling birds. The marsh tit differed from all of them
(LSD tests, $P < 0.05$) by very low number of handling birds.

Marsh tits have not killed any nonaposematic firebugs.
However, the killing significantly differed among the other
species ($G^2 = 28.88$; df = 4; $P < 0.001$). With the only one
exception, blue tits handled the prey carefully and did not kill
any nonaposematic firebugs. The reaction of blue tits differed
significantly from those of great tits, crested tits, and willow tits
(LSD tests, $P < 0.05$), which killed the nonaposematic prey
more frequently (Table 1, Figure 2A). Coal tits differed nei-
ther from blue tits nor from great tits, crested tits, and willow
tits (LSD tests, not significant [NS]).

Interspecific comparison of hand-reared birds

Reaction to aposematic firebugs
All the hand-reared great tits handled the aposematic firebugs.
The handling was similar ($G^2 = 3.614$; df = 3; $P = 0.16$) in the
group consisting of the crested tits, coal tits, and blue tits but less
frequent than in great tits (Table 1, Figure 2B).

Killing of aposematic firebugs differed significantly among
the tit species ($G^2 = 68.98$, df = 3, $P < 0.0001$). Great tits
nearly always killed the handled firebugs. The proportion of
birds that killed aposematic firebugs decreased in the follow-
ing direction: great tit → crested tit → coal tit → blue tit
(Table 1, Figure 2B). However, great tits did not differ from
crested tits and the latter did not differ from coal tits (LSD
tests, NS). Only a small proportion of hand-reared blue tits
and coal tits killed aposematic firebugs. The behavior of these

2 species was similar (LSD test, NS) and jointly differed from
great tits (LSD test, $P < 0.05$).

Reaction to nonaposematic firebugs
All the hand-reared great tits handled the nonaposematic fire-
bug at least once. The differences in handling among the other
3 species were only marginally significant ($G^2 = 5.369$, df = 3,
$P = 0.068$). Nevertheless, hand-reared blue tits and coal tits
handled the nonaposematic firebugs less frequently than
crested tits (Table 1, Figure 2B).

Killing the nonaposematic firebugs differed significantly
among tit species ($G^2 = 52.38$; df = 4; $P < 0.0001$, Figure 2B).
The 2 homogenous groups (great tits and crested tits vs. coal
tits and blue tits) differed significantly (LSD test, $P < 0.05$).
Great tits and crested tits included the highest proportions
of birds that killed at least one nonaposematic firebug. Their
reactions toward nonaposematic prey did not differ signifi-
cantly (LSD test, NS). The proportion of birds that killed the
nonaposematic firebugs was low both in the blue tits and
coal tits (LSD test, NS).

Intraspecific comparison—importance of firebug coloration and predator's age category (hand-reared vs. wild-caught birds)

Blue tits (Cyanistes caeruleus)
The age category of tested birds and coloration of offered
firebugs had no statistically significant influence on the num-
ber of firebugs handled by the bird (2-way GLM ANOVA: $F =$
1.742; df = 3,104; NS; Figure 3). Reactions of hand-reared
blue tits were essentially similar to those of wild-caught indi-
viduals; birds of both age categories did not accept firebugs as
a prey.

