Parental preference for red mouth of chicks in a songbird

F. GÖTMARK and M. AHLSTRÖM

Department of Zoology, University of Göteborg, Medicinaregatan 18, S-413 90 Göteborg, Sweden
(`f.gotmark@zool.gu.se`)

SUMMARY

Parental preferences during feeding and care-giving may select for ornamental traits in young, such as bright coloration. For chicks of coots, there is experimental evidence for this idea. We examined the hypothesis that bright yellow, orange and red mouths of chicks of songbirds have been favoured by feeding preferences in parents. In a field experiment, the orange–yellow mouths of great tit nestlings were dyed brightly red, and the feeding response of parents recorded. In nest boxes with extra daylight through a window, experimental chicks were on average given twice as much food (biomass) as control chicks (sham dyed). In normal nest boxes, the tendency was similar, but not significant. Thus, at least in good light, great tit parents prefer to feed young with red mouths, a preference for colourfulness that helps explain the evolution of bright gapes in chicks of songbirds (passerine birds).

1. INTRODUCTION

Ornaments such as huge feather plumes and fins, song, and bright colours, have been favoured in adult individuals of many animals by sexual selection (Andersson 1994). Young individuals, on the other hand, are usually cryptic in both appearance and behaviour (e.g. Harrison 1985; Booth 1990). In the absence of reproductive ability, predation and other factors favour dull or unornamented plumages and coats in the early life stages of many animals (Booth 1990). However, at least in primates and in some birds, young individuals have bright colour patterns. Alley (1980) described young primates with distinctively coloured and patterned coats and flesh. Observational evidence indicated that these colour patterns elicit attention, protection, tolerance and care-giving in older conspecifics. In birds, chicks of coots (*Fulica* spp.) have modified conspicuous orange feathers on the front of their bodies and bright red patterns on their heads and bills (Harrison 1985). Recently, Lyon *et al.* (1994) showed that American coot (*F. americana*) parents prefer to feed ornamented chicks over unornamented ones (chicks with trimmed orange feathers), leading to higher growth rates and greater survival for ornamented chicks. Lyon *et al.* (1994) suggested that parental choice in this way can select for ornamental traits in offspring.

The importance of such parental preferences is unclear. Chicks in some grebes and other rails, such as the moorhen, *Gallinula chloropus*, have similar ornaments, but otherwise the young of most birds appear to be cryptic (Harrison 1985). However, Götmark & Olsson (1997) suggested that the brightly coloured mouth of nestlings of many passerine birds is an ornamental trait, selected at least in part through parental choice. While begging for food from the parents, the young passerines display a large gape in conspicuous yellow, orange, or red colour (Swynnerton 1916; Harrison 1985). The bright mouths are usually viewed as 'directive marks' and 'releasers' of parental feeding (Ticehurst 1910; Swynnerton 1916; Armstrong 1965; Lack & Cambell 1985, pp. 99, 599). Such a proximate function does not, however, explain the evolution of the colour patches, nor does it explain why yellow, orange, and red predominate (Harrison 1985); other colours could also release feeding. White, bright green, or black mouths occur in other young and adult birds (Swynnerton 1916; Armstrong 1965; Harrison 1985; Lack & Campbell 1985), indicating that a reddish mouth is no physiological necessity.

In our earlier study, where we had manipulated plumage coloration of recently fledged great tits, *Parus major*, the parents fed red-painted fledglings more often than controls (yellow-painted fledglings) (Götmark & Olsson 1997). This surprising result indicated a parental preference for red in the feeding situation. To test directly whether great tit parents prefer to feed young with a colourful red mouth, we conducted a field experiment where nestlings were manipulated in the nest, and the feeding response in parents was recorded.

2. METHODS

The experiment was done in May–July 1996, near Göteborg in south-western Sweden. The study area at the Gunnebo nature reserve (municipality of Mölndal) consists of deciduous forest, mostly of oak (*Quercus robur*). We studied nestlings of 27 pairs of great tits breeding in wooden nest boxes. Nestlings in this species have orange–yellow mouths, with red blood vessels visible in the throat in small nestlings. In tits, most of the mouth opening consists of a 'horny covering sheathing the bones of the bill' (Wetherbee 1961). Colour pigments are prob-

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ably deposited in this horny covering. The mouth is surrounded by enlarged light yellow flanges, as in many other passerine nestlings (Swynnerton 1916; Clarke 1969). The flanges are almost always lighter than the mouth cavity and may 'serve as outlines of the opened mouth to guide the adult in feeding young' (Clarke 1969). They tend to be larger in hole-nesting birds (Clarke 1969), but gradually shrink in chicks older than two weeks (Gosler 1993, p. 80).

