

Mouth colour is a reliable signal of need in begging canary nestlings

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SUMMARY

Begging passerine chicks display brightly coloured mouths as they solicit food from their parents. Despite a range of hypotheses, the function of vivid nestling mouth colour remains unknown. Here I report that mouth colour functions as a signal of need in canary nestlings, in the days immediately following hatching. Changes in mouth colour accurately reflect a nestling's state of need: the more food deprived the chick, the more intensely coloured its mouth. In controlled experiments with two nestlings, parents were offered the opportunity to choose which nestling to feed. When the mouth colour of one offspring was artificially reddened using food colouring, parents gave it more food. These results demonstrate a novel function for nestling mouth colour and are consistent with recent models of the resolution of parent-offspring conflict.

1. INTRODUCTION

Begging passerine chicks display brightly coloured mouths as they solicit food from their parents. For example, canary (*Serinus canaria*) nestlings display deep pink mouths, but mouths are orange in dunnocks (*Prunella modularis*) and yellow in robins (*Erithacus rubecula*). Despite a range of hypotheses (Pycraft 1907; Swynnerton 1916; Lorenz 1937; Pullen 1945; Armstrong 1947; Wetherbee 1961; Payne 1973; Dawkins & Krebs 1979), the function of vivid nestling mouth colour remains unknown. In this paper, I present experimental evidence that canary nestling mouth colour functions to signal need and that parents adjust their food allocation behaviour among the brood in response.

The striking mouth coloration of nestlings is one component of a suite of solicitation behaviours that make up the begging display. Young birds in the nest assume vigorous begging postures and call loudly at parents in a way that seems paradoxically exuberant. Why do chicks employ such apparently energetically costly behaviours (although, see Leech & Leonard 1996), which potentially attract the attention of predators (Haskell 1994; Redondo & Castro 1992), when communicating with a parent who is merely centimetres away? One possibility is that begging displays reflect an underlying conflict of interest between parents and their young over resource allocation at the nest since, in theory, offspring are selected to demand more resources than parents are selected to provide (Trivers 1974). Early models suggested that vigorous begging may be the means by which offspring wheedle additional resources from highly sales resistant parents (e.g. Parker & Macnair 1979). By contrast, recent analyses of ESS models find that the apparent costliness of solicitation

displays creates a signalling equilibrium which resolves parent-offspring conflict over resource distribution (Godfray 1991, 1995). The suggestion is that at equilibrium, begging serves to advertise some component of offspring condition, which parents are otherwise unable to assess directly. Parents use this information to allocate resources to young who stand to gain the greatest fitness benefits from receiving food. Honest signalling models of offspring solicitation thus yield the following three main predictions: (i) begging intensity should reflect offspring need; (ii) parents should provision young in relation to begging intensity; and (iii) begging should be costly. Empirical work has found some support for these predictions. Chick begging posture and calling are now known to change reliably in the short-term with recent feeding experience and some experimental work suggests that parents alter their pattern of food distribution in response (see Kilner & Johnstone (1997) for review). The function of bright nestling mouth coloration, however, remains unknown.

The mouths of canary nestlings are relatively unusual in that, following the onset of each begging bout, they exhibit a rapid change in colour intensity. I call this rapid change 'the flush'. Swynnerton (1916) describes a similar phenomenon in his observations of a bulbul species: 'The mouth is ... sometimes brighter than at others, even nearly carmine ... I found, in fact, that when I opened the mouth myself it was dull brownish in coloration, the bright colour ... being evidently due not to pigment but to a rush of blood to the mouth under the stimulus of eagerness'. The effect has also been seen in house finch (*Carpodacus mexicanus*) nestlings (A. Lotem, personal communication). Such rapid changes in mouth colour are probably the result of changes in blood flow to the mouth and they have only been observed

in species which have red or pink mouths. In canaries, flushing is most pronounced when nestlings are less than four days old (personal observation).

The dynamic nature of canary nestling mouth colour indicated that it may function as a signal of need. Using experiments on captive canaries, I tested the following two predictions based on Godfray's models: first, that mouth colour should vary reliably with need; and second, that parents should allocate food in relation to nestling mouth colour, preferring to feed chicks signalling they are in greatest need.

