

Signals of profitability? Food colour preferences in migrating juvenile blackcaps differ for fruits and insects

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Received: 6 March 2006 / Accepted: 16 May 2006 /

Published online: 28 September 2006

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Abstract Red is a common colour signal in both aposematic warning displays, and in fruit displays. One common feature is that red is conspicuous against the natural background of the prey and fruits. However, there is a potential conflict between fruits and aposematic prey in how a bird predator should react to red colours, where fruits aim to attract birds and aposematic insects aim to ward off, often the same bird individuals. Here we investigate possible differences in red/green colour preferences of frugivorous, wild-caught, young blackcaps (*Sylvia atricapilla*), when food is either a fruit or an insect. Birds in two groups were presented with a series of pairs of food items that had been artificially painted red and green, in the order of (I) fruits, crickets and maggots, or (II) crickets, fruits, and maggots. Birds first presented with crickets or fruits differed in first attacks directed at the two colours: They showed no colour preference between fruits, but showed a clear preference for green over red crickets. Also, birds in both experimental groups clearly preferred green to red maggots. These results provide evidence that wild, frugivorous birds are able to differentiate between prey types, and show different colour preferences depending on whether food is insect or fruit. We conclude that blackcaps show an attack bias against red insects, and that one important function of the signal in insects, is to inhibit attack after discovery. However, the lack of preference for red fruits suggests other functions to red fruit displays, such as facilitating discovery per se, rather than directly stimulating attack after discovery.

Keywords Colour preference · Colour signals · Foraging · Frugivory · Fruit colour · Warning coloration

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Introduction

Many aspects of bird behaviour are influenced by colour signals. For instance, certain colours are important as attractants in partner choice and/or to deter competitors (Darwin 1871; Butcher and Rohwer 1988; Radwan 1993; Maynard Smith and Harper 2003), and colours may stimulate feeding of nestlings (Swynnerton 1916; Harrison 1985; Jourdie et al. 2004). In a foraging context, colours play an important role when searching for profitable foods, such as insects and fruits, and when recognizing unprofitable defended prey. Prey coloration has often evolved to either work against the perception of predators, as in the case of crypsis (Cott 1940; Edmunds 1974; Ruxton et al. 2004), or to be easily perceived, as in the case of aposematism (Cott 1940; Guilford 1990; Ruxton et al. 2004) and attractive fruit colours (Ridley 1930; Willson and Whelan 1990).

Here we concentrate on insect aposematic coloration and fruit colours, which use similar signals intended for more or less the same predators. Red is a common colour in warning displays, as well as in fruit displays, at least partly because this hue is conspicuous against most natural backgrounds (Lee et al. 1994; Schmidt et al. 2004). Herein lies a potential conflict between fruits on one hand, aiming to attract birds, and, on the other hand, aposematic insects using the coloration to ward off birds (Schuler and Roper 1992). A common argument is that these signals have evolved to function as efficiently as possible for their purpose, and thus have been shaped by the sensory systems of consumers (Guilford and Dawkins 1991). Predators show learned and unlearned aversions to aposematically coloured prey (Rubinoff and Kropach 1970; Smith 1975, 1977; Wiklund and Järvi 1982; Sillén-Tullberg 1985a; Schuler and Hesse 1985). However, it is more difficult to find conclusive evidence for colour preferences in fruit consumers (Gamberale-Stille and Tullberg 2001; Schmidt et al. 2004). Black and red fruit-colours dominate in temperate areas, and are the colours mainly used by bird-dispersed fruits (Wheelwright and Janson 1985; Willson and Whelan 1990; Traveset et al. 2004). Many of these fruits also reflect in the UV (Burkhardt 1982; Willson and Whelan 1989; Altshuler 2001), but a majority of red fruits do not (Willson and Whelan 1989), indicating that red functions as an important fruit signal in its own right. Again, fruit colours are generally thought to be an adaptation to attract dispersers (Willson and Whelan 1990 and references therein). There is some evidence that wild-caught frugivorous birds prefer common fruit colours (McPherson 1988; Willson 1994; Puckey et al. 1996; Hartley et al. 2000; Siitari et al. 1999), but the inconsistency in preferences is striking (Willson et al. 1990; Willson and Comet 1993; Willson 1994) and shown preferences may well have been an effect of differences in conspicuousness against the background. Conclusive evidence of innate fruit colour preferences is even scarcer (but see Schmidt and Schaefer 2004, Honkavaara et al. 2004).

