



# Nestling mouth colour: ecological correlates of a begging signal

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## ABSTRACT

The mouths of begging nestlings vary widely in colour, ranging from yellow in robins, *Erithacus rubecula*, to red in reed buntings, *Emberiza schoeniclus*. Two functions have been suggested for bright nestling mouth colour: (1) it may improve the detectability of chicks, particularly in poorly lit nests and (2) within species, it may signal need. We tested these hypotheses in a comparative analysis, measuring the mouth colours of nestlings from 31 species under conditions of standardized light availability and food deprivation. Changes in mouth colour signalled need only among the seed-regurgitating finches. In these species there was a 'red flush' at the onset of begging, which became redder with increasing food deprivation. No other species showed these changes, including the closely related chaffinch, *Fringilla coelebs*, which feeds its young insects. We found no evidence that mouth colour was correlated with the light available in the nest. We did find, however, that nestlings in darker nests improved their conspicuousness through the relative colour and size of the flange that borders their brightly coloured mouths. Nestlings from darker nests had relatively wider flanges, which were whiter and less densely coloured in relation to their mouth colour, than those of chicks reared in better illuminated nests. Clutch size was not related to mouth or flange colour, or relative flange size. We suggest that nestling mouth colour has not been selected to make chicks detectable, but that this is the function of the surrounding flange. We also discuss reasons why signals of need through mouth colour are not more widespread.

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Begging nestlings from a variety of species use similar, exuberant, multicomponent displays when soliciting food from their parents. Typically, offspring present brightly coloured mouths, call incessantly, stand up and flap their wings. The details of the solicitation display, however, vary between species. Begging calls may be short and high pitched as in chaffinches, *Fringilla coelebs*, or lower and longer as in starlings, *Sturnus vulgaris* (Redondo & Arias de Reyna 1988). Nestling mouth colour is equally variable between species, ranging from yellow in robins, *Erithacus rubecula*, to orange in pied wagtails, *Motacilla alba*, and red in reed buntings, *Emberiza schoeniclus*.

Variation in bright nestling mouth colour between species did not go unnoticed by early ornithologists. Swynnerton (1916), for example, suggested that bright nestling mouths functioned as warning coloration for potential predators, an idea that he tested by asking his manservant to report on the palatability of different species. The taste of young birds was apparently so obnoxious that Swynnerton concluded their vivid mouth colours must serve an aposematic function. Pycraft

(1907), meanwhile, proposed that mouth colour functioned to guide parents to their nestlings, particularly in darker cavity nests. Ficken (1965) also suggested that nestling mouth colour is related to nest type, and that species with yellow mouths are more likely to be found in cavity nests.

More recently, nestling mouth colour has been shown to vary within a species. Specifically, in canary, *Serinus canaria*, nestlings, it is a signal of need (Kilner 1997). Canary chicks have pink, highly vascularized mouths which rapidly intensify in colour after the onset of begging, a process called the 'flush'. The extent to which mouths change colour during the flush increases as a chick becomes more food deprived, so that nestling mouth colour can reliably indicate a chick's nutritional state to parents poised at the side of the nest with food. Variation in the mouth colour of canary nestlings with need is relatively small, and much less than the variation in mouth colour between species.

We combined recent progress in understanding the function of nestling mouth colour with earlier ideas to test the following hypotheses. First, we investigated whether changes in nestling mouth colour are a signal of need in a wide variety of species. Some birds build their nests in dark cavities (e.g. great tit, *Parus major*), under

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overhangs (e.g. barn swallow, *Hirundo rustica*) or in domed nests (e.g. longtailed tit, *Aegithalos caudatus*), while others construct cup nests that are placed in more brightly lit sites, under tussocks (e.g. meadow pipit, *Anthus pratensis*) or in bushes (e.g. blackbird, *Turdus merula*). We predicted that changes in mouth colour should signal need only in species where such visual cues would be easily detected by parents, that is in species that rear their young in open nests. Second, we tested whether (for a given state of food deprivation) nestling mouth colour varied between species to ensure maximum detectability by parents. Clearly, chicks in dark nests are under different selection pressures to be detectable than chicks in well-lit nests (cf. Endler 1987; Guilford & Dawkins 1991; Marchetti 1993). Equally, the pressure to be detected, and chosen by parents with food, may vary with the intensity of sibling competition. We therefore predicted that between species, nestling mouth colour should vary with light availability at the nest and mean clutch size. Third, as well as considering the colour of the mouth lining, we also examined the colour and size of the paler fleshy flange that commonly borders the gapes of nestlings. Ingram (1920) observed that the nestling flange of hole-nesting jackdaws, *Corvus monedula*, was much more prominent than in the congeneric open-nesting carrion crow, *C. corone*, and concluded that the flange functioned to guide parents to nestlings in dark holes. We tested this hypothesis for a wider range of species, and also considered the possibility that flange size and colour might be related to the intensity of sibling competition.