2. METHOD

(a) *The study species*

Domesticated canaries rear broods of three to four chicks which hatch asynchronously, generating a noticeable size hierarchy. Both parents feed the young, by regurgitation, and nest visits are relatively infrequent, usually about five times an hour at unmanipulated nests. Nest visits are relatively long, lasting about 60 s, during which time parents typically regurgitate 25 times, often feeding each chick in the brood at least once per nest visit. Chicks were fed Nectarblend rearing mix, a blend of ground seed, egg, honey and water concocted by Haith's Seeds of Cleethorpes, UK. Further details on canary breeding habits can be found in Kilner (1996).

(b) *Does nestling mouth colour vary with the extent of food deprivation?*

Domesticated canaries were bred in captivity at Madingley, at the Sub-Department of Animal Behaviour, in Cambridgeshire in the summers of 1994 and 1995 under conditions described elsewhere (Kilner 1995, 1996). To examine whether mouth colour varies with the extent of food deprivation, a simple pilot experiment was performed on seven pairs of siblings, from seven different broods, 2–4 days after hatching (i.e. $N = 7$). In both this test and the one described below, colour quantification is based on human vision. Unlike humans, birds have UV photoreceptors which may alter their perception of colours we see as red (Bennett *et al.* 1994). There is a small risk that the difference between human and avian vision may introduce artefacts which manipulate avian colour traits, but as yet the seriousness of these potential dangers is not known (see Hill 1991; Bennett *et al.* 1994; Götmark & Olsson 1997). Both chicks were removed from their nest and kept warm. One of the pair received 0.25 ml of warm, liquid consistency Nectarblend rearing mix from a syringe, while the other received nothing. After 30 min, both chicks were placed in an artificial nest, induced to beg and their gapes were photographed using slide film. Since it was impossible to control daylight quality, chicks were photographed in a blacked out room, with the artificial nest illuminated by four 275 W Photoflood light bulbs. To quantify the colours of the chicks' mouths, the slides were digitized and the images imported into the Macintosh application Adobe Photoshop. In this program, hue represents position across the spectrum and is measured on a wheel in degrees, 0° (360°) is the reddest measure; saturation represents colour density, least dense (0%) to most dense (100%); brightness is the grey-scale value of the colour where 0% is white and 100% is black. Mouth colour was quantified by placing ten arbi-