Great tits breed in natural holes or in nest boxes, in which the light is restricted, coming only from the entrance hole. Our nest boxes had a 35–40 mm wide and 65 mm deep opening (deeper than normal to reduce nest predation by marten, *Martes martes*, which otherwise may reach the nestlings). We studied 14 tit pairs breeding in such nest boxes and 13 pairs breeding in nest boxes where we had put in a (plastic) window on the side, about 3.5 cm × 9 cm. It ensured that feeding parents could see the young well in the extra light, and was used in case a parental preference for red would be difficult to detect in the other, darker nest boxes (in the study of Götmark & Olsson (1997), recently fledged young were fed in daylight). To avoid disturbing the nesting birds, this window was first covered by tape. The tape was removed (at night) at about the second day after hatching. We observed no negative effects of the window on behaviour or breeding success of the great tits.

The eggs of the tits hatched between mid May and mid June. Newly hatched young are poorly developed, but grow rapidly, and reach adult weight after about 14 days (see, for example, Orell 1983). We studied the chicks when they were on average 3.5 days old (s.d. $= 0.9$, range 1.5–5, $n = 27$) and weighed on average 6.1 g (s.d. $= 1.4$, range 3.2–8.0, $n = 27$). To alter mouth coloration, we used a non-toxic red food dye, sold for household use ('Ekströms Hushållsfärg', Procordia Food AB, Färjestaden, Sweden). It contains water (75%), glycerol (10%), ethyl alcohol (5%) and red pigment (carmine, 10%). When a chick gaped, its mouth cavity and tongue were carefully 'painted' with a very small amount of dye, using a thin brush that the chicks tended to suck (which made application of the dye easy). For control chicks, we used the same liquid without any pigment (this 'control liquid' was obtained from Procordia Food AB, Färjestaden). Controls were manipulated in the same way as experimentals, and there were no apparent differences in the behaviour of the two categories after manipulation. The liquid used for controls did not alter mouth coloration. The red dye had a slight bluish tinge on white paper, but together with the orange–yellow background of the mouth it produced a bright red mouth. The dye showed high reflectance in the red part of the spectrum, low reflectance in the remaining part of the 'visible' spectrum (400–550 nm) and similar low reflectance in the near ultraviolet (300–400 nm; checked by spectroradiometer, see Götmark (1996) for methods). Birds are able to perceive UV light (between 320 and 400 nm), but most red colours in birds seem to lack strong UV-reflecting components (Götmark 1996; S. Andersson, personal communication; see Finger & Burkhardt (1994) for exceptions). The mouth spectra of experimentals, therefore, should be representative for red signals in birds.

The red mouths of experimentals faded with time and were barely visible after about 2 h. We therefore started the trials directly after manipulation, ending after on average 44 min (s.d. $= 15.0$, range 20–69 min, $n = 27$). In each brood, we selected two chicks (of 4–12 young, mean $= 7.5$) for observations, those that were most similar in mass and bill width (including flanges). Bill width was measured with a ruler. To measure mass and changes in mass during the trials, we used a 10 g Pesola spring balance. Measurements were taken to the nearest 0.05 g; tests were made with the balance to ensure that such accuracy was possible to achieve (in the field, the following factors are important: shelter from wind, a firm object against which the balance is held, and no movements in the chick). In recording data, we paid attention to the possibility of psychological bias; for instance, when we had to round off mass measurements, we tended to choose conservative values (opposite the direction predicted by our hypothesis).

During all trials the remaining chicks in the nest were temporarily removed from the nest box (but kept warm). One of the two chosen chicks was selected as an experimental by using random numbers; the other became a control. After manipulation, the two chicks were placed in the nest box side by side in front of the hole. We retreated to a distance of about 25 m, where it was possible to observe the parents arriving with food in the bill. We recorded the sex of the parent, if possible the kind of food it brought (if any), whether it fed young (entered and left nest box, food in the bill disappeared), and whether it left the nest box with a faecal sac from the young. The trial ended when the parent(s) had entered the nest box and fed young at least three times and maximally five times (mean $= 4.0$, s.d. $= 0.85$, $n = 27$).