## METHODS

### General Methods

We measured the mouth colours of nestlings under conditions of standardized light availability and food deprivation. By travelling around Cambridgeshire, Suffolk, Oxfordshire and Cumbria, U.K. in April–July 1996, we collected data on 31 European species from 17 families (see Table 1). To avoid pseudoreplication, we sampled a maximum of two chicks from each nest. All chicks were at approximately the same stage of development with closed eyes and no pin feathers. Across species the age range was 3–6 days. When the parents were absent, we removed the chicks from the nest (under licence from English Nature) and took them to the laboratory nearby for measurement. We always left at least one chick with the parents during the experiment. The laboratory was always set up within 30 min travelling distance of the nest and we carried the chicks on a hot water bottle, insulated with fake fur, during transport. In the laboratory, we weighed individuals to the nearest 0.5 g using a 50 g Pesola spring balance. For all of the species we measured, the brightly coloured nestling mouth lining was bordered with a paler fleshy flange. We used vernier callipers to measure the distance between the proximal corners of the mouth flange to the nearest 0.5 mm. These gape measurements were made when the mouth was shut.

We then placed the chicks in a plastic canary nest pan (bought from Porters, London, U.K.), lined with felt and wrapped with aluminium foil underneath, which was supported on a wooden stand and heated from below with an insulated jar of hot water. The chicks were supported and covered with Sanitary Nesting Material (also bought from Porters, London, U.K.) for insulation. We induced the chicks to beg, by removing the covering nesting material and lightly tapping the box with plastic forceps. Begging chicks were fed balls of Nectarblend rearing mix, a blend of egg, honey and ground seed (available only from Haith's of Cleethorpes, U.K.) until they stopped begging, presumably having reached satiation. We called this point 0 min. We then covered the chicks again with nesting material and moved them in their heated nest into a wooden, light-proof box (30 × 30 × 45 cm) which was painted white on the inside. The lid of the box was fitted with a Sony CCD-TR680E Hi-8 video camera, with the lens pointing down into the box at the chick in the nest. The box could be lit with a halogen light bulb, which was attached to the inside of the box lid and powered by a 12 V battery. The light from the bulb was dispersed by passing it through diffuser paper.

Every 10 min, for the next 110 min, we tested the begging performance of each chick. We turned on the light and induced the chick to beg by tapping the side of the nest with the plastic forceps. Access to the nest during each test was by means of a sleeve attached to the side of the box. The chicks were supported with nesting material so that their open gapes were approximately perpendicular to the plane of the video camera. During each test, all begging activity was filmed and recorded with Fuji Hi-8 MP videotapes. Between tests, we checked that the nestling was warm and replaced the hot water under the nest when necessary. Previous work on canaries (Kilner 1997) and blackbirds (unpublished data) has established that repeated testing of chicks has no independent effect on mouth colour. We assume that this is also true of other species. After 110 min, we removed the nestling from the wooden box and fed it Nectarblend, again until it stopped begging. We then transported it back to its nest on the hot water bottle and replaced it when the parents were absent. At this point, we measured the light available at the nest (in  $\text{cd/m}^2$ ) with a photographic light meter with the end pointing towards and approximately 5 cm above the chicks. Although we measured nest light availability under a range of weather conditions, we are confident that this did not bias our data set in a systematic way. We used the light meter scores to estimate the light available at the nest as perceived by parents arriving to feed chicks.

### Measuring Mouth Colour

Unlike humans, birds have UV photoreceptors which may alter their perception of colours that we see as red, orange or yellow (Bennett et al. 1994). Ideally, we should have measured nestling mouth colour using a reflectance spectrophotometer which measures into the ultraviolet. In pilot tests on canary young, however, we found it impossible to position gaping chicks to take accurate

**Table 1.** The nestling mouth colours of 31 European bird species, organized by the clades identified by Sibley & Ahlquist's (1990) molecular phylogeny