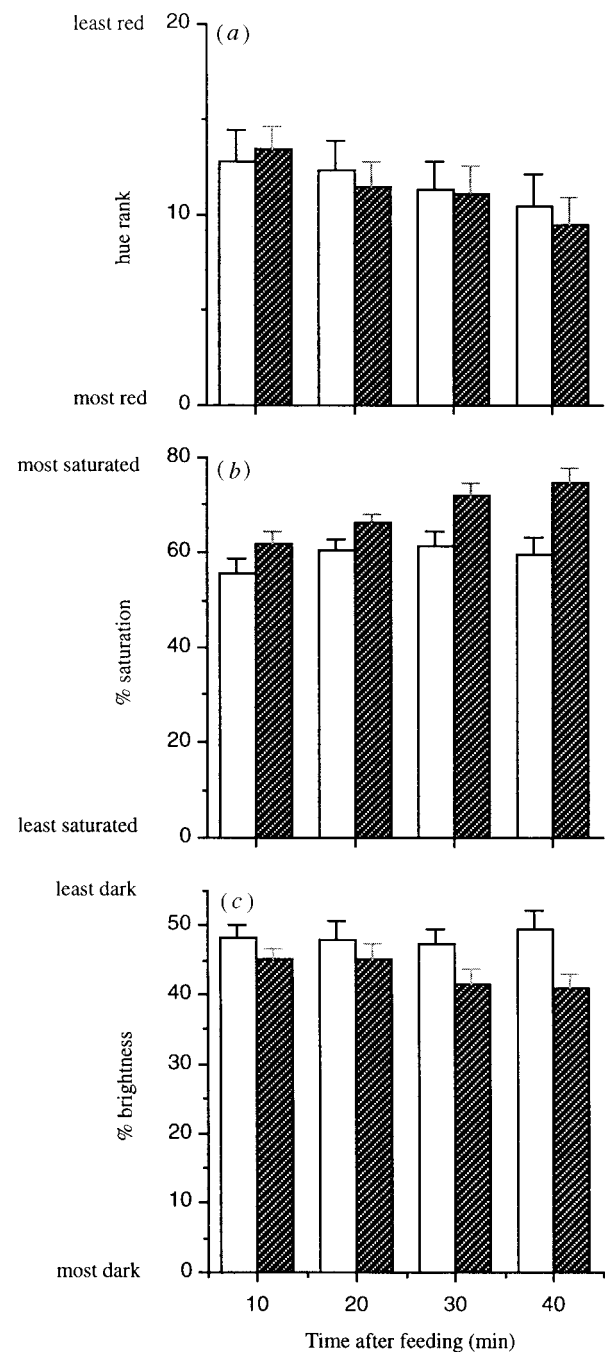


Figure 1. The effect of food deprivation and the mouth flush on mouth colour. (a) Mouth hue. (b) Mouth saturation. (c) Mouth brightness. Hatched bars show mouth colour after the flush, unhatched bars mouth colour before the flush. Means and standard error bars are shown ($N = 8$).

trarily arranged dots over the mouth image on the screen and scoring hue, saturation and brightness at each point. Means of the ten values were calculated to give the colour scores for each mouth image. Using a two-tailed paired *t*-test, the mean mouth colours of food-deprived chicks were compared with their less needy siblings.

(c) *How does 'flushing' influence mouth colour?*

In a second experiment, I investigated the effect of the mouth flush and extent of food deprivation on changes in mouth colour. Eight nestlings were removed from seven

different broods ($N = 8$), 2–4 days post-hatching, and fed 0.25 ml of warm, liquid consistency Nectarblend rearing mix from a syringe at 0 min. The chicks were placed in a heated nest under a Sony Hi-8 Camcorder, in the same constant lighting conditions as the pilot test. Chicks were induced to beg at 10, 20, 30 and 40 min and all begging activity was filmed. At the end of the test, chicks were fed until they stopped begging and returned to their parents.

The videotapes were analysed frame by frame using a Macintosh computer and mouth images were selected and imported into Adobe Photoshop for colour quantification using the technique described above. Within each of the four times at which begging was induced, mouth colour was measured twice, once as the chick opened its mouth to beg and again at least 2 s later, after the flush. These data were tested for normality and analysed using a split-plot ANOVA to investigate the effect of the mouth flush and extent of food deprivation on mouth colour (Sokal & Rohlf 1995). The ANOVA was designed so that mouth colour measurements made before and after the flush (before and after) were nested within time since feeding (10, 20, 30, 40 min).

(d) Does nestling mouth colour influence food allocation among the brood?

I tested whether offspring with more intensely coloured mouths attracted increased feeding by parents, while controlling chick size and chick hunger, factors that have previously been shown to influence food distribution among the brood (Kilner 1995). It was not possible to standardize chick size empirically, so this had to be done statistically, a process made easier by testing pairs of differently sized chicks where one chick was always at least 1.5 g heavier than the other. Chick hunger was controlled by depriving both chicks of food for 90 min and then feeding them 0.25 ml warm, liquid consistency Nectarblend rearing mix. Mouth colour was manipulated by adding Tesco's cochineal food colouring to the rearing mix. The dyed food intensified the colour of the chicks' mouth lining for 45–60 min within the range occurring naturally (painted mouth mean \pm s.e.; hue, 9.2 ± 1.1 ; saturation, 76.6 ± 1.5 ; brightness, 37.1 ± 3.5 ; see figure 1 for comparison with natural range). The experiment was divided into four different treatments: (i) control—both chicks hand-fed red rearing mix; (ii) control—both chicks hand-fed uncoloured rearing mix; (iii) experimental—larger chick fed red rearing mix, smaller chick hand-fed uncoloured rearing mix; and (iv) experimental—larger chick fed uncoloured rearing mix, smaller chick hand-fed red rearing mix.

Each treatment was replicated with eight different pairs of parents using two of their chicks (i.e. $N = 8$). Remaining chicks from the brood were fostered out to other nests for the duration of the experiment. The experiment was conducted 5–8 days post-hatching, with one treatment per day. The order in which treatments were carried out was stratified between nests, such that a control treatment always alternated with an experimental treatment.