Despite the fact that the effect of firebug coloration was not
significant in the total model, the proportions of wild-caught
birds that handled the aposematic and nonaposematic fire-
bugs were statistically different ($\chi^2 = 6.31$; $P = 0.012$, Table 1,
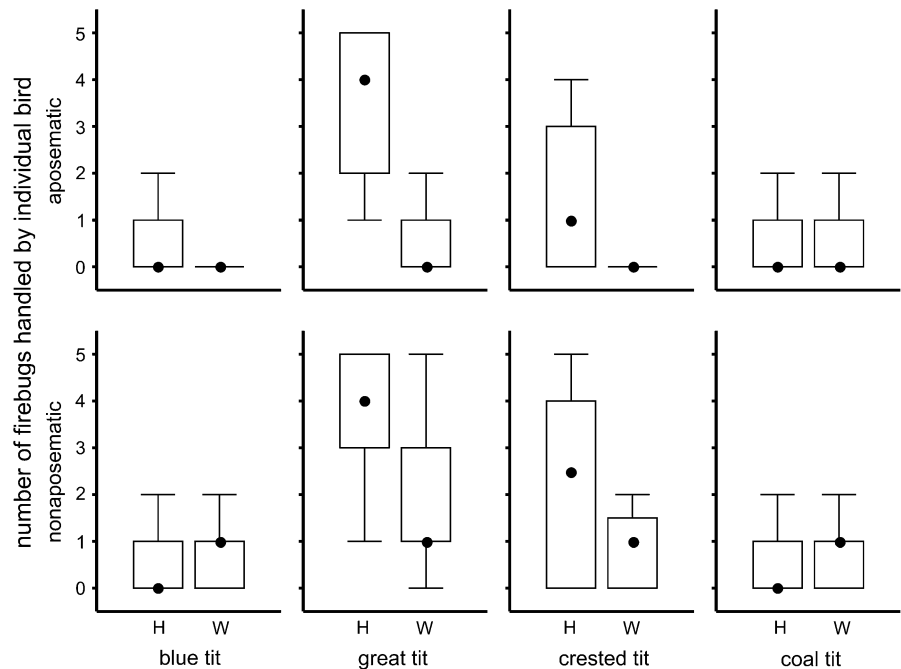Figure 2A). On the other hand, similar proportions of

Figure 3
Number of aposematic and non-
aposematic firebugs (*Pyrrhocoris
apterus*) handled by an individual
hand-reared (H) or wild-caught
(W) bird during 5 successive trials
(point = median; box = lower
and upper quartile; whiskers =
nonoutlier range).

hand-reared birds handled aposematic and nonaposematic firebugs ($\chi^2 = 2.03$; $P = 0.154$, Figure 2B).

Great tits (*Parus major*)

As shown by 2-way GLM ANOVA, wild-caught and hand-reared great tits behaved differently ($F = 57.32$; df $= 1,96$; $P < 0.0001$), and the reaction of birds was influenced by firebug coloration ($F = 4.78$; df $= 1,96$; $P < 0.05$). There was also a significant interaction between the age category and color of the firebug ($F = 11.63$; df $= 1,96$; $P < 0.01$). Therefore, we divided our data set according to the age and the color and assessed influence of color or age in the 2 categories separately.

Wild-caught great tits discriminated clearly between the aposematic and nonaposematic firebugs (One-way ANOVA, $F = 16.32$; df $= 1,48$; $P < 0.001$). Majority of birds avoided attacking the aposematic firebugs, but a large proportion of birds handled, killed, and even ate artificially nonaposematic firebugs (see Figure 3 and also Table 1).

Contrastingly, hand-reared great tits attacked equally both aposematic and nonaposematic firebugs. Consequently, there was no statistically significant effect of firebug coloration on the number of firebugs handled by one bird (One-way ANOVA, $F = 0.078$; df $= 1,48$; NS; see Figure 3). Hand-reared great tits handled significantly more both aposematic (One-way ANOVA: $F = 54.57$; df $= 1,48$; $P < 0.001$) and nonaposematic (One-way ANOVA: F $= 14.37$; df $= 1,48$; $P < 0.001$) firebugs than wild-caught great tits.

Crested tits (*Lophophanes cristatus*)

The total model revealed a highly significant effect of age category of the tested bird (2-way GLM ANOVA for unequal sample sizes, $F = 8.18$; df $= 1,49$; $P = 0.006$) and significant effect of the firebug color (2-way GLM ANOVA for unequal sample sizes, $F = 4.14$; df $= 1,49$; $P = 0.047$) on the number of firebugs handled by a bird. The interaction between the 2 factors was not significant (2-way GLM ANOVA for unequal sample sizes, $F = 0.136$; $P = 0.714$, Figure 3). The birds of both age categories handled more often the nonaposematic firebugs than the aposematic ones. The hand-reared crested tits were in this respect less cautious than wild-caught individuals, and they learned faster to avoid aposematic than nonaposematic firebugs.

Coal tits (*Periparus ater*)

There was no influence of age category of tested birds and of the firebug coloration on the number of firebugs handled by a bird (2-way GLM ANOVA, $F = 0.41$; df $= 3,96$; NS). Large proportions of coal tits in both age categories avoided both aposematic and nonaposematic firebugs (Figure 3). More wild-caught birds than hand-reared birds handled, killed, and ate firebugs (both aposematic and nonaposematic ones) (Table 1), but these differences were not statistically significant.

