



Through experience to boldness? Deactivation of neophobia towards novel and aposematic prey in three European species of tits (Paridae)



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ABSTRACT

European tits (Paridae) exhibit species-specific levels of initial wariness towards aposematic prey. This wariness may be caused by neophobia, dietary conservatism or innate bias against particular prey traits. We assessed the contribution of these three mechanisms to the behaviour of juvenile tits towards novel palatable prey and novel aposematic prey. We compared levels of initial wariness in great tits (*Parus major*), blue tits (*Cyanistes caeruleus*) and coal tits (*Periparus ater*), and tested how the wariness can be deactivated by experience with a palatable prey. One group of birds was pre-trained to attack familiar naturally coloured mealworms the other one, novel red-painted mealworms. Then all the birds were offered a novel palatable prey of different colour and shape: cricket (*Acheta domestica*) with blue sticker, and then a novel aposematic firebug (*Pyrrhocoris apterus*). The three species of tits differed in how the experience with a novel palatable prey affected their behaviour towards another novel prey. Great tits and coal tits from experienced groups significantly decreased their neophobia towards both palatable prey and aposematic prey while blue tits did not change their strongly neophobic reactions. The interspecific differences may be explained by differences in body size, geographic range, and habitat specialisation.

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1. Introduction

Aposematic prey signal their noxiousness or unprofitability to potential predators by a conspicuous warning signal (reviewed in Ruxton et al., 2004). Bird predators usually learn to avoid aposematic prey, and many experimental studies have focused on factors affecting the mechanisms of avoidance learning, memory and generalisation (e.g. Sillén-Tullberg, 1985; Roper and Redston, 1987; Gamberale and Tullberg, 1996; Lindström et al., 1999a; Riipi et al., 2001; Gamberale-Stille and Guilford, 2003; Ham et al., 2006; Exnerová et al., 2010; Aronsson and Gamberale-Stille, 2008, 2012; Svádová et al., 2009; Barnett et al., 2012). The avoidance of aposematic prey may also have an inherited component, which causes even inexperienced individuals to avoid aposematic prey or at least to hesitate longer before attacking them (Smith, 1975, 1977; Lindström et al., 1999b; Exnerová et al., 2007), and is important for the evolution of aposematic prey (Marples et al., 2005; Marples and Mappes, 2011). Recent studies on the phenomenon of innate wariness have shown that it may vary between bird species (Exnerová et al., 2007) and individuals (Exnerová et al., 2010), may often

include hidden biases that are manifested only when a combination of visual and chemical signals of a prey are involved (Rowe and Guilford, 1996, 1999a; Jetz et al., 2001; Lindström et al., 2001; Kelly and Marples, 2004; Rowe and Skelhorn, 2005), and that the wariness may in fact be a complex of several, partly independent mechanisms (Marples et al., 1998; Marples and Kelly, 1999; Exnerová et al., 2003; Marples and Mappes, 2011). Innate wariness towards aposematic prey may include three mutually not exclusive processes: (1) food neophobia, (2) dietary conservatism and (3) specific innate biases against warning signals of aposematic prey. All these processes may contribute to some degree to the predator's response and, in a natural situation, it is difficult to distinguish them.

Neophobia, usually defined as a tendency to avoid novel objects and situations (Barrows, 2011), is a widespread phenomenon first described in rats tested with novel objects (Barnett, 1958). It has since been observed in many animal taxa also as a response to novel food (Honey, 1990; Galef, 1993; reviews in Kelly and Marples, 2004; Mappes et al., 2005; Marples et al., 2005). Food neophobia has been measured as a hesitation to approach a new food and come into a physical contact with it, which lasts usually only several minutes, and is followed by investigation of the novel food (Marples and Kelly, 1999). In some bird species, food neophobia may be correlated with object neophobia (e.g. blacked-capped chickadees

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(*Poecile atricapillus*)—An et al., 2011), whereas in others the correlation may be absent or present only in some populations (e.g. great tits (*Parus major*)—Exnerová et al., 2010, 2015; house sparrows (*Passer domesticus*)—Bókony et al., 2012). After the first contact with novel food, birds may no longer show neophobia, but they may still refuse to consume the novel food. This reaction was termed dietary conservatism, and is usually measured as the time from initial contact with the novel food item to its incorporation into the diet (Marples et al., 1998; Kelly and Marples, 2004). Dietary conservatism (DC) has been defined as a relatively long lasting refusal (persisting for days to months) of some individuals to accept novel food into their diet (Marples et al., 1998; Thomas et al., 2003; Thomas et al., 2004). Individual variation in dietary conservatism has been shown to have a genetic basis (Marples and Brakefield, 1995). Neophobia and dietary conservatism together are usually referred to as dietary wariness (Mappes et al., 2005; Marples et al., 2005; Marples et al., 2007) and the evidence that neophobia but not dietary conservatism can be reduced through experience with food of various colours in chicks (Jones, 1986; Marples et al., 1998) and turkeys (Lecuelle et al., 2011) supports the idea of the existence of two distinct processes.

