Evolutionary Ecology Research, 2004, **6**: 919–925

Unlearned preference for red may facilitate recognition of palatable food in young omnivorous birds

Veronika Schmidt[1,2] and H. Martin Schaefer[1]*

[1]*Institut für Biologie I, Albert-Ludwigs-Universität Freiburg, Hauptstr. 1, 79104 Freiburg and* [2]*Institute of Avian Research, 'Vogelwarte Helgoland', An der Vogelwarte 21, 26386 Wilhelmshaven, Germany*

ABSTRACT

Unlearned colour choices by consumers are generally interpreted as an adaptation to avoid unprofitable prey, often involving red warning coloration. However, red colour is a context-dependent stimulus. It signals palatability in ripe fruits, but unlearned fruit colour preferences have rarely been assessed. Therefore, we tested unlearned preferences and the effect of experience on differently coloured artificial fruits in an omnivorous bird. Naïve hand-raised blackcaps (*Sylvia atricapilla*) preferred red to blue, green, yellow and white artificial fruits, while adult wild-caught birds had no colour preference. In the area from which the experimental birds originated, red ripe fruits are present in 53% of the species with fleshy fruit displays in summer. In these circumstances, unlearned preferences for red might facilitate food recognition in inexperienced fruit-eating birds. Unlearned colour choices should thus be interpreted in a broader context of foraging and not only to explain warning coloration. The contrasting choices of adult and naïve birds imply, however, a low potential for directional selective pressures on fruit colour evolution in this system.

Keywords: aposematism, blackcap, frugivory, fruit colour, naïve preferences, plant–animal interactions.

INTRODUCTION

As an essential part of visual signals, colour is used commonly in a variety of contexts – for example, for predator avoidance in aposematism or for consumer attraction in pollination and seed dispersal. The same colour stimulus may then convey different messages to the same receiver. Red, for instance, is a warning signal in insects but often signals palatability in ripe fruits. Because experience may strongly impact colour preferences (Coppinger, 1970; Roper, 1990), testing unlearned responses of naïve birds should provide insight otherwise not available (Alatalo and Mappes, 1996; Lindström *et al.*, 1999a; Gamberale-Stille and Guilford, 2003). Thus far known, naïve birds have often unlearned avoidance of red (Roper and Cook, 1989; Roper, 1990; Mastrota and Mench, 1995). It is assumed that this unlearned

* Author to whom all correspondence should be addressed. e-mail: martin.schaefer@biologie.uni-freiburg.de

response serves as an adaptation to avoid unprofitable or harmful prey, and it may play a crucial role in explaining the evolution of warning colours (Lindström *et al.*, 1999b; but see Guilford, 1990).

By contrast, 50–70% of all ripe fruits are either red or black both in temperate and tropical regions (Willson and Thompson, 1982; Wheelwright and Janson, 1985; Traveset *et al.*, 2004), which are the most conspicuous colours against natural backgrounds (Lee *et al.*, 1994; Schmidt *et al.*, in press). In Europe, red fruits are particularly common, accounting in total for 40–60% of the species of bird-dispersed fruits (Turcek, 1963; Martin, 1965). Thus, for frugivores, it might be advantageous to prefer red objects instead of avoiding them. Fittingly, naïve chicks (*Gallus gallus domesticus*) were shown only to avoid red in round, dead insects but not in artificial fruits (Gamberale-Stille and Tullberg, 2001).

To track fruit colour evolution, preferences for fruit colours have been studied intensively in wild-caught but rarely in naïve birds (but see Willson and Comet, 1993). Birds showed mainly weak and transient colour preferences with strong intra- and interspecific differences (Willson and Whelan, 1990; Willson *et al.*, 1990; Willson and Comet, 1993; Willson, 1994; but see Puckey *et al.*, 1996). However, the interpretation of these results was hampered by the birds' unknown previous experience. To assess the effect of experience, we conducted an experiment focusing on the fruit colour preferences of adult and of hand-raised, naïve birds. We tested blackcaps (*Sylvia atricapilla*), an omnivorous bird feeding on both fruits and insects (Glutz von Blotzheim, 1991), to determine (1) whether colour choices were dependent on birds' experience and (2) whether naïve birds had an unlearned avoidance of or preference for red. We also surveyed fruit displays in summer, when juvenile birds start to forage independently, to correlate birds' unlearned colour responses with fruit colour diversity.