Wilow tits (*Poecile montanus*)

The effect of prey coloration on the proportion of wild-caught willow tits that handled the firebugs was marginally significant ($\chi^2 = 3.71$; $P = 0.0541$). Smaller number of birds handled the aposematic than nonaposematic firebugs (Table 1, Figure 2A).

Marsh tits (*Poecile palustris*)

The proportion of wild-caught marsh tits that handled any color form of firebugs was extremely low (Table 1, Figure 2A). None of the birds handled the aposematic firebugs, and only 4 birds handled the nonaposematic ones ($\chi^2 = 4.35$; $P = 0.0371$).

DISCUSSION

Wild-caught individuals of all tit species avoided aposematic firebugs. However, individual species differed in the origin of the avoidance behavior. Naive great tits and crested tits had no initial unlearned bias and had to learn to avoid the aposematic prey. On the other hand, most of the naive blue tits and coal tits avoided aposematic firebugs at their first encounter, and their behavior did not differ from the behavior of wild-caught, potentially experienced birds. Our results thus show that the origin of avoidance may differ even in closely related species. Such a difference is probably specific for a particular aspect of behavior. In contrast to our results, Sasvári (1979, 1985) did not find any differences among juveniles of 3 tit species (great tits, blue tits, and marsh tits) in the ability to learn location of food by observing other individuals; however, in the same experiments with adult birds, he found that great tits performed better in observational learning than the other 2 species.

Innate avoidance

Hand-reared blue tits and coal tits mostly refused to attack both aposematic and nonaposematic firebugs. We suppose that their avoidance behavior was innate because the birds had no previous experience with any kind of unpalatable prey. In contrast to some previous studies (Smith 1975, 1977; Schuler and Hesse 1985; Roper 1990; Ingalls 1993; Mastrota and Mensch 1995; Lindström et al. 1999), the avoidance was not specifically directed against warningly colored prey. Hence, we do not interpret the avoidance behavior as a specific innate bias against warning colors. More likely, it is a novelty of the prey what makes the birds to hesitate to attack it. This interpretation is consistent with the fact that those birds, which attacked the firebugs during the experiment, handled them very carefully, and the firebugs mostly survived the attack. Avoidance of a novel prey was found in naive birds in several previous studies. Coppinger (1970) found nonspecific neophobic behavior concerning various species of butterflies in naive individuals of 3 passerine species (blue jays *C. cristata*, grackles *Quiscalus quiscula*, and red-winged blackbirds *A. phoeniceus*). Domestic chicks avoided food and drink scented with pyrazine, when it was associated with a novel color (Marples and Roper 1996), and avoided novel odors (Jetz et al. 2001). Almost all naive blue tits and coal tits inspected the firebugs in our experiments from a very short distance (2–3 cm) before they decided not to attack it. Therefore both the appearance and the defensive smell possibly influenced birds' reaction—results similar to those obtained in domestic chicks (Marples and Roper 1996) and zebra finches *Taeniopygia guttata* (Kelly and Marples 2004). As the avoidance of naive blue tits and coal tits did not disappear after repeated exposure to the novel prey (5 times), there is also the possibility to interpret their reaction as dietary conservatism, which lasts much longer than neophobia (Marples and Kelly 1999). However, it is uncertain whether dietary conservatism may exist at birds in such an early age. Other experiments are necessary for unequivocal interpretation.

The initial neophobia of young birds may, at least in some cases, change over the time. Langham (2006) found that older rufous-tailed jacamars (*Galbula ruficauda*) were more likely to sample novel morphs of aposematic *Heliconius erato* butterflies than were the younger birds. Similar change was observed also in great tits—yearlings were more cautious than older birds in contact with aposematic prey (Lindström et al. 1999; Exnerová et al. 2006). Our results with blue tits and coal tits seem to show similar tendency. Thus, the initial avoidance present in neophobic birds may be later fine-tuned by their experience with various prey types.

Influence of phylogeny and ecology

Having comparative data about 4 species only, we cannot decide whether neophobia is primitive or derived character within the Paridae. Provided the phylogeny suggested by Gill et al. (2005) is correct (Figure 1A), then the hypotheses that neophobia is primitive (2 independent losses—Figure 1B or one loss and one reversal—Figure 1C) or that it is derived (2 independent gains—Figure 1D) are equally parsimonious. Using the competing phylogenetic hypotheses (e.g., Kvist et al. 1996; Garamszegi and Eens 2004) provides similarly ambiguous interpretation.