In a previous study, we showed that an omnivorous bird differ in unlearned preference for green over red, depending on whether the food item is an insect or a fruit (Gamberale-Stille and Tullberg 2001). Young domestic chicks (*Gallus gallus domesticus*) preferred green to red insect prey, which can be interpreted as an innate avoidance of red aposematic prey. However, when offered fruit-sized pastry spheres, the birds did not show any preference, suggesting that the relative avoidance of red is not general for all food types. Noticeably, we found no preference for red fruits. However, the domestic fowl is not frugivorous in the sense that it is expected to have

special adaptations to forage for fruits. It is descended from the red jungle fowl (*Gallus gallus*), a bird that eats almost anything edible found by pecking and scratching the ground (Collias and Collias 1967). Thus, it is possible that different preferences can be found in more specialized frugivores (Gamberale-Stille and Tullberg 2001). Fittingly, in a recent study, Schmidt and Schaefer (2004), actually found an unlearned preference of red artificial food items in frugivorous, hand-raised young blackcaps (*Sylvia atricapilla*), although no preference could be found in wild-caught adults. However, in this study, the total consumption from 5 g square-shaped, fruit tasting food items was compared. Thus, initial preference was not measured, nor was birds' reactions to natural fruit-shaped stimuli, which could possibly have an effect on birds' reactions.

In the present study, we aim to further investigate the potential conflict between insects and fruits that use the same signalling colours for opposing purposes. We aim to investigate red/green colour preference/avoidance in frugivorous birds, to get an idea of the generality of the effects of food-type on red/green colour preferences, with regard to the degree of bird frugivory. In contrast to fruits, insect prey show a variety of shapes and behaviours. Therefore, we were also interested to see whether a colour preference regarding one type of insect prey is also found for an entirely different prey type. We use wild caught, (pre-) migrating juvenile blackcaps as predators. The diet of blackcaps consists of both invertebrates and fruits (Bairlein 1996 and references therein), and they forage for both types of food when in the migrating phase (Eggers 2000).

Methods

The experiment was conducted at Tovetorp Zoological Research Station (58°56' N, 17°08' E) in SE Sweden during September 2002 (under permit from Linköpings djurförsöksetiska nämnd, D-nr: 34-02). Juvenile blackcaps (EURING code 3) were captured at dawn using mist nets and playback of blackcap song. Ageing and sexing followed Svensson (1992). All birds were ringed, had their wing length measured to the nearest millimetre (maximum chord, Svensson 1992), weighed on a Pesola balance to the nearest 0.1 g and had their fat scores estimated on a scale from 0 to 6 following Pettersson and Hasselquist (1985). Mainly birds with low fat scores (1–3, with a few exceptions) were brought into the lab and housed individually in cages that measured 80 × 40 × 60 cm. The cages contained two higher and two lower perches. All sides of the cages except the front were made out of opaque white plastic, and the front was made out of steel-wire. Six cages, in piles of 2 × 3 had been placed in each of three experimental rooms so that the birds could not see each other or into each other's cages. Birds were left undisturbed for a minimum of 2 h with free access to food and water. They were fed with a mixture of dried insects and pieces of dried fruit (Biofood, RAFF) and mealworms (*Tenebrio molitor*). The testing of a bird started after a 30–60 min period of food deprivation. Directly after testing (max 60 min), birds had free access to food again, and were released in the late afternoon the same day.

As experimental food we used ripe fruits of black elder (*Sambucus nigra*, ca 6 mm in diameter), dead cricket nymphs (*Gryllus bimaculatus*, ca 6–7 mm in length) that had been killed by freezing, and live maggots (*Calliphora* sp., ca 11–12 mm in length). We painted the prey items red or green using a mixture of one part "glue",

made out of flour and water, and two parts children's paint, Gouache tempera (Colour and co, Lefranc and Bourgeois, Le Mans, France). As green we used a 1:1 mixture of "emerald green" and "leaf green", and as red we used a 1:1 mixture of "brilliant orange" and "primary red". These were the same paints used in a previous study (for reflectance spectra see Gamberale-Stille and Tullberg 2001). The green and red paints peak within the green and red part of the spectrum, respectively and neither paints reflect any UV light. Also, the reflectance of the paints is consistent to that of natural fruits and insects. The paint coated the whole of the fruits and maggots, and the upper, visual side of the crickets. The movement of the maggots did not seem to be inhibited by the paint.

Birds were filmed with video cameras connected to TV monitors. In this way we were able to observe the birds' behaviour from the TV monitors outside of the experimental rooms, without disturbing them. One green and one red food item of the same type were presented simultaneously to the birds. Food items were placed in two separate Petri-dishes with the diameter of 5 cm. The two dishes were placed on a white podium, approximately 2 cm from each other, and at the same distance from one of the lower perches within the cage from which prey could closely be observed by the birds. We varied the individual location of the two colours (left or right Petri-dish) between presentations for each bird and between birds, but the maggots were always presented in the same way as the fruits.