Species	N	Mouth			Flange		
		Hue	Saturation	Brightness	Hue	Saturation	Brightness
Nonpasserines							
Common swift, <i>Apus apus</i>	9	9.8	80.7	57.5	16.8	64.9	71.1
Common cuckoo, <i>Cuculus canorus</i>	3	13.6	99.9	56.0	28.6	78.6	82.0
Passerines							
Superfamily							
Corvoidea							
Jackdaw, <i>Corvus monedula</i>	6	8.0	87.4	50.8	47.7	67.3	86.1
Superfamily							
Muscicapoidea							
Robin, <i>Erithacus rubecula</i>	29	33.3	99.7	80.2	48.4	70.5	98.2
Pied flycatcher, <i>Ficedula hypoleuca</i>	9	22.3	99.7	47.1	35.8	62.6	84.6
Blackbird, <i>Turdus merula</i>	36	38.7	93.8	77.7	49.4	75.3	85.9
Song thrush, <i>T. philomelos</i>	5	31.3	97.5	74.1	40.7	73.2	90.9
Starling, <i>Sturnus vulgaris</i>	8	41.6	99.3	89.6	48.9	73.7	84.4
Superfamily							
Sylvioidea							
Wren, <i>Troglodytes troglodytes</i>	2	25.4	99.6	47.1	34.8	57.5	83.9
Nuthatch, <i>Sitta europaea</i>	2	29.4	91.8	60.5	46.9	44.7	92.2
Treecreeper, <i>Certhia familiaris</i>	2	21.6	100.0	51.5	35.9	63.5	82.1
Barn swallow, <i>Hirundo rustica</i>	8	36.0	92.5	71.2	41.0	55.1	88.9
Longtailed tit, <i>Aegithalos caudatus</i>	6	24.8	99.0	63.9	40.1	67.9	93.4
Blue tit, <i>Parus caeruleus</i>	6	21.5	99.6	45.3	44.0	75.4	84.2
Great tit, <i>P. major</i>	12	26.5	99.3	56.6	47.9	69.0	90.7
Grasshopper warbler, <i>Locustella naevia</i>	2	16.5	100.0	76.0	41.7	77.4	96.3
Willow warbler, <i>Phylloscopus trochilus</i>	9	21.9	99.7	56.5	32.6	75.1	82.2
Reed warbler, <i>Acrocephalus scirpaceus</i>	26	23.8	99.5	55.2	37.9	60.5	88.3
Sedge warbler, <i>A. schoenobaenus</i>	6	17.9	99.8	53.4	35.6	77.3	83.1
Blackcap, <i>Sylvia atricapilla</i>	2	9.7	83.2	52.1	25.6	32.5	85.5
Lesser whitethroat, <i>S. curruca</i>	2	18.7	100.0	59.9	34.4	77.4	83.7
Superfamily							
Passeroidea							
Pied wagtail, <i>Motacilla alba</i>	4	12.8	100.0	57.5	33.2	70.5	89.4
Meadow pipit, <i>Anthus pratensis</i>	4	18.6	97.1	54.8	30.2	77.3	71.9
Dunnock, <i>Prunella modularis</i>	10	11.6	99.5	75.5	21.9	67.3	90.2
House sparrow, <i>Passer domesticus</i>	5	18.4	96.0	57.8	43.7	75.0	94.4
Chaffinch, <i>Fringilla coelebs</i>	7	7.0	80.9	59.0	23.1	36.1	93.6
Linnet, <i>Acanthis cannabina</i>	2	6.5	89.0	56.0	18.2	41.1	90.9
Greenfinch, <i>Carduelis chloris</i>	4	11.0	94.3	57.3	20.4	58.4	84.3
Goldfinch, <i>C. carduelis</i>	4	9.5	96.7	43.1	19.4	66.0	66.0
Bullfinch, <i>Pyrrhula pyrrhula</i>	2	5.6	91.3	46.9	21.8	51.5	76.4
Reed bunting, <i>Emberiza schoeniclus</i>	8	10.4	90.5	47.9	24.1	49.2	82.6
Total	240						

N refers to the number of nestlings measured for each species. Mean mouth and flange hue, saturation and brightness scores (see Methods) were measured with the Macintosh application Adobe Photoshop. All means are derived from second measurements made 60 min after feeding to satiation.

measurements of their mouth colours using this equipment. Instead, we measured nestling mouth colour by playing our video recordings of nestlings begging on to a computer. Images of nestling mouths were selected, digitized and imported into the Macintosh application Adobe Photoshop. For each species, we measured mouth colour twice during each test session when chicks were induced to beg, to investigate the existence of a canary-like 'flush' in mouth colour. There is a small risk that the difference between human and avian vision may introduce artefacts into these measurements but as yet the seriousness of these dangers is not known (Hill 1991; Bennett et al. 1994).