There is no trait in the biology of the tit species, which could unequivocally explain their differences in behavior to aposematic prey. Differences in the habitats occupied suggest only that wild-caught individuals in species inhabiting mainly coniferous forests (the coal tit and crested tit) have smaller chance to encounter *P. apterus* and other similar red-and-black aposematic insects (spittle bugs, lygaeid bugs, similarly colored ladybirds) than the species living in the deciduous woodlands (the marsh tit) or in a wide range of habitats (the great tit, blue tit, and willow tit). This could explain the difference between wild-caught blue tits and coal tits in their reactions to firebugs. Although hand-reared birds of both species avoided firebugs, irrespectively of their color, the behavior of wild-caught birds seems to reflect different experience with the prey encountered in their habitats. Wild-caught coal tits, in contrast to blue tits, did not avoid aposematic firebugs more frequently than nonaposematic ones.

Foraging strategy is another possible factor influencing the attitudes of birds to a novel prey. Greenberg (1983) found that dietary specialists are more neophobic than generalists among *Dendroica* warblers. All tit species studied are rather generalists than specialists, and differences among them are small. Great tits and blue tits have more specialized nestling diets (mainly caterpillars and spiders) than other tit species, which feed the nestlings with diverse invertebrate food similar to those of adult birds (Gibb and Betts 1963; Krištín 1992; Cramp and Perrins 1993). Blue tits have even more restricted diet than great tits in the breeding season (Török 1986), but individuals of both species living in urban environment regularly bring food from bird tables (e.g., peanuts) to their nestlings (Cowie and Hinsley 1988). Moreover, the difference is restricted to the food brought to nestlings and disappears in the nonbreeding season (Sasvári 1988), when all tit species forage on a variety of invertebrates and seeds (Cramp and Perrins 1993 and references therein), visit bird tables, and most of them exploit unusual food sources such as milk bottles (Fisher and Hinde 1949). Therefore, the foraging strategy does not explain the differences observed in the behavior to a novel prey in our experiments.

Individual tit species differ in the prevailing size of their prey, ranging from 15–20 mm in great tits to 5–10 mm in coal tits and blue tits (Gibb and Betts 1963; Török and Tóth 1988; Krištín 1992; Cramp and Perrins 1993). However, the ranges of consumed prey items of all the species broadly overlap, and Carlson (1992) did not find any difference in the size of preferred prey (mealworms) among captive great tits, coal tits, and willow tits; all birds preferred the largest prey. Moreover, reactions of wild-caught great tits and blue tits to different instars of the firebug (L3, L5, and adults) were not affected by the size of the prey (Prokopová M, unpublished data). Thus, it is unlikely that the size of the firebug could influence interspecific differences in our results.

Greenberg (1990) proposed that neophobia might be a trait influencing phenotypic plasticity of a species. Species with low degree of neophobia are likely to explore and exploit novel food sources and habitats. Our data are only partly consistent with this hypothesis. Great tits, which were far less neophobic than other tits in our experiments, are known to be an innovative birds frequently exploiting new habitats and food sources. However, blue tits, which are similar to great tits in plasticity of their behavior and habitat selection, differed substantially from great tits in the reaction to a novel prey. Coal tits and crested tits, which differed one from another in their attitude to a novel prey, are species with conservative preference for coniferous forests.

Personality and neophobia

Attitude to a novel prey may be linked with a general personality of an individual—a complex of heritable correlated traits including aggressive behavior, risk-taking, exploratory behavior, wariness, and others. Personality characteristics have been extensively studied in great tits (Verbeek et al. 1994, 1996; Dingemanse et al. 2002; Drent et al. 2003; Carere et al. 2005; van Oers et al. 2005), in which 2 personality types were defined. "Fast" individuals are bold, aggressive, noninnovative, and explorative; "slow" individuals are cautious, nonaggressive, and innovative. Neophobic individuals are expected to belong to a "slow" personality type. Unfortunately, comparative data for other species of tits are not available. Nevertheless, it is possible to expect that individual species of tits may differ in proportion of individuals belonging to different personality types, and, consequently, also in different proportions of neophobic individuals within each species. Winkler and Kothbauer-Hellmann (2001) have found in coal tits and crested tits different searching strategies, which may be linked to the 2 personality types extended to a species level: crested tits being largely fast explorers and coal tits slow ones. This result is consistent with greater proportion of neophobic individuals among coal tits than among crested tits observed in our experiments. Individual differences in personality may be responsible for within-species variation in our data.