All birds were presented with all food types, but in different order. There were two treatment groups. Group 1 first received fruits, followed by crickets and then maggots, and Group 2 first received crickets, followed by fruits and then maggots. The presentation of maggots served to check whether the preference for insect prey coloration was repeatable using an entirely different prey type from the crickets and independently of the previous order of presentation. The birds were presented with the first food type for a maximum of 10 min without attacking, after which the trial was terminated. Did the bird attack one of the food items of the pair, the trial was continued and terminated 5 min after that attack, unless the bird attacked the second food item in the presentation. Were both food items attacked, we waited 5 min after the last attack before presenting the bird with the next food type. The procedure was repeated with the subsequent food types. Only birds that attacked a food item in the first presentation received the following food types, thus non-attacking birds were excluded from the experiment. As we were mainly interested in the behaviour of attacking birds, and as quite a large group of birds did not attack the experimental food, we kept the number of attacking birds as equal as possible between the treatment groups each experimental day. That is, for each bird in one treatment group accepting to feed on the experimental food, we tested birds successively with the other treatment until a bird accepted to feed on that food type. In total, 91 birds were tested of which 43 attacked a food item and took part in the whole experiment. The final sample sizes of attacking birds were $N = 22$ for Group 1 (fruits first), and $N = 21$ for Group 2 (crickets first).

We collected data about the colour of the first food item attacked from each of the presentations, and whether or not the other colour also was attacked. We noted the total number of attacks and whether or not the item was eaten, for each food type. The weight and fat scores of the birds at capture were noted and compared with regard to the birds' willingness to attack. Please note that weight and fat data for two of the attacking birds are missing and are not included in the analysis.

As mentioned above, many birds brought into the lab were reluctant to eat the experimental food, which is probably partly related to their preparedness to migrate. Birds' willingness to feed on the experimental food was related to their body mass and fat scores, birds attacking being both lighter (18.40 ± 0.142 vs. 19.01 ± 0.19 , mean (g) \pm S.E., Mann–Whitney $U_{(41, 48)} = 737$, $P = 0.042$) and having less visual body fat (1.90 ± 0.15 vs. 2.79 ± 0.15 , mean score \pm S.E., Mann–Whitney $U_{(41, 48)} = 518$, $P = 0.0001$). For instance, blackcaps at the island of Gotland, SE Sweden, left on migration with approximately 23% fat load (Ellegren and Fransson 1992). In comparison, the attacking birds in the present experiment had on average 16% fat load (range 5.0–27.2%, $N = 41$) and the non-attacking birds had on average 20% fat load (range 8.2–39.9%, $N = 48$) estimated as fat load in relation to the size-specific lean body mass (Ellegren and Fransson 1992). Non-attacking birds were immediately given back the pre-experimental food mixture and released together with the experimental birds later the same day.

Results

In the first presentation, birds presented with crickets and fruits differed in the proportion of first attacks directed at the two colours (Fisher Exact Test: $P = 0.045$, Fig. 1a). They did not prefer either colour in the fruit presentation (Goodness of fit, $\chi^2 = 0.182$, d.f. = 1, $P > 0.5$), but they significantly preferred green to red cricket prey (Goodness of fit, $\chi^2 = 10.71$, d.f. = 1, $P < 0.005$). Thus, colour preference in juvenile blackcaps is dependent on food-type.

In the second presentation (Fig. 1b) some birds were reluctant to attack at all and the reaction to the food items differed close to significantly between the experimental groups ($\chi^2 = 5.88$, d.f. = 2, $P = 0.053$). Among the attacking birds in this trial, birds with previous experience of fruits did not show any significant colour preference when presented with crickets (Goodness of fit, $\chi^2 = 0.4286$, d.f. = 1, $P < 0.5$) and birds with previous cricket experience did not prefer any colour when encountering fruits (Goodness of fit, $\chi^2 = 0.2857$, d.f. = 1, $P > 0.5$). Because the experience in the first presentation might have influenced the birds' choice in the second presentation we tested whether individual birds tended to prefer the same colour in both trials. In Group 1 with previous experience of fruits 14 preferred the same and 7 a different colour in the cricket, and in Group 2 with previous experience of crickets 8 preferred the same and 5 preferred a different colour of the fruits. Pooling these numbers there is no indication of consistent individual colour preferences over the two trials (Goodness of fit, $\chi^2 = 2.38$, $P = 0.12$).