The first measurement was made as soon as the mouth was fully open and perpendicular to the plane of the video camera; the second was made at least 2 s after this, again when the plane of the mouth was perpendicular to the plane of the video camera. Adobe Photoshop can describe colour by measuring an area five pixels by five pixels in terms of hue, saturation and brightness. Hue is a circular variable, depicting position on a colour wheel, where red is at 0° and green is at 180°. Nestling mouth colours fall within a sufficiently narrow sector (see Table 1) for hue to be treated as a linear variable in these analyses. Using this technique, the red mouths of reed buntings, for example, had a mean hue score of 10.4,

while the mean hue of yellow-mouthed robins was 33.3. Saturation describes the density of the colour and ranges from 0% (least dense) to 100% (most dense). Brightness describes the grey-scale value of the colour and ranges from 0% (black) to 100% (white). Because Adobe Photoshop can describe the colour of only a small patch at each sampling, each nestling mouth image was sampled in eight different sites to derive mean hue, saturation and brightness scores for each image. (The variance for each mean was very small.) The sites where colour was measured were scattered around the inside of the mouth in an approximate circle and avoided the tongue and darker areas towards the centre of the image where the mouth lining stretched down into the throat of the chick. To avoid biased data collection, arbitrary sampling sites were chosen for each image using dots attached to the computer screen. As well as measuring the colour of the mouth lining, we also measured the colour of the bordering flange in eight different places again to derive mean hue, saturation and brightness scores for each image. We checked that colours were consistent between images by measuring the hue, saturation and brightness of the orange plastic nest pan that held the begging chicks.

Finally, we used the images of begging chicks to measure relative flange width. By placing Perspex rulers over the computer screen we measured the width of the gape (from corner to corner, including the flange) and the width of the paler flange when chicks had their mouths open. To control for the possibility that the mouths were not perfectly perpendicular to the plane of the video camera, we measured the width of the flange at its four widest points, and derived a mean score. Because we had focused the camera at different distances for chicks of different size, we standardized flange measurements by relating them to gape width.

### Comparative Analyses

There are problems with treating individual species as independent data points (Harvey & Pagel 1991), which we avoided by using the Comparative Analysis by Independent Contrasts (CAIC) technique, with the CAIC 2.0 program (Purvis & Rambaut 1994). The program calculates statistically independent contrasts by first searching a phylogeny for independent evolutionary changes in the variable in question, in this case mouth colour. For each node in the phylogeny at which there is variation in the test variable, the corresponding evolutionary change in the predictor variable, for example light availability, is calculated. If evolutionary change in the predictor variable has driven evolutionary change in the test variable, the two sets of linear contrasts should be strongly correlated. We measured the degree of association between the two by regressing contrasts in nestling mouth colour on contrasts in the predictor variables, forcing the regression through the origin as recommended (Purvis & Rambaut 1994). To meet the statistical assumptions of the CAIC method, the light meter readings were logarithmically transformed. Where the effects of a predictor variable were examined with several different nestling mouth colour parameters in a single

CAIC analysis, *P* values were adjusted with Bonferroni corrections. All statistical tests were two-tailed.

Because the outcome of a comparative analysis by independent contrasts can depend on the phylogeny used, we repeated each CAIC analysis three times, with three different phylogenies: the molecular phylogeny of Sibley & Ahlquist (1990), the molecular phylogeny constructed by Sheldon & Gill (1996) and a morphological phylogeny (based on Howard & Moore 1991). The phylogenies differed principally in the relative arrangement of three of the clades (Muscicapoidea, Sylvioidea and Passeroidea) identified by Sibley & Ahlquist's (1990) molecular phylogeny (see Table 1). Pairs of closely related species were virtually identical in each phylogeny. In each phylogeny, branch lengths were assumed to be equal.

### Ethical Note

We used pilot tests on blackbird and robin nestlings to decide that the period of food deprivation, after feeding to satiation, should last 110 min. We chose this period for a number of reasons. First, these insectivorous species rarely began begging again until approximately 40 min after the start of the test (seed-eaters did not start begging until approximately 60 min after the start of the test). Second, begging activity changed continuously after this point until 110 min, and did not appear to plateau. Third, after 110 min food deprivation, chicks did not appear to be begging very differently to their siblings in their natural nest. For example, we found that natural, unmanipulated reed warbler broods begged at the same intensity in the field as broods that we had fed to satiation and then food deprived for 80–90 min in our box set-up (unpublished data). Fourth, individuals used in the pilot tests were still alive and healthy 4 days after they had experienced our experimental treatment. We decided to test chicks every 10 min during their 110 min of food deprivation because, on average across species, this best mimicked the rate at which parents would induce begging naturally by visiting the nest with food.