The degree of neophobia may depend on potential risk associated with the consumption of noxious prey, and such a risk is probably greater for birds with a smaller body size relative to the prey. In our previous study, we have found negative correlation between the body size and the avoidance of aposematic prey (firebugs) among 9 species of passerine birds (Exnerová, Landová et al. 2003). Differences in the body size are also congruent with the results of our present study: the neophobic coal tit and blue tit are the smallest species and the nonneophobic great tit is the largest one. Consequently, the weight-dependent risk of consumption of a novel prey may constrain the possibility of decrease of food-related neophobia in, otherwise, behaviorally plastic species such as the blue tit.

Controversial results concerning behavior of naive great tits

We have not found any innate components of avoidance behavior in naive great tits. All naive birds attacked aposematic as well as nonaposematic firebugs immediately after they were presented, and they usually required several trials to learn to avoid them. This result is surprising because Lindström et al. (1999) found in naive great tits from Finland innate avoidance against yellow-and-black–striped mealworms. In both cases, the birds were taken from nests at the same age, rearing conditions were similar, and the birds tested were about the same age. We suggest 3 alternative explanations. 1) The reactions may be population specific; birds from Finland and Sweden may be more cautious in contact with brightly colored prey. Differences between birds coming from different geographic regions in the presence or absence of innate avoidance have already been found in birds avoiding the coral snake pattern (Smith 1975, 1977, 1980). However, the different bird

species were tested in different areas. 2) Innate avoidance may be specific to yellow color or to the striped yellow-and-black pattern. Majority of other studies showing the inborn avoidance dealt with such a color pattern (Smith 1975, 1977, 1980; Schuller and Hesse 1985). 3) Differences may result from different experimental designs. In each experimental design, birds face different foraging tasks resulting from either a) simultaneous offer of aposematic and nonaposematic prey items (Lindström et al. 1999) or b) offer of only one prey type at the moment (present study). Having a choice, the bird makes a decision, which prey it will attack first, and it may start with a more familiar prey. The results are then relative measures of choice between different prey types. Having no choice, the bird has to decide whether to attack the particular prey or not. Naive great tits from southern Sweden, tested in experiments with red-and-black aposematic insects (*Lygaeus equestris*, *P. apterus*, *Coccinella septempunctata*, *Zygaena filipendula*) presented simultaneously with palatable prey, mostly did not attack the aposematic prey at the first encounter (Wiklund and Jarvi 1982; Sillén-Tullberg 1985). These results suggest a population-specific reaction or effect of an experimental design.

Suitability of a species as a model for experimental studies

Most of our knowledge about behavior of the bird predators to aposematic prey is based on the experiments with rather few model species of birds, namely, domestic chicks (e.g., Gamberale and Tullberg 1996; Marples and Roper 1996; Rowe and Guilford 1996; Rowe and Skelhorn 2005), quails (e.g., Evans et al. 1987; Marples et al. 1994), and great tits (e.g., Sillén-Tullberg 1985; Alatalo and Mappes 1996; Lindström, Alatalo et al. 2001). Lindström et al. (1999) have pointed out that the evidence in studies of innate component of the avoidance is based almost entirely on precocial species. As the psychological development of precocial and altricial birds is substantially different (Starck and Ricklefs 1998), one may expect also differences in the acquisition of the avoidance of noxious prey. Moreover, our results suggest that even closely related altricial species may greatly differ in this respect. The same experiment performed with naive birds of different species may lead to different or even contradictory results. Comparative studies taking into account also development of the behavior are necessary for the assessment of the general scope of results obtained in experiments with a particular predator species. Fortunately, great tits, which are frequently used in studies focused on learning of the avoidance of aposematic prey, are suitably chosen because their avoidance is based entirely on learning. Other species (blue tits and coal tits) would be more suitable models for the study of innate avoidance.

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