In each treatment, following mouth colour manipulation, the two nestlings were returned to their parents and all feeding activity at the nest in the next 30 min was filmed with a video camera. Each time a parent inserted its beak into the mouth of a nestling, one feed was scored. The feeding decisions of parents were compared by counting the number of feeds, of the first 25 delivered to both nestlings after the start of the test, that were allocated to the larger nestling. By examin-

ing the number of feeds given to the larger chick alone, pseudo-replication was avoided. Furthermore, the effects of chick size became statistically irrelevant and the effect of mouth colour could be investigated in isolation. Twenty-five feeds was selected as the cut-off point, because for 30 of the 32 tests this restricted the analysis to visits in the first ten minutes of the test when nestlings were more equally fed, when both nestlings begged so parents were forced to choose which to feed and when artificially reddened mouths were most strikingly red. The data were tested for normality and analysed using a repeated measures ANOVA, where the four different treatments were the repeated measure. Differences between pairs of treatments were analysed using Fisher's PLSD *post hoc* tests (Sokal & Rohlf 1995).

I also examined whether parents increased their food delivery rate in response to nestling mouth colour, by comparing the number of feeds delivered to broods in each control treatment. The number of feeds delivered in each of the 16 tests ranged widely (25–283), could not be analysed using parametric statistics, and so were compared using two-tailed Wilcoxon signed rank tests.

3. RESULTS

(a) Does nestling mouth colour vary with the extent of food deprivation?

Needier chicks had significantly redder ($n = 7$, d.f. = 6, paired t -test, $t = 6.18$, $p < 0.001$), more saturated ($n = 7$, d.f. = 6, paired t -test, $t = -4.07$, $p < 0.01$) and less bright (darker) ($n = 7$, d.f. = 6, paired t -test, $t = 6.09$, $p < 0.001$) mouths than their more recently fed siblings.

(b) How does 'flushing' influence mouth colour?

Mouth colour changed significantly each time that begging was experimentally induced as a result of the flush, and with increasing time since feeding. Mouth hue changed significantly with time since feeding ($F_{3,21} = 3.24$, $p = 0.04$). However, each time that begging was induced, mouth hue did not change as a result of the flush ($F_{1,28} = 0.33$, $p = 0.6$), nor was there an interaction between these two factors ($F_{3,28} = 1.6$, $p = 0.21$). Mouth saturation did not change significantly with the extent of food deprivation, although there was a strong trend in that direction ($F_{3,21} = 2.91$, $p = 0.058$), but it did change significantly as a result of the flush each time that begging was induced ($F_{1,28} = 94.3$, $p < 0.001$). The same pattern held for mouth brightness. Although it did not change significantly with time since feeding ($F_{3,21} = 0.94$, $p = 0.4$), it did change significantly as a result of the flush each time that begging was experimentally induced ($F_{1,28} = 46.3$, $p < 0.001$) (figure 1).

Changes in mouth saturation and brightness as a result of the flush increased in magnitude with increasing time since feeding. There was a significant interaction between time since feeding and the effect of the flush on both mouth saturation ($F_{3,28} = 5.36$, $p = 0.005$) and brightness ($F_{3,28} = 3.27$, $p = 0.04$) (figure 2).