In the third presentation with maggots (Fig. 1c), there was no significant difference in food preference between the experimental groups (Fisher Exact Test: $P = 0.412$). All birds attacked the prey and birds in both experimental groups clearly preferred green to red maggots (Group 1: Goodness of fit, $\chi^2 = 6.545$, d.f. = 1, $P < 0.025$; Group 2: Goodness of fit, $\chi^2 = 13.76$, d.f. = 1, $P < 0.001$).

Over the whole experiment consumption of preferred food items was lower for crickets (32/42) than for fruits (35/36) and maggots (42/43) (Contingency table, $\chi^2 = 13.90$, d.f. = 2, $P = 0.001$). Also, a greater proportion of attacking birds attacked both food items in the fruit and maggot presentations, respectively, whilst most birds attacking crickets stopped after one attack (Contingency table, $\chi^2 = 39.58$, d.f. = 2, $P < 0.0001$).

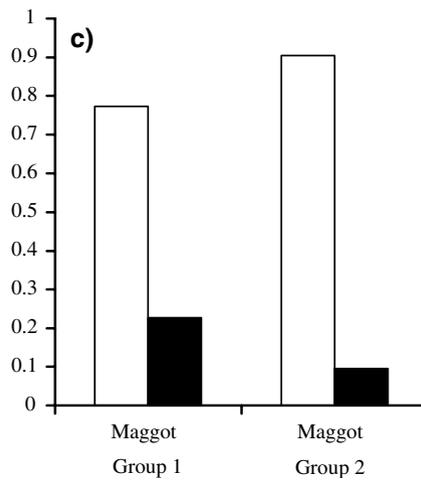
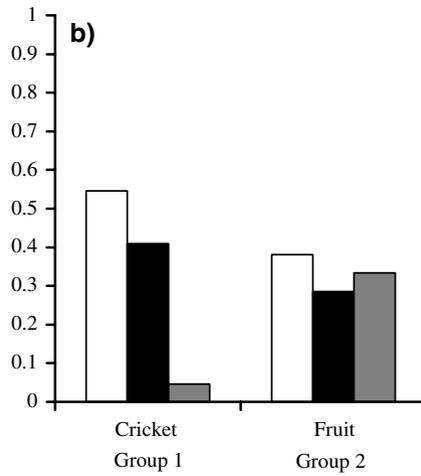
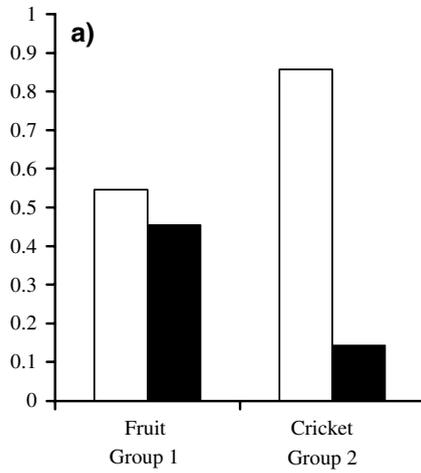


Fig. 1 The proportion of birds in Group 1 ($N = 22$) and Group 2 ($N = 21$) first attacking green (open bars) or red (closed bars) food items in three consecutive presentations (a–c). Grey bars represent non-attacking birds

As mentioned in the Methods section, only birds that attacked food items in the first presentation were included in the experiment and these birds were lighter in weight than the rest. It is therefore interesting to investigate whether there is an effect of the state of a bird, in terms of body weight, on its food choice. Of all the captured birds first tested, a greater proportion presented with fruits (Group 1, 22/34) attacked within the set time than did birds presented with crickets (Group 2, 21/57, Fisher's Exact $P = 0.028$). However, we found no significant difference in weight between attacking birds in these two groups (Group 1: 18.45 ± 0.20 ; Group 2: 18.36 ± 0.21 , mean (g) \pm S.E.; $t = 0.32$, d.f. = 39, $P = 0.75$). Furthermore, green-red colour preference of fruits in Group 1 was not significantly related to weight ($t = -0.52$, d.f. = 18, $P = 0.60$) and neither was colour preference of crickets in Group 2 ($t = -1.77$, d.f. = 19, $P = 0.09$), or colour preference in the first presentation for both groups combined ($t = -1.24$, d.f. = 39, $P = 0.22$). We also found no significant weight difference between birds that attacked and those that did not attack fruits in Group 2 (Fig. 1b, $t = -0.95$, d.f. = 19, $P = 0.35$).