METHODS

We mist-netted 10 adult blackcaps at the end of the breeding season in August and September 1999 and took 10 juveniles from the nests in Wilhelmshaven, northern Germany, 3–5 days after hatching in June 2000 (permit 503.82-22201-1-05-199901 under Weser-Ems District, Germany). Birds were held individually in cages $62 \times 40 \times 40$ cm under constant conditions (light : dark 14 : 10; 20 ± 1°C; ~60% relative humidity). All birds were fed a beige standard maintenance diet (Bairlein, 1986) and mealworms (*Tenebrio molitor* larvae) with water available *ad libitum*. Juveniles were hand-raised and had no experience with any coloured food object before the trial. The trial was performed in week 7 of juvenile development. Juveniles and adults were held in different rooms to prevent imitation of feeding behaviour by juveniles. The adult birds were released within 5 km of their original trapping site at the beginning of the breeding season in April 2001 with a higher than average body mass. Previous studies have demonstrated that the release of long-term captive blackcaps is reasonable because they had lower than average mortality (Bairlein and Berthold, 1984). First-year birds were held captive for further studies and released in April 2002. For fruit colour surveys, we monitored all fruits from June to August at a 100-ha plot in the woodland from which the birds originated.

The colour preference trial lasted for 45 min at the beginning of the light phase on four consecutive days. Artificial fruits consisted of agar, cellulose and fructose based on the recipe of Levey and Grajal (1991). We dyed fruits with tasteless food colour (Crazy colours, Brauns Heitmann GmbH, Germany) and titanium white for white fruits. We did not test for black colour as it was not available in trade. The same colour shades were used on all days. The colours of artificial fruits were checked with a spectrometer and a DH 2000 deuterium-halogen lamp as a light source (both from Ocean Optics S2000, FL). The spectrometer only allowed for measurements at 350 nm and above. We measured reflectance as the proportion of a standard white reference tile (Top Sensor Systems WS-2). Colours of artificial fruits fell within the range of natural fruit colours (Fig. 1). Birds were simultaneously exposed to five differently coloured fruit cubes. Each cube weighed 5 g, exceeding the birds' consumption within the exposure time, and birds pecked bits from the cubes. The fruits were presented in petri dishes on a tray against brown background at the lattice side of the cage for equal light conditions (illuminated by daylight tubes, Osram, Munich). Colour positions changed randomly on consecutive days. At the end of the trial, we collected the unconsumed fruits and food spills and determined the amount eaten of each colour. To assess whether birds prefer a certain colour, we tested the amount eaten of each colour in a Hotelling's T^2-test modified for multiple-choice preference trials (Lockwood, 1998).

RESULTS

Naïve birds preferred red to white, yellow, green and blue artificial fruits (Hotelling's $T^2 = 42.57$, d.f. (4,6), $P = 0.018$; Fig. 2). Adults did not prefer any fruit colour (Hotelling's $T^2 = 21.93$, d.f. (4,6), not significant). During summer in northern Germany, when immature blackcaps start to forage independently, 83% of the species with fleshy fruit displays involve red colour as ripe (53%) or as unripe fruits or coloured accessory structures (Table 1).

DISCUSSION

Juvenile blackcaps did not experience colour stimuli in foods before the experiments because they were taken very early from the nests and were hand-raised without coloured food items. We conclude that juvenile blackcaps have an initial unlearned preference for red fruits. A similar study on hand-raised northwestern crows also yielded a slight tendency to

