FAMILY CONFLICTS AND THE EVOLUTION OF NESTLING MOUTH COLOUR

by

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Summary

A variety of family conflicts can influence provisioning behaviour at the passerine nest. There can be sexual and parent-offspring conflict over the amount of food provided for young, and sibling conflict over how food is allocated among the brood. Whatever the type of conflict, its resolution may be determined by nestling begging displays, and its intensity will vary between species with variation in % EPY. Begging intensity is therefore predicted to vary with % EPY. One component of the begging display, that varies widely between species, is nestling mouth colour. Recent empirical work on canaries and great tits has shown that parents prefer to feed young with redder mouths, even if offspring naturally possess yellow gapes. I use comparative analyses to explain the diversity of nestling mouth colour between species in terms of the various family conflicts. In species where there are high rates of % EPY, and sibling and sexual conflicts are more intense, offspring that are reared in well-lit nests display redder mouths. Offspring reared in dark nests, however, show no such relationship and have yellower mouths generally. A comparison of Cuculinae species and host nestling mouth colour showed that cuckoo young have the redder mouths, which might be the result of more intense parent-offspring conflict. I suggest that nestling mouth colour reflects the intensity of family battles waged in the past, but only at nests where there is sufficient light for such visual displays to be perceived by parents. The diversity of nestling mouth colour can therefore be explained by both 'strategic' and 'tactical' influences on signal design. I conclude by discussing how variation in the choice of nest site within species might cause family differences in conflict resolution.

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Introduction

Parent birds returning to the nest with food face a brood of begging young. Nestlings posture and call, jostle and display brightly coloured mouths to solicit parental resources. The apparently happy scene of parent birds feeding young at the nest conceals a variety of family conflicts, however (Mock & Parker, 1997). There may be sexual conflict between the provisioning male and female, for example, a bartering contest over how much food each should bring their young, with a reduction in investment by one partner causing an increase in provisioning by the other, and *vice versa* (Parker, 1979; Houston & Davies, 1985). Experiments suggest that the outcome of the bidding competition may be determined by each parent's response to nestling begging intensity (Ottoson *et al.*, 1997).

Parent-offspring conflict can similarly influence the amount invested by each parent. Parents are selected to strike the optimal balance between current and future reproduction, providing sufficient resources for their current brood to grow well and survive yet withholding enough resources to reproduce again successfully (Clutton-Brock, 1991). Individual offspring, however, balance the costs and benefits of their parents' reproductive attempts differently, effectively devaluing the costs by at least one half (Hamilton, 1964; Trivers, 1974). Consequently, optimal investment levels for offspring are greater than for parents, and offspring may be selected to employ manipulative begging displays to wheedle additional resources from parents (Trivers, 1974; Mock & Parker, 1997).

Finally, sibling conflict can influence the allocation of investment within the brood. Such conflict could take the form of jostling or jockeying for a location in the nest favoured by parents when distributing food (*e.g.* Parker & Macnair, 1978; McRae *et al.*, 1993). Alternatively, parents may play a more active role in selecting which nestling to feed (*e.g.* Godfray, 1995a; Kilner, 1995), and chicks could compete by signalling to capture their parent's attention (Kilner, 1997). Parents might respond to offspring begging signals because they supply accurate information about the state of their young (see Godfray, 1991, 1995a) or because their sensory system predisposes them to favour particular displays (see Kilner *et al.*, 1999), perhaps because some are more detectable than others (Guilford & Dawkins, 1991). Indeed, complex nestling begging displays may have evolved because some elements carry information about chick state, while others simply enhance chick detectability.

In short, family conflicts over the level and allocation of parental investment arise because parental care carries fitness costs (Gustaffson & Sutherland, 1988; Nur, 1988) and because sexual reproduction means that parents and their young have an average coefficient of relatedness of one half at most (Hamilton, 1964). Importantly, the outcome of such family disputes is likely to depend on parental response to the begging display. Between species, the potential intensity of family disputes will vary with the fitness cost of parental care and the genetic mating system. These two factors can therefore have a profound influence on the design of nestling begging displays (see Briskie *et al.*, 1994).

One component of the begging display, that varies widely between species, is nestling mouth colour. Minute variation in the mouth colour of canary (*Serinus canaria*) nestlings (Kilner, 1997), and just a few other species (Kilner & Davies, 1998), accurately signals chick nutritional state to parents. However, between species there is far greater variation in mouth colouration. For example, alpine accentor (*Prunella collaris*) nestlings display red mouths, whereas in the closely-related dunnock (*P. modularis*), chick mouths are orange (Harrison & Castell, 1998). In other passerines, such as robins (*Erithacus rubecula*) and corn buntings (*Miliaria calandra*), chicks have yellow and flesh-coloured mouths respectively (Harrison & Castell, 1998).

In general, such variation in signal design may be accounted for by selection on the signaller for efficient information transfer (Johnstone, 1997; Bradbury & Vehrencamp, 1998). Species differences in the visual signalling environment, such as the ambient light quality (*e.g.* Endler, 1991) or the background against which the signal is sent (*e.g.* Endler & Théry, 1996), mean that the most efficient signal design may vary between species. For example, a comparative study of *Phylloscopus* warbler species found that the number of white patches adults displayed against their yellow-green body plumage was correlated with brightness of the habitat in which they lived (Marchetti, 1993). Species from dark evergreen forest habitat displayed more patches than those living in better illuminated open montane shrub.

In a previous study (Kilner & Davies, 1998), we similarly attempted to explain variation in nestling mouth colour between species by examining the relationship between the signalling environment and mouth colouration. Just as in Marchetti’s (1993) study, we quantified nest light availability using a photographic light meter. Using data from 31 British species, we found that the fleshy white border of nestling mouths was wider in species from darker nests and also showed the greatest brightness contrast with the colour of the mouth interior. However, we found no correlation between our measurements of nestling mouth colour and photographic light meter readings at the nest. Whether mouth colour is correlated with ambient nest light colour, or the colour of the background against which the chick displays remains unknown (Kilner & Davies, 1998).

In this paper, I suggest that the diversity of nestling mouth colour reflects both the intensity of family conflicts and selection for signal efficacy, a combination of the so-called 'strategic' and 'tactical' influences identified in previous work (Guilford & Dawkins, 1991; Johnstone, 1997). The predictions I test are based on two experimental recent studies, one on domesticated canaries (Kilner, 1997), the other on great tits (*Parus major* — Götmark & Ahlström, 1997), which suggest that nestling mouth colour may play a role in resolving family conflicts.

Experiments with these two species have shown that parents allocate more food to offspring with redder mouths (Kilner, 1997), even if their young do not naturally display red mouths as they beg (Götmark & Ahlström, 1997). Red mouths may give offspring a competitive advantage because parents have a preference for red *per se*, (see Tinbergen, 1951; Lyon *et al.*, 1994), or because of a more subtle interaction with the signalling environment that promotes detectability. In the greenish ambient light of cup nests placed in shrubs, for example, parents may perceive red mouths as black. Reddening mouths artificially may therefore heighten the brightness contrast between the mouth interior and its white fleshy border (Kilner & Davies, 1998) promoting chick detectability and thereby competitive ability. Whatever the subtleties of ambient nest light colour, young signalling in near darkness can gain little by displaying a red mouth where there is insufficient light for colour to be seen. Not surprisingly, Götmark & Ahlström (1997) found a significant preference for red nestling mouths only when a window was installed in their great tit nestboxes, and not when it was absent. The evidence to date therefore suggests that reddening