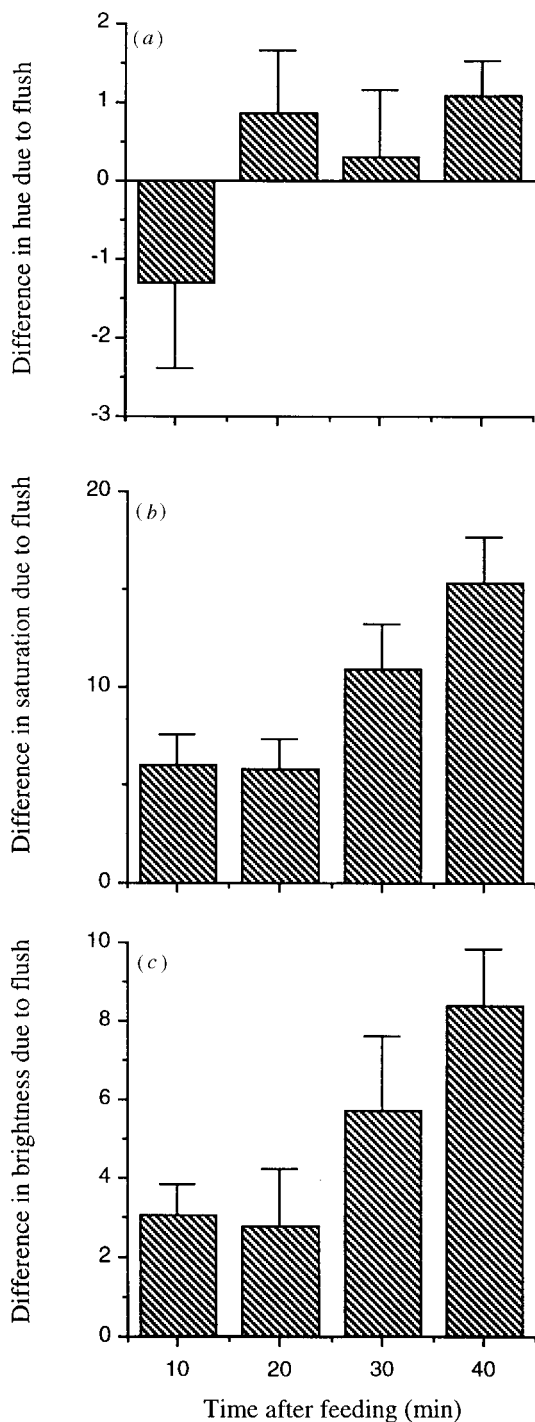


Figure 2. The interaction between food deprivation and the mouth flush on changes in mouth colour. (a) Mouth hue. (b) Mouth saturation. (c) Mouth brightness. The magnitude of the difference as a result of the flush is shown. Means and standard error bars are shown ($N = 8$).

To exclude the possibility that repeated testing of individual chicks alone accounted for the observed changes in mouth colour, I compared the mouth colours of chicks from the first experiment (where chicks were tested once) with those from the second experiment (where chicks were tested repeatedly). Both sets of chicks had been food deprived for 30 min since being fed 0.25 ml food. There was

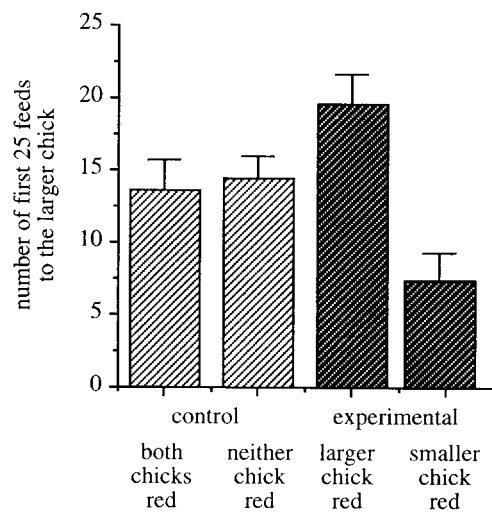


Figure 3. The results of the mouth colour manipulation experiment. Means and standard error bars are shown ($N = 8$).

no significant difference between chick mouth colours measured after repeated testing and those measured after a single test (hue: d.f. = 13, unpaired t -test, $t = 1.36$, $p > 0.19$; saturation: d.f. = 13, unpaired t -test, $t = 0.711$, $p > 0.48$; brightness: d.f. = 13, unpaired t -test, $t = 1.41$, $p > 0.18$).

(c) *Does nestling mouth colour influence food allocation among the brood?*

Nestling mouth colour significantly influenced food distribution among the brood. There was a significant difference between the four mouth colour treatments ($F_{3,21} = 8.31$, $p < 0.001$). When the mouth colour of the larger nestling was artificially reddened, parents gave it significantly more food than in the control tests (larger chick red versus both nestlings red: Fisher PLSD = 5.12, $p < 0.05$; larger chick red versus neither nestling red: Fisher PLSD = 5.12, $p < 0.05$). When the mouth colour of the smaller nestling was artificially reddened parents gave the larger nestling significantly less food than in the control tests (larger chick uncoloured versus both nestlings red: Fisher PLSD = 5.12, $p < 0.05$; larger chick uncoloured versus neither nestling red: Fisher PLSD = 5.12, $p < 0.05$) (figure 3).

Parents delivered more food to the brood when both chicks had reddened mouths than when they did not. In the control treatment where both nestlings had reddened mouths, the total number of feeds given to both nestlings in the course of the experiment was significantly greater than the total amount of food given to both nestlings in the control treatment where their mouths were uncoloured ($N = 8$, Wilcoxon, $Z = -2.03$, $p = 0.04$).