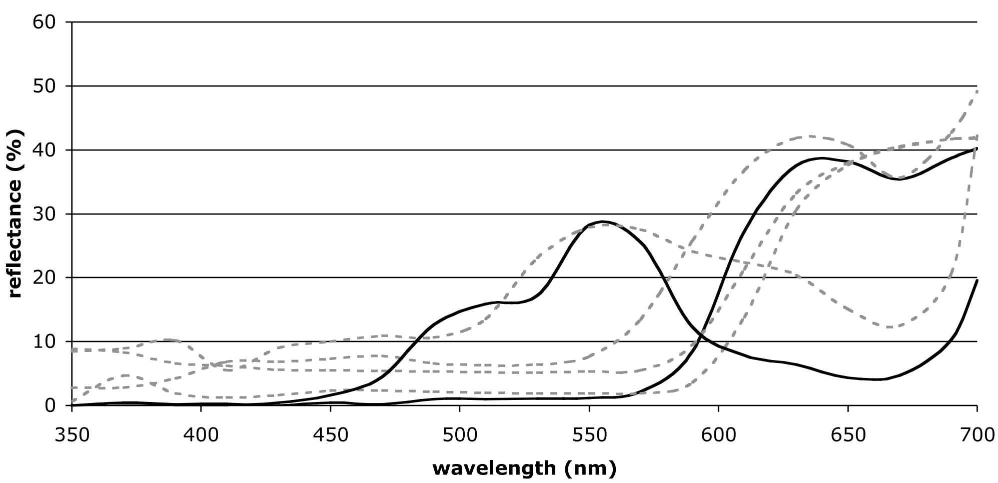

Fig. 1. The colours of green and red artificial fruits (solid lines) compared with examples of natural fruit colours (dotted grey lines).

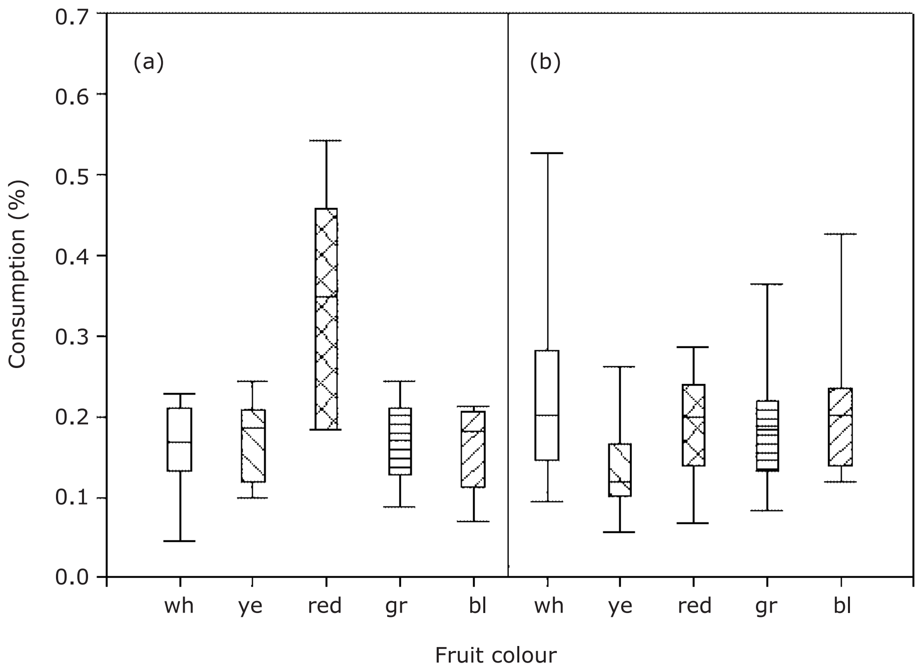

Fig. 2. Colour choices by hand-raised juvenile (a) and adult wild-caught (b) blackcaps. wh = white, ye = yellow, gr = green, bl = blue. Boxes indicate 2nd and 3rd interquartiles; bars represent the 5th and 95th percentiles.

Table 1. Colours of fleshy fruit displays of indigenous plants in northern Germany during summer; the colours of unripe fruits and stems of infructescences are given if non-green