## RESULTS

### Changes in Nestling Mouth Colour as a Signal of Need

We began by investigating whether changes in nestling mouth colour were a widespread signal of need. We examined mouth colours at three stages of food deprivation: the first time chicks begged after feeding to satiation, 60 min after feeding to satiation and 110 min after feeding to satiation. For species where  $N > 4$  (see Table 1), we compared the second set of mouth colour measurements made at these three stages of food deprivation to see whether mouth colour changed with the extent of food deprivation in the same way as canary nestling mouths (Kilner 1997). We also compared the first set of mouth colour measurements made after 60 min of food deprivation with the second set, to detect the possible existence of a canary-like mouth colour flush (Kilner

1997) after the onset of begging. In both comparisons, each species was analysed separately. We excluded the seed-regurgitating finches (linnet, greenfinch, goldfinch and bullfinch) from these preliminary analyses because we had observed fluctuations in mouth colour in these species during the experiments. For the remaining 18 species (see Table 1), including chaffinches, which feed

their young insects, we found no evidence that mouth colour changed with increasing period of food deprivation when we compared mouth colours the first time chicks started to beg with colours measured at 60 and 110 min since feeding to satiation (mouth hue, saturation and brightness: Friedman two-way ANOVAs:  $0.32 < \chi^2_2 < 3.5$ ,  $0.18 < P < 0.87$ ), irrespective of nest type. Nor was there any evidence of a canary-type flush in mouth colour after the onset of begging in any of these species (Wilcoxon signed-ranks tests:  $-0.85 < Z < -0.10$ ,  $0.41 < P < 0.96$ ).

In all four seed-regurgitating species, however, we observed the canary-like mouth flush at the onset of begging, which we did not see in the other species measured. When chicks opened their mouths to beg there was a rapid change in mouth colour which became redder and more intense. Unfortunately, we were unable to find enough nests of the seed-regurgitating finches to analyse changes in mouth colour with need separately for each species so we pooled the data from the four species ( $N=12$ ). This might have introduced confounding phylogenetic effects. Since the species are all members of the subfamily Fringillinae, however, these artefacts may be minimal given Ficken's (1965) suggestion that most variation in nestling mouth colour between species occurs at the family level. The data did not fit the assumptions of parametric statistical tests, could not be transformed, and so were analysed with nonparametric statistics. First, we compared the first set of mouth colour measurements made at each stage of food deprivation with the second set, using Wilcoxon signed-ranks tests, again to detect the possible existence of a canary-like mouth colour flush. Mouth hue (60 min:  $Z = -3.06$ ,  $P < 0.01$ ; 80 min:  $Z = -3.06$ ,  $P < 0.01$ ; 100 min:  $Z = -3.06$ ,  $P < 0.01$ ), saturation (60 min:  $Z = -1.26$ , NS; 80 min:  $Z = -1.96$ ,  $P < 0.05$ ; 100 min:  $Z = -2.39$ ,  $P < 0.02$ ) and brightness (60 min:  $Z = -2.04$ ,  $P < 0.05$ ; 80 min:  $Z = -2.15$ ,  $P < 0.05$ ; 100 min:  $Z = -0.47$ , NS) all changed as a result of a canary-like flush at the onset of begging (Fig. 1). There was no equivalent change in flange hue ( $-0.89 < Z < -0.22$ , NS), saturation ( $-1.73 < Z < -0.85$ , NS) or brightness ( $-0.90 < Z < -0.08$ , NS).

We then compared the first and second sets of mouth colour measurements made at 60, 80 and 100 min after feeding to satiation using Friedman two-way ANOVAs, to see whether there was greater mouth colour change with increasing need in the same way as in canary nestlings. Mouth hue ( $\chi^2_2 = 15.5$ ,  $P < 0.001$ ), saturation ( $\chi^2_2 = 9.04$ ,  $P < 0.02$ ) and brightness ( $\chi^2_2 = 6.5$ ,  $P < 0.05$ ) measured after the flush all changed with time. Mouth hue and saturation became respectively redder and denser with increasing food deprivation (Fig. 1 a, b), while the change in mouth brightness was less clearly associated with increasing food deprivation (Fig. 1c). By contrast, mouth hue ( $\chi^2_2 = 0.5$ , NS), saturation ( $\chi^2_2 = 1.5$ , NS) and brightness