The third process contributing to innate wariness of aposematic prey is a specific innate bias against particular warning signals and their combinations. This type of inherited avoidance of warning signals has been found in birds from several taxa (Galliformes, Momotidae and Passeriformes) and is usually associated with conspicuous aposematic colour patterns. Naive domestic chicks (*Gallus gallus domesticus*) avoid red painted mealworms (larvae of *Tenebrio molitor*) (Roper and Cook, 1989; Roper, 1990) and mealworms with black-and-yellow stripes (Schuler and Hesse, 1985); naive northern bobwhites (*Colinus virginianus*) avoid red-and-yellow pinheads (Mastrota and Mench, 1995); naive hand-reared turquoise-browed motmots (*Eumomota superciliosa*) and great kiskadees (*Pitangus sulphuratus*) avoid the coral snake pattern (Smith, 1975, 1977); and hand-reared juveniles of great tits (*Parus major*) avoid black-and-yellow striped mealworms (Lindström et al., 1999b). Furthermore, warning signals are often multimodal and innate biases may emerge only when visual signals are combined with olfactory, gustatory or acoustic cues (Rowe and Guilford, 1999a). These hidden biases have been intensively studied mainly in domestic chicks, in which a combination of warning coloration and smell (Rowe and Guilford, 1996, 1999b; Jetz et al., 2001), taste (Rowe and Skelhorn, 2005; Skelhorn et al., 2008) or sound (Rowe and Guilford, 1999a; but see Siddall and Marples, 2011) triggers manifestation of innate biases.

The degree of innate wariness may differ even between closely related bird species, and also the mechanisms responsible for the wariness may be species specific (Exnerová et al., 2007). Moreover, predator species may differ not only in their initial degree of innate wariness, but also in how easily it is modified by further experience with palatable or unpalatable prey. Considerable variation in innate wariness exists among European species of tits (Paridae). While naive hand-reared great tits (*Parus major*) and crested tits (*Lophophanes cristatus*) readily attack aposematic red-and-black firebugs, *Pyrrhocoris apterus*, naive hand-reared coal tits (*Periparus ater*) and blue tits (*Cyanistes caeruleus*) avoid them (Exnerová et al., 2007). The fact that naive coal tits and blue tits avoided not only aposematic firebugs, but also non-aposematic brown-painted ones, suggests an effect of neophobia. However, the potential role of dietary conservatism and specific biases against warning colours remain to be studied.

In this study we compared the degree of innate wariness towards novel prey in three European species of tits and attempted to assess the roles of neophobia, dietary conservatism and specific bias against aposematic coloration in an overall wariness. Specifically, we compared the reactions of hand-reared juveniles of great

tits (*Parus major*), coal tits (*Periparus ater*) and blue tits (*Cyanistes caeruleus*) towards two types of novel prey: (1) novel palatable prey (a cricket *Acheta domestica* with a blue sticker) and (2) novel aposematic prey (the red-and-black firebug *Pyrrhocoris apterus*). Within each species, we tested whether the previous positive experience with another novel palatable prey (red-painted mealworms) affects willingness of the birds to attack and consume the two novel prey types.

2. Material and methods

2.1. Birds

Hand-reared juveniles of three European tit species were tested: 85 great tits (*Parus major* L. 1758), 65 coal tits (*Periparus ater* (L. 1758)) and 85 blue tits (*Cyanistes caeruleus* (L. 1758)). All three species are sedentary, and their diet includes mainly small arthropods, supplemented with seeds and berries (Cramp and Perrins, 1993). Preferred prey length of all the three tit species is around 1 cm, with coal tits preferring slightly smaller prey than the other two species (Cramp and Perrins, 1993). Coal tits cache their food regularly, whereas blue tits and great tits do not (Štorchová et al., 2010). Great tits and coal tits are widespread thorough the whole Palaearctic (Cramp and Perrins, 1993). Great tits inhabit a wide range of woodland habitats including urban and suburban areas, whereas coal tits are restricted to coniferous and mixed woodlands (del Hoyo et al., 2007). Blue tits are endemic to the West Palaearctic (Harrap and Quinn, 1996), inhabiting mostly lowland and submontane deciduous woodlands (Cramp and Perrins, 1993; del Hoyo et al., 2007). The great tit is the largest of the three species (weight: 14.0–22.0 g, body length: 140 mm), followed by blue tit (weight: 7.5–14.7 g, body length: 115 mm) and coal tit (weight: 7.2–12.0 g, body length: 115 mm) (Cramp and Perrins, 1993; del Hoyo et al., 2007). The weight of the juveniles tested in our experiment ranged 14–18 g in great tit (mean = 16.2 ± 0.8 g), 9.5–13 g in blue tits (mean = 11.1 ± 0.8 g) and 8.5–10.5 g in coal tits (mean = 9.5 ± 0.5 g).

The nestlings were taken from nest boxes at the age of 12–16 days, when they had only very limited visual experience with prey brought to the nest by their parents. The nest boxes were placed in large parks at the outskirts of Prague (50°04'N, 14°26'E) and in mixed woods near Hradec Králové (50°12'N, 15°50'E). Not more than two nestlings were taken from a single brood. Nestlings were kept in artificial nests and were fed every two hours from 6 AM to 10 PM for several days, until they were able to feed themselves. Their diet consisted of mealworms, boiled eggs, handmix (Orlux), egg mixture Oké-bird (Versele-Laga), mixtures for insectivorous birds Uni patee (Orlux), Nutribird (Versele-Laga), Insect patee (Orlux) and vitamins Roboran (Unisvit), Vitamin plus V (Sera) and Activ plus W (Sera). After fledging, the birds were housed individually in plastic home cages (50 × 40 × 40 cm) with wire-mesh front wall. Each cage was equipped with three perches, two water bowls with drinking and bathing water *ad libitum*, and two feeders placed on the bottom of the cage. Birds were kept under natural light conditions (16:8 h light/dark) and were daily provided with fresh water and food. All birds were tested when they were fully independent, most of them at the age of 38–65 days (minimum 35 days and maximum 73 days).

2.2. Prey

Naturally coloured mealworms (larvae of *Tenebrio molitor*, Fig. 1), which were familiar to the birds, were used to check their foraging motivation during the experiment and for training the birds from non-experienced experimental group (see below). We

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