When the trial ended, we immediately reweighed the two chicks to determine the change in mass from the start of the trial, indicative of the amount of (or absence of) food brought by the parents. If we saw parents leaving the nest box with a faecal sac during a trial, it was ended and a new trial was done later (faecal sacs would have biased estimates of mass change). For each chick, the change in biomass (which could be positive, zero, or slightly negative) was used as a test variable. Only one trial was conducted for each great tit pair. We tested the (directed) prediction that great tit parents prefer ornamental coloration in chicks, and therefore used one-tailed tests, unless otherwise specified.

3. RESULTS

The great tits fed the young mainly with dipterans, spiders and geometrid larvae. Males and females differed in parental behaviour (see also Gosler 1993, p. 81). The young were quite small and the females still brooded them for periods of *ca.* 5–15 min. The females more often stayed near the nest box and fed the nestlings less than did the males. For 17 trials where we were able to determine the sex of feeding parents, males fed nestlings on average 2.9 times (s.d. $= 1.0$, range 1–5) and females 0.9 times (s.d. $= 0.7$, range 0–2). In total, males were seen feeding 50 times and females 15 times.

Parents might preferentially feed the larger nestlings in the brood, that is, the ones with larger gapes (Price & Ydenberg 1995; but see Leonard & Horn 1996). In our study, experimentals and controls did not differ in body mass or size (gape width) when the trials began (normal nest boxes, mass: $p = 0.28$, gape: $p = 0.94$; nest boxes with window, mass: $p = 0.64$, gape: $p = 0.69$, randomization test for matched pairs, two-tailed; Siegel (1956)). These results were expected, as the nestlings were matched

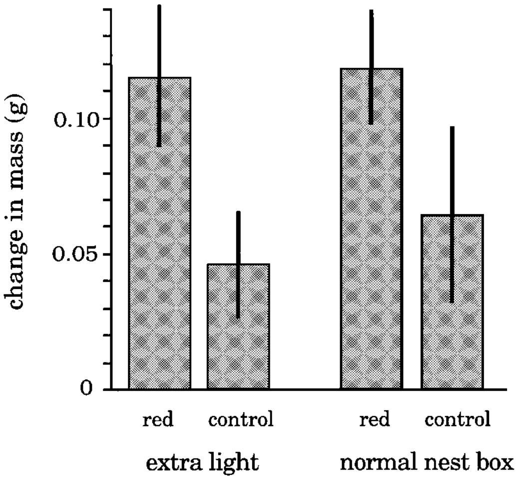

Figure 1. Mean (±s.e.) change in body mass (g) of great tit chicks, experimentals (red mouth) and controls (normal mouth), fed by parents during trials. Based on 13 pairs breeding in nest boxes with extra light through a window and 14 pairs breeding in normal nest boxes (one experimental and one control chick studied in each nest box). One trial was conducted per pair.

in mass and size, and manipulation was randomized within pairs.

For nest boxes with windows, experimentals increased in mass on average more than twice as much as controls (figure 1; $p = 0.017$, randomization test for matched pairs, one-tailed). For normal nest boxes, the tendency was similar (figure 1), but the difference was not significant ($p = 0.074$, same test, one-tailed), apparently due to slightly higher and more variable feeding of the controls in these nest boxes (figure 1). For an alternative analysis, we used mass change of chicks per feeding (3–5 feedings were recorded per trial) as a test variable, but the results were essentially the same.

4. DISCUSSION

The result of our experiment suggests that great tit parents give more food to nestlings with a bright red mouth than to those with a normal orange–yellow mouth. As in the study by Götmark & Olsson (1997), experimental chicks received about twice as much food (biomass) as control chicks. For nest boxes with extra light as well as normal nest boxes, parents fed chicks with red mouths at approximately double the rate of control chicks, but the difference was significant only for nest boxes with extra light. Taking into account other factors such as parasites, begging intensity, start rank, and nestling position, that have been shown to affect parental feeding of nestlings (e.g. Price & Ydenberg 1995; Leonard & Horn 1996; Christe *et al.* 1996), the feeding difference recorded in our experiment suggests that parents have a strong preference for red. Because mostly males fed the young, the preference was probably mainly due to them; more work is needed to establish whether females show a similar preference (from about day 6 after hatching, the females feed nestlings as much as the males do (Gosler 1993)).