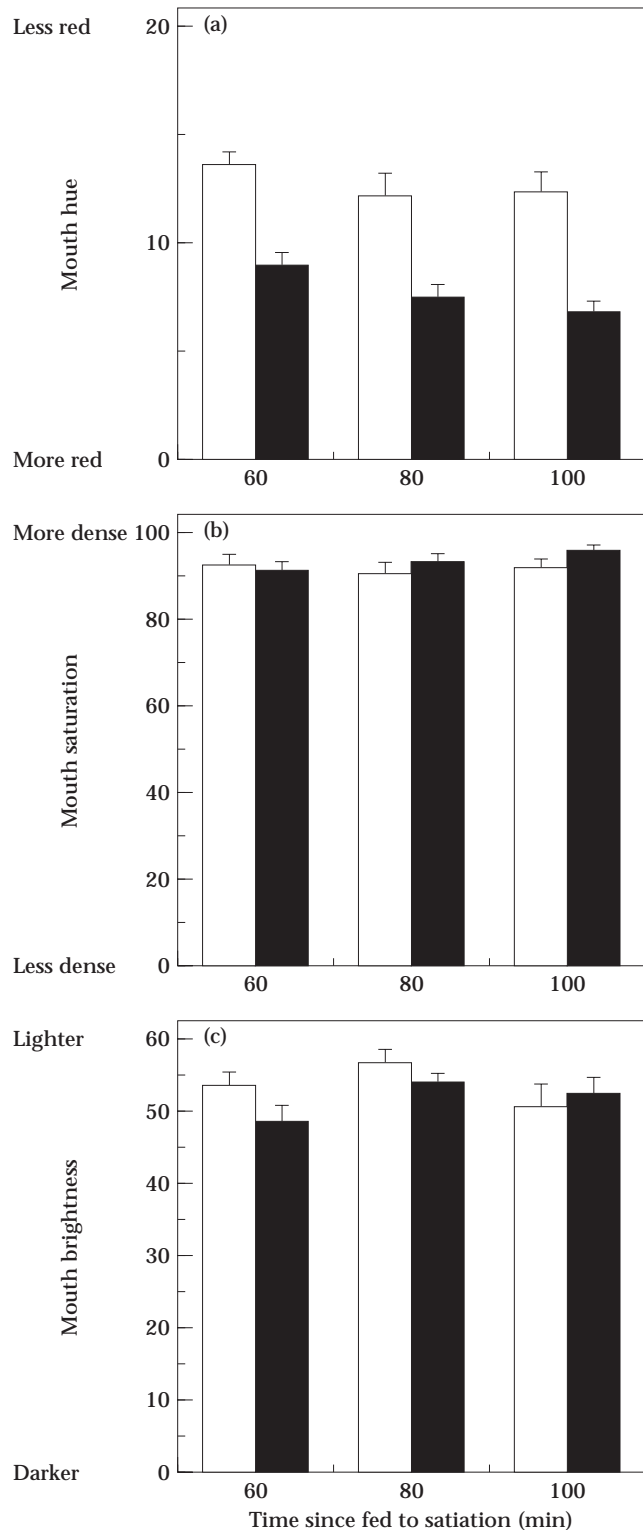


Figure 1. The change in nestling mouth (a) hue, (b) saturation and (c) brightness of the seed-regurgitating finches (linnet, bullfinch, greenfinch and goldfinch;  $N=12$ ) with increasing food deprivation. □: Mouth colours measured before the flush; ■: mouth colours measured after the flush. Means and standard error bars are shown.

**Table 2.** The results of the regression of contrasts in various mouth colour variables on contrasts on nest light meter readings calculated by CAIC 2.0

Mouth colour variable	Sibley & Ahlquist		Sheldon & Gill		Howard & Moore	
	$F_{1,29}$	$P$	$F_{1,24}$	$P$	$F_{1,20}$	$P$
Mouth hue	1.53	NS	1.58	NS	7.20	NS
Mouth saturation	1.26	NS	1.11	NS	0.83	NS
Mouth brightness	1.79	NS	1.66	NS	3.21	NS
Flange hue	0.18	NS	0.25	NS	1.40	NS
Flange saturation	7.95	NS	7.10	NS	7.43	NS
Flange brightness	5.60	NS	4.73	NS	2.45	NS
Flange-mouth hue	0.90	NS	0.83	NS	3.26	NS
Flange-mouth saturation	11.62	<0.01	10.4	<0.01	11.40	<0.01
Flange-mouth brightness	24.95	<0.01	23.6	<0.01	60.13	<0.01

Sibley & Ahlquist, Sheldon & Gill and Howard & Moore refer to the phylogenies used in each CAIC analysis. All  $P$  values are adjusted for significance with Bonferroni corrections.

( $\chi^2_2=3.11$ , NS) measured before the flush did not change with increasing food deprivation (Fig. 1). There was no change in flange hue ( $1.44 < \chi^2_2 < 1.57$ , NS), saturation ( $1.11 < \chi^2_2 < 2.00$ , NS) or brightness ( $1.57 < \chi^2_2 < 3.5$ , NS) with increasing food deprivation, before or after the flush.

### Ecological Correlates of Nestling Mouth Colour

Next, we examined the relationship between nestling mouth colour parameters (derived from 'second' measurements taken 60 min after feeding to satiation) and either nest light availability or sibling competition. We considered nine measures of mouth colour: mouth hue, saturation and brightness, flange hue, saturation and brightness and the difference in hue, saturation and brightness between the mouth lining and the flange. Light meter readings were significantly related to the differences between mouth and flange in saturation and brightness. Mouth flanges were significantly less densely coloured and had whiter grey-scale scores in relation to the mouth lining, in species where nestlings were reared in darker nests (see Table 2; Fig. 2). There was no significant relationship between the light meter readings taken at each nest and the remaining seven mouth colour variables in the analysis (see Table 2).