Discussion

This study demonstrates that a strongly frugivorous bird, the blackcap, differentiates between food types and shows different colour preferences for insects and fruits. This result supports the findings of Gamberale-Stille and Tullberg (2001), and shows that also wild birds adjust their responses to the type of signaller when dealing with colour stimuli. In first presentations, green crickets were clearly preferred over red, but no preference was shown in fruits, neither as first nor as second presentations (Fig. 1). Further, the blackcaps were consistent in their preference of green to red insects also with the live maggot prey. Why birds presented with crickets after fruits did not significantly prefer green to red crickets is uncertain. One reason could be that the previous positive experience of both colour stimuli overrode any bias for green insects, albeit temporarily, as green maggots were later preferred over red. The bias for green maggots in the last trial, suggests that birds may recognise insect prey per se, which then elicit a green to red bias, and not some other factor (e.g. presence of black in the stimulus or the presence of insect legs, cf. Gamberale-Stille and Tullberg 2001).

It should be noted that the blackcaps in our experiment were young, but hardly naïve and had most likely encountered both red and green insects and fruits in the wild. Thus, the preference of green over red insects shown here could well have been acquired through learning. Regardless, these results, as well as the results of Gamberale-Stille and Tullberg (2001), reflect a predator bias against attacking red insects, which is a common signal in unprofitable prey, and supports that one important function of the signal is to inhibit attacks when already discovered by a predator. On the other hand, the lack of conclusive evidence to a preference for common fruit colours (this experiment, Willson et al. 1990; Willson and Comet 1993; Willson 1994; Gamberale-Stille and Tullberg 2001; Schmidt and Schaefer 2004), suggests other functions than directly stimulating

attack. One function of red and black fruit colours seems to be to maximize conspicuousness against the background (Burns and Dalen 2002; Schmidt et al. 2004). Conspicuousness makes the fruit easily perceived at a distance, and fruits that contrast against the background may be preferred also on close range (e. g. Schmidt et al. 2004). On the contrary, experiments with insect prey show that red hue per se may be more important than contrast to produce an avoidance effect in birds (Sillén-Tullberg 1985b). One reason for this difference in the strength of association of red hue to unpalatability in insects compared to profitability in fruits may be that the consequences from making the wrong decision differ. We hypothesize that catching and consuming an aposematic, potentially toxic insect is more time consuming and harmful than sampling an unprofitable fruit. Another possible reason for weak associations of profitability with red fruit colours is the fact that not all red fruits are ripe, as many eventually black fruits are red when immature (Willson and Thompson 1982). This suggests that birds would need ancillary cues to determine the profitability of red fruits.

Recently, Schmidt and Schaefer (2004) found a preference for red (over white, yellow, green and blue) coloured food-items in young hand-raised blackcaps, but found no colour preferences at all in adult wild-caught birds. Our experiment, using fruit-shaped prey, supports their results for adult birds in that no fruit colour preference was found. Schmidt and Schaefer (2004) suggest that the preference for red colour in the very young birds may act to facilitate food recognition, and that this preference is later overruled by experience, as blackcaps may feed on a variety of differently coloured fruits during migration. Our blackcaps were migrating yearlings and were probably more experienced than the younger, hand-raised birds used by Schmidt and Schaefer (2004), but they also lacked the considerable experience of different fruit signals gained by adults that have returned from migration. If there is an innate preference for red fruits, our results suggest that it disappears very early. This implies that there is more to be known to fully understand the colour preferences (or lack thereof) in blackcaps.

Only about half of the birds brought in from the field attacked in the first presentations and were used in the experiment. The most obvious difference between attacking and non-attacking birds was that non-attacking individuals were heavier and possessed more visual body-fat. Although we did not use really fat birds, but mainly such with fat scores 1–3, it is possible that the heavier birds were more interested in leaving than in feeding. However, and especially in light of the fact that a smaller proportion of tested birds attacked crickets than fruits in the first presentation, it is important to consider a possible difference in body weight between the two experimental groups, or, whether body weight is a factor that might influence colour preferences. Because we found no such weight differences between experimental groups or between birds with different colour preferences we find it unlikely that our results are biased with respect to the state of a bird during migration.

In conclusion, we have shown that red-green colour preferences in young blackcaps are dependent on food type, in that they show a preference for green to red in two very different types of insect prey, but no evident preference among fruits. This indicates that signals in fruits and insects are functionally different, with fruit signals mainly facilitating detection and insect signals deterring attack after detection. The generality of this finding should, however, be investigated using other common fruit colours such as black and ultraviolet.

Acknowledgments We would like to thank the anonymous referees for their valuable comments on the manuscript. This study was financed by the Swedish Research Council (VR) to GGS and BT.

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