Species	Ripe fruits	Unripe fruits	Stems
Arum maculatum	orange		
Bryonia dioica	red		
Frangula alnus	black	red	
Fragaria vesca	red		
Lonicera nigra	black		
Lonicera xylosteum	red		
Prunus avium	black	red	
Ribes rubrum	red		
Rubus idaeus	red		
Rubus fruticosus	black	red	
Sambucus nigra	black		red
Sambucus racemosa	red		
Solanum dulcamara	red		
Sorbus aria	red		
Taxus bacchata	red		
Vaccinium myrtillus	blue/UV		
Viburnum lantana	black	red	

favour red and blue food despite prior experience with a uni-coloured (red, yellow, natural) maintenance diet (Willson and Comet, 1993). These results contrast with the unlearned feeding behaviour of other omnivorous birds whose avoidance of red was thought to facilitate recognition of noxious insect prey (Lindström *et al.*, 1999b). Blackcaps are more frugivorous than most other species thus far tested on unlearned preferences. In the period from June to February, fruits form up to 90% of blackcaps' diet (Glutz von Blotzheim, 1995; Herrera, 1995). Because of the high proportion of red fruits in summer, an innate avoidance of red would conflict with the recognition of palatable fruits in this species. Juveniles' preference for red suggests that the birds' innate association with coloured food operates either according to the birds' main type of diet (fruit *vs* insects) or according to a yet unidentified stimulus that distinguishes 'red' in insects and fruits (Gamberale-Stille and Tullberg, 2001). According to the former conjecture, naïve frugivorous, but not insectivorous, birds should consistently prefer red colour to less common fruit colours. Assessing innate colour preferences in various frugivorous birds will consequently help to determine which of the two possible mechanisms leads to the formation of innate colour preferences in consumers.

In temperate areas, the majority of fruit displays in summer involve red colour (e.g. Turcek, 1963; Burns and Dalen, 2002). Since red fruits may be ripe or unripe, inexperienced birds have to learn using taste or context to avoid unripe fruits, which have lower digestibility and a higher allelochemical content (Schaefer and Schmidt, 2002; Schaefer *et al.*, 2003). Red colour is thus not an assessment signal that reliably reveals the quality of fruit (palatability); this contrasts with insects, where colour seems to convey the content (unpalatability) except for mimics. This may explain why colour and not conspicuousness determined avian food choice on insects (Lindström *et al.*, 1999b), but the latter and not the former on fruits (Schmidt *et al.*, in press).

The random consumption of adult blackcaps in our study implies that the innate (i.e. without prior experience) preference for red colour in fruits disappears, probably being overruled by experience. Blackcaps feed on a variety of differently coloured fruits during migration (Jordano and Herrera, 1981) and it is probably not adaptive for experienced birds to choose fruit principally according to colour. Consequently, red fruit colour operates more strongly as a cue for food recognition in inexperienced birds. This would also explain the inconsistent and transient colour preferences of other wild-caught birds in previous trials (Willson and Whelan, 1990; Willson *et al.*, 1990; Willson, 1994).

In conclusion, the innate preference for red in juvenile blackcaps might facilitate food recognition. However, preferring red was age-related and is therefore unlikely to translate into fruit colour evolution. Owing to a differential receiver response, we emphasize the need to control for experience when testing dispersers' selective pressures on fruit colours. Furthermore, to understand the adaptive significance of unlearned colour choices, it is essential to examine not only receivers' responses to noxious prey but also to include food recognition of palatable prey. Broadening the current research focus will reveal currently hidden mechanisms of colour preferences as well as their context dependence.

ACKNOWLEDGEMENTS

F. Bairlein kindly provided birds and facilities and commented on an earlier version of the manuscript. The study was financed by grants from the Deutsche Studienstiftung to H.M.S. and the Bischöfliche Studienförderung Cusanuswerk, e.V. to V.S. The experiment complies with current German law.

REFERENCES

Alatalo, R.V. and Mappes, J. 1996. Tracking the evolution of warning signals. *Nature*, **382**: 708–710.

Bairlein, F. 1986. Ein standardisiertes Futter für Ernährungsuntersuchungen an Singvögeln. *J. für Ornithol.*, **127**: 338–340.

Bairlein, F. and Berthold, P. 1984. Rückkehr und Brut einer handaufgezogenen freigelassenen Mönchsgrasmücke Sylvia atricapilla. *J. für Ornithol.*, **125**: 484–486.

Burns, K.C. and Dalen, J.L. 2002. Foliage color contrasts and adaptive fruit color variation in a bird-dispersed plant community. *Oikos*, **96**: 463–469.

Coppinger, R.P. 1970. The effects of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies: reactions of naïve birds to novel insects. *Am. Nat.*, **104**: 323–335.