We then considered the relationship between nestling mouth colour and sibling competition, using mean clutch sizes for each species, as described in Cramp (1995), as an index of competition. We found no significant relationship between clutch size and any of the nine mouth colour variables (Sibley & Ahlquist:  $0.01 < F_{1,30} < 4.05$ , NS; Sheldon & Gill:  $0.002 < F_{1,24} < 5.25$ , NS; Howard & Moore:  $0.0009 < F_{1,21} < 2.64$ , NS). There was no significant relationship between clutch size and light meter readings taken at each nest (Sibley & Ahlquist:  $F_{1,30}=3.4$ ,  $P < 0.1$ ; Sheldon & Gill:  $F_{1,24}=0.62$ , NS; Howard & Moore:  $F_{1,21}=2.89$ , NS).

### Ecological Correlates of Relative Flange Width

Finally, we considered the relationship between relative flange width and the light available in the nest. Relative

flange width was significantly related to the light meter readings taken in the nest (Sibley & Ahlquist:  $F_{1,30}=3.75$ ,  $P < 0.1$ ; Sheldon & Gill:  $F_{1,24}=9.56$ ,  $P < 0.01$ ; Howard & Moore:  $F_{1,21}=6.92$ ,  $P < 0.02$ ) and flanges were relatively wider in darker nests than lighter nests (Fig. 3). There was no significant relationship between absolute gape width and light meter readings taken in the nest (Sibley & Ahlquist:  $F_{1,30}=0.61$ , NS; Sheldon & Gill:  $F_{1,24}=0.62$ , NS; Howard & Moore:  $F_{1,21}=0.50$ , NS) which suggests that our results are not confounded by variation in body size between species. We also found no significant relationship between mean clutch size and relative flange width (Sibley & Ahlquist:  $F_{1,30}=3.20$ ,  $P < 0.1$ ; Sheldon & Gill:  $F_{1,24}=2.66$ , NS; Howard & Moore:  $F_{1,21}=1.96$ , NS).

## DISCUSSION

Two functions that have been suggested for bright nestling mouth colour are that it improves the detectability of chicks, particularly in poorly lit nests (Pycraft 1907;

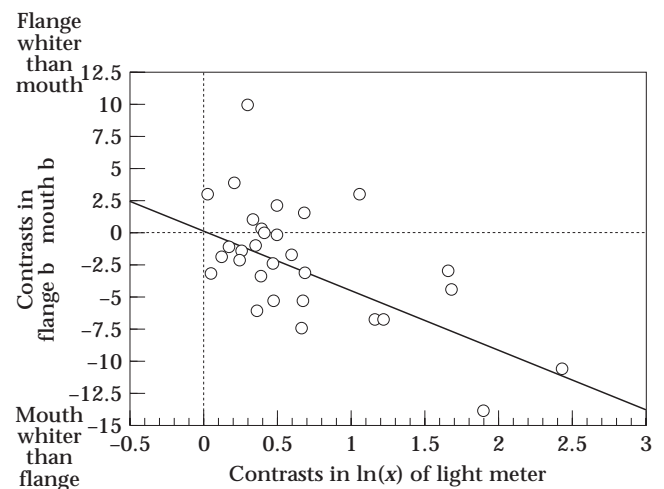


Figure 2. The relationship between contrasts in nest light availability and contrasts in the difference between flange and mouth lining brightness. Contrasts were calculated using the Sibley & Ahlquist phylogeny. The regression line is shown.

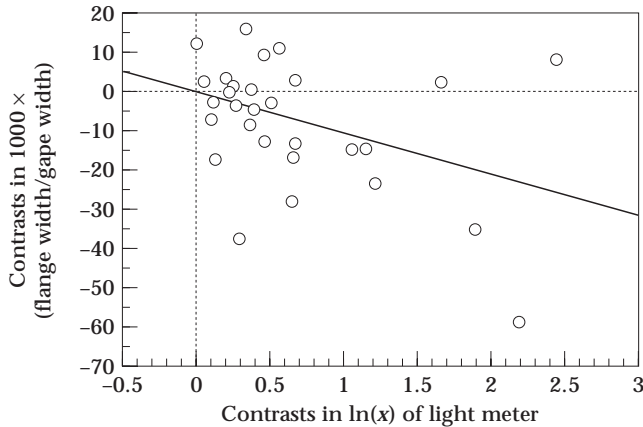


Figure 3. The relationship between contrasts in nest light availability and contrasts in relative flange width. Contrasts were calculated using the Sibley & Ahlquist phylogeny. The regression line is shown.