Lyon *et al.* (1994) gave three possible explanations for a feeding preference for orange chicks in coot parents: (1) the colour of chicks may signal individual quality (genetic and/or phenotypic); (2) it may indicate chick age and nutritional need, since it varies with age and disappears after three weeks; and (3) the preference may stem from sensory exploitation of a parental preference favoured for other reasons. Below, we discuss these three explanations. First, yellow, orange and red colours are usually due to carotenoid pigments, obtained from the food and involved in vision, physiology, immunology and behavioural ecology (Andersson 1994; Lozano 1994; Hill 1996; Gray 1996, and references therein). In the house finch, males vary in colour from yellow to red, and females prefer the reddest males, which provide more food to offspring and seem to be of higher quality (Hill & Montgomerie 1994). The mouth colours of young are probably due to carotenoids in the integument or in blood vessels in the mouth (Ficken 1965; Hill *et al.* 1994) and might signal individual quality. The preference for red in great tit parents has not, however, led to evolution of bright red mouths in nestlings of this species (that have orange–yellow mouths). There seems to be little variation in mouth coloration in the nestlings (personal observation), and it remains to study whether mouth coloration signals individual quality.

Second, although we did not quantify mouth coloration in relation to age of nestlings, we observed no apparent changes in colour with age (personal observation). Age may also be assessed by the parents from the size of nestlings. In small canary (*Serinus canaria*) nestlings, mouth coloration seems to signal short-term need (Kilner 1997). The colour is controlled by blood flow, becoming more saturated when a chick starts begging. The more food-deprived, the more intensely coloured are the mouths of the chicks. As in the great tit, the parents prefer to feed nestlings with (dyed) red mouths (Kilner 1997).

Third, a bright mouth in nestlings occurs in nearly all passerine birds (Harrison 1985). The trait may reflect exploitation in the young of a parental preference for bright colour evolved earlier, in a different context (Basola 1990; Kirkpatrick & Ryan 1991; Andersson 1994; see also Kear 1966). In the great tit, perhaps costs of obtaining and processing red pigments (Hill 1996) or other factors limit selection for a red mouth. Hole-nesting may be one factor, if parents respond weakly to red in dark nests. In two other hole-nesting species, the blue tit and pied flycatcher, nestlings had mouth coloration similar to that of the great tit (personal observation).

Comparative data would be valuable for analysis of mouth coloration in relation to ecology, behaviour and phylogeny, but unfortunately such data are not available. Harrison (1985) presents data for many European species, but our experience of nestlings in four species and colour photographs of nestlings in many other species suggests that his colour categories are unreliable (within the range from yellow to red). Swynnerton (1916) presented a nice colour plate of a variety of mouth colour patterns of young and adult birds. He suggested that the bright gapes of nestlings represent warning colours, deterring nest predators. However, as the gapes are mainly directed at parents, evolution through parental choice is probably a more important mechanism. In addition, mouth coloration may relate to species recognition, as in the parasitic *Vidua* finches that mimic complicated mouth colour patterns of host nestlings (Nicolai 1974). For discussion of mouth signals in adults, see Armstrong (1965).

Except in Passeriformes, red or orange–red mouths of chicks have evolved in Cuculiformes, at least in two European brood parasites (Wyllie 1981, pp. 36, 46; Harrison 1985). Given the feeding preference documented above, the mouth colour of cuckoo chicks may be important for triggering feeding in host parents. Chicks of the parasitic brown-headed cowbird, *Molothrus ater*, also have red mouths, and they are often found in nests of hosts where the other young have yellow mouths (Rothstein 1978, p. 157).

In conclusion, great tit parents gave more food to chicks with red mouths than to those with normal, orange–yellow mouths, as predicted if parental choice selects for bright coloration in offspring (Lyon *et al.* 1994). Comparative studies, and studies of species with red mouths in chicks should help clarify the function and evolution of ornamental mouth coloration in young birds.