Gamberale-Stille, G. and Guilford, T. 2003. Contrast versus colour in aposematic signals. *Anim. Behav.*, **65**: 1021–1026.

Gamberale-Stille, G. and Tullberg, B.S. 2001. Fruit or aposematic insect? Context-dependent colour preferences in domestic chicks. *Proc. R. Soc. Lond. B*, **268**: 2525–2529.

Glutz von Blotzheim, U. 1991. *Handbuch der Vögel Mitteleuropas*, Band 12. Wiesbaden: Aula Verlag.

Guilford, T. 1990. The secrets of aposematism: unlearned responses to specific colours and patterns. *TREE*, **5**: 323.

Herrera, C.M. 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary and historical determinants. *Annu. Rev. Ecol. Syst.*, **26**: 705–727.

Jordano, P. and Herrera, C.M. 1981. The frugivorous diet of blackcap populations wintering in southern Spain. *Ibis*, **123**: 502–507.

Lee, W.G., Weatherall, I.L. and Wilson, J.B. 1994. Fruit conspicuousness in some New Zealand *Coprosma* (Rubiaceae) species. *Oikos*, **69**: 87–94.

Levey, D.J. and Grajal, A. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.*, **138**: 171–189.

Lindström, L., Alatalo, R.V., Mappes, J., Riipi, M. and Vertainen, L. 1999a. Can aposematic signals evolve by gradual change? *Nature*, **397**: 249–251.

Lindström, L., Alatalo, R.V. and Mappes, J. 1999b. Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behav. Ecol.*, **10**: 317–322.

Lockwood, J.R., III. 1998. On the statistical analysis of multiple-choice feeding preference experiments. *Oecologia*, **116**: 475–481.

Mastrota, F.N. and Mench, J.A. 1995. Colour avoidance in northern bobwhites: effects of age, sex and previous experience. *Anim. Behav.*, **50**: 519–526.

Martin, W.K. 1965. *The Concise British Flora in Colour*. London: Ebury Press and M. Joseph.

Puckey, H.L., Lill, A. and O'Dowd, D.J. 1996. Fruit color choices of captive silvereyes (*Zosterops lateralis*). *Condor*, **98**: 780–790.

Roper, T.J. 1990. Reponses of domestic chicks to artificially coloured insect prey: effects of previous experience and background colour. *Anim. Behav.*, **39**: 466–473.

Roper, T.J. and Cook, S.E. 1989. Responses of chicks to brightly coloured insect prey. *Behaviour*, **110**: 276–293.

Schaefer, H.M. and Schmidt, V. 2002. Feeding strategies and food intake of Blackcaps consuming ripe or unripe fruits and insects. *J. für Ornithol.*, **143**: 341–350.

Schaefer, H.M., Schmidt, V. and Winkler, H. 2003. Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, **102**: 318–328.

Schmidt, V., Schaefer, H.M. and Winkler, H. in press. Conspicuousness, not colour as foraging cue in plant–animal signalling. *Oikos*.

Traveset, A., Willson, M.F. and Verdú, M. 2004. Characteristics of fleshy fruits in southeast Alaska: phylogenetic comparison with fruits from Illinois. *Ecography*, **27**: 41–48.

Turcek, F.J. 1963. Color preferences in fruit- and seed-eating birds. *Proc. Int. Ornithol. Congr.*, **13**: 285–292.

Wheelwright, N.T. and Janson, C.H. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.*, **126**: 777–799.

Willson, M.F. 1994. Fruit choices by captive American robins. *Condor*, **96**: 494–502.

Willson, M.F. and Comet, T.A. 1993. Food choices by northwestern crows: experiments with captive, free-ranging and hand-raised birds. *Condor*, **95**: 596–615.

Willson, M.F. and Thompson, J.N. 1982. Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are 'green'? *Can. J. Bot.*, **60**: 701–713.

Willson, M.F. and Whelan, C.J. 1990. The evolution of fruit color in fleshy-fruited plants. *Am. Nat.*, **136**: 790–809.

Willson, M.F., Graff, D.A. and Whelan, C.J. 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. *Condor*, **92**: 545–555.