Ficken 1965), and that it signals need (Kilner 1997). The comparative analyses presented here found no support for the first hypothesis, and only limited support for the second.

### Chick Detectability

There was no evidence that variation in nestling mouth colour between species could be explained by the environment in which offspring solicit food. We did find, however, that nestlings in darker nests improved their conspicuousness through the relative colour and size of the flange that borders their brightly coloured mouths. Nestlings from darker nests had relatively wider flanges which were whiter, and less densely coloured in relation to their mouth colour, than those of chicks reared in better illuminated nests. Our evidence supports Ingram's (1920) hypothesis that the flange acts as a beacon around nestling mouths, functioning to make chicks detectable as they gape in dark nests.

Despite earlier work that suggested a correlation between nest type and nestling mouth colour (Ficken 1965), we found no evidence that mouth colour was related to either the number of young, or the amount of light available in the nest. We consider three explanations. First, we might have measured mouth colour and nest light availability incorrectly. Even if we assume no artefacts from the differences in human and avian vision (Bennett et al. 1994), which is by no means certain, there remains the possibility that parental perception of gape colour at the nest is very different from the colours that we measured under standardized conditions of light availability. In addition, we did not correlate measures of nestling mouth colour with the ambient light available at the nest (cf. Endler 1987). Accounting for either or both of these problems might yet reveal that variation in nestling mouth colour can be explained by the lighting conditions in which parents view gaping nestlings. Alternatively, the conspicuousness of nestlings may be entirely governed by the relative size and colour of the flange surrounding the mouth, independently of mouth

colour itself. It may be that mouth colour is arbitrarily determined by pigments available in the diet, which could vary widely between species. Or it could be that mouth colour serves a different function, and has been selected to give offspring a competitive edge over half-siblings, rather than to improve visibility in a dark nest (R. Kilner, unpublished data).

### Signal of Need

Our results suggest that nestling mouth colour is not a widespread signal of need. Great tit nestlings, in particular, showed no need-driven fluctuations in mouth colour, which is interesting given the recent experimental evidence that parents prefer to feed young whose naturally orange mouths have been artificially reddened (Götmark & Ahlström 1997). It may be that by reddening the mouths of great tit nestlings, Götmark & Ahlström increased the contrast in brightness between the mouth lining and the mouth rim, effectively making the 'beacon' around the mouth more prominent. Perhaps it was this manipulation, rather than the red colour itself, that affected the parents' feeding decision at the nest.

It is intriguing that we found changes in nestling mouth colour with need, which was previously described in canaries (Kilner 1997), only in other seed-regurgitating finches (linnet, bullfinch, greenfinch and goldfinch). Moreover, it is striking that these changes were absent in the closely related chaffinch, which provisions its young with insects rather than seeds. However, changes in mouth colour with need are unlikely simply to be a correlate of a diet of seeds. Raven, *Corvus corax*, nestlings, which are fed primarily on scraps of carrion, also show 'flushing' in their red mouth linings when they are hungry (E. Gwinner, personal communication). The key correlate with the mouth flush may be parental provisioning by regurgitation. Seed-eating finches regurgitate food to their young from a crop, while ravens regurgitate food from their beak pouch (E. Gwinner, personal communication). From the parents' perspective, feeding nestlings by regurgitation takes much longer than it does to deliver a single item or bill full of prey. This may give parents more time to make careful decisions about which offspring to feed, and this in turn may have selected for finely graded offspring signals of need. Furthermore, parents are able to feed more than one individual as they regurgitate. In canaries, about 25 regurgitations are spread among the brood at each nest visit (Kilner 1995), while in ravens parents usually feed more than one nestling at each nest visit (E. Gwinner, personal communication). In these regurgitating species then, parents spend long enough at the nest each time they deliver food to be able to assess chick need accurately, and because they make several regurgitations per visit, rather than delivering a single load, they can fine-tune their response to offspring signals. It may be that precise offspring signals of need can only benefit parents and young in a system like this. Time constraints in species that deliver single loads of prey at each nest visit may have selected for a simpler laissez-faire pattern of food distribution (McRae et al.

1993; Mock & Parker 1997), determined by sibling competition rather than offspring signalling.

While the time required to regurgitate food may explain when signals of need govern the pattern of food distribution at each nest visit, it does not explain when need should be signalled through mouth colour. Our original hypothesis, that mouth colour can only signal need in nests where there is sufficient light for parents to perceive differences in the signal, may be appropriate here. This would explain why we found that the hole-nesting jackdaw, which feeds its young by regurgitation and which is closely related to the open-nesting raven, nevertheless shows no changes in nestling mouth colour with need.

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