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REFERENCES

Alley, T. R. 1980 Infantile coloration as an elicitor of caretaking behaviour in old world primates. *Primates* **21**, 416–429.

Andersson, M. 1994 *Sexual selection.* Princeton University Press.

Armstrong, E. A. 1965 *Bird display and behaviour.* New York: Dover.

Basolo, A. L. 1990 Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808–810.

Booth, C. L. 1990 Evolutionary significance of ontogenetic colour change in animals. *Biol. J. Linn. Soc.* **40**, 25–163.

Christe, P., Richner, H. & Opplinger, A. 1996 Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behav. Ecol.* **7**, 127–131.

Clarke Jr, G. A. 1969 Oral flanges of juvenile birds. *Wilson Bull.* **81**, 270–279.

Ficken, M. S. 1965 Mouth colour of nestling passerines and its use in taxonomy. *Wilson Bull.* **77**, 71–75.

Finger, E. & Burkhardt, D. 1994 Biological aspects of bird coloration and avian colour vision including ultraviolet range. *Vision Res.* **34**, 1509–1514.

Gosler, A. 1993 *The great tit.* London: Hamlyn.

Götmark, F. 1996 Simulating a colour mutation: conspicuous red wings in the European blackbird reduce the risk of attacks by sparrowhawks. *Funct. Ecol.* **10**, 355–359.

Götmark F. & Olsson, J. 1997 Artificial colour mutation: do red-painted great tits experience increased or decreased predation? *Anim. Behav.* **53**, 83–91.

Gray, D. A. 1996 Carotenoids and sexual dichromatism in North American passerine birds. *Am. Nat.* **148**, 453–480.

Harrison, C. 1985 *A field guide to the nests, eggs and nestlings of European birds.* London: Collins.

Hill, G. E. 1996 Redness as a measure of the production cost of ornamental coloration. *Ethol. Ecol. Evol.* **8**, 157–175.

Hill, G. E. & Montgomerie, R. 1994 Plumage colour signals nutritional condition in the house finch. *Proc. R. Soc. Lond.* B **258**, 47–52.

Hill, G. E., Montgomerie, R., Inouye, C. Y., Dale, J. 1994 Influence of dietary carotenoids on plasma and plumage colour in the house finch: intra- and intersexual variation. *Funct. Ecol.* **8**, 343–350 .

Kear, J. 1966 The pecking response of young coots *Fulica atra* and moorhens *Gallinula chloropus. Ibis.* **108**, 118–122.

Kilner, R. 1997 Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond.* B **264**, 963–968. (Following paper.)

Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Lack, E. & Campbell, B. (eds) 1985 *A dictionary of birds.* Calton: Poyser.

Leonard, M. & Horn, A. 1996 Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.* **38**, 341–347.

Lozano, G. A. 1994 Carotenoids, parasites, and sexual selection. *Oikos.* **70**, 309–311.

Lyon, B. E., Eadie, J. M. & Hamilton, L. D. 1994 Parental choice selects for ornamental plumage in American coot chicks. *Nature* **371**, 240–243.

Nicolai, J. 1974 Mimicry in parasitic birds. *Scientific American* October 1974, 93–98.

Orell, M. 1983 Nestling growth in the great tit *Parus major* and the willow tit *P. montanus. Ornis. Fenn.* **60**, 65–82.

Price, K. & Ydenberg, R. 1995 Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behav. Ecol. Sociobiol.* **37**, 201–208.

Rothstein, S. I. 1978 Geographical variation in the nestling coloration of parasitic cowbirds. *Auk.* **95**, 152–160.

Siegel, S. 1956 *Non-parametric statistics for the behavioural sciences.* Tokyo: McGraw-Hill.

Swynnerton, C. F. M. 1916 On the coloration of the mouth and eggs of birds. I. The mouths of birds. *Ibis* **4**, 264–294.

Ticehurst, C. B. 1910 On the down-plumage and mouth-coloration of neonatal birds. *Brit. Birds* **4**, 70–73.

Wetherbee, D. K. 1961 Observations on the developmental condition of neonatal birds. *Am. Midl. Nat.* **65**, 413–435.

Wyllie, I. 1981 *The cuckoo.* London: Batsford.

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