4. DISCUSSION

These experimental results demonstrate that in canaries, nestling mouth colour functions to signal need by becoming more intensely coloured with increasing

food deprivation. Parents adjust their food allocation among the brood in relation to mouth colour, preferring to feed chicks apparently signalling they are in greatest need. In addition, since parents delivered more feeds when both chicks displayed reddened mouths than when neither did, parents must respond to absolute, rather than relative, changes in mouth colour when assessing brood need. The data are certainly consistent with two of the predictions of Godfray's models, but in isolation are not sufficient to merit the conclusion that canary nestling mouth colour functions to resolve parent-offspring conflict. After all, the data are also consistent with the type of cooperative signalling system, with no conflicts of interest expected between young and their parents, envisaged by Pullen (1945) and other traditional ethologists (e.g. Armstrong 1947) long before the concept of parent-offspring conflict was derived. We cannot be certain that mouth colour signals function to resolve parent-offspring conflict until the costs of signalling are measured.

(a) What maintains signal reliability?

If it pays offspring to display a perpetually intensely coloured mouth, what maintains signal reliability? It could be that presenting an intensely colourful mouth is costly and this prohibits less needy chicks from displaying at maximum intensity. For example, if changes in blood flow to the mouth are responsible for changes in mouth colour with need, chicks may pay a digestive cost for channelling blood away from a full gut to the mouth. It is known that blood is diverted from other tissues to the digestive organs in recently fed sheep (e.g. Barnes *et al.* 1983). Similar processes in birds may explain why more satiated chicks display paler mouths as they beg. If it is the costliness of diverting blood from a full gut that maintains signal reliability, then it is likely that mouth colour functions explicitly as a signal of need in the way described by Godfray's models (Godfray 1991, 1995). However, an intriguing complication in this scenario is that chicks would not only vary in the amount they stand to gain, but also in the costs of displaying, making it difficult to predict exactly how parents should respond to the signal (see Johnstone & Grafen 1993). An alternative possibility is that mouth colour is a low cost or cost-free signal and its reliability is ensured by a strong proximate link, physiologically preventing blood passing in high quantities to the mouth when the gut is full. Mouth colour could still be a signal of need resolving parent-offspring conflict in this scenario. The conflict would be then resolved through selection on offspring gut capacity, or the relevant proximate link to mouth colour, rather than the costliness of the signal itself.

(b) Why does nestling mouth colour no longer change with need in older chicks?

As canary chicks grow and develop other begging behaviours such as posturing and calling, mouth

colour ceases to change with need. This may be because blood can flow freely to the mouth and the gut in older chicks; there is no longer a cost of signalling through mouth colour so chicks can display perpetually at maximum intensity. Or, it may be that the newer suite of multiple begging behaviours provide parents with more information than can be obtained through mouth colour alone, making it redundant as a signal of need.

(c) Why do chicks of other species have yellow or orange mouths?

The mouths of canary chicks are highly vascularized which gives them their deep pink colour. Unless changes in blood flow can also permeate through the densely pigmented yellow and orange mouths of other species to alter mouth colour, it is unlikely that nestling mouth colour functions in all passerines as a signal of need. What, then, could be the function of bright nestling mouth coloration in species such as dunnocks and robins (see Götmark & Ahlström 1997)? Perhaps nestling mouth colour functions to improve the efficacy of transmission of other begging behaviours (Guilford & Dawkins 1991). Mouth colour may function in a relatively straightforward way to define targets for parents (Pycraft 1907), either by making chick mouths more visible in a dark nest or by creating maximum contrast between the chick and the nest background in open nests. Alternatively, nestling mouth colour may interact with other components of the begging display to amplify their meaning (Hasson 1989), or modify parental response (see Rowe & Guilford 1996).

In summary, this study has revealed a novel function for bright nestling mouth colour as a signal of need in canary nestlings. Whether all passerine nestlings signal need through mouth colour remains to be seen. It may be that only red, vascularized mouths can signal need, or that such visual signals have only evolved in open-nesting species where parents can clearly see their young. The challenge for future work is to explain why nestling mouth colour signals are reliable and why mouth colours are so diverse between species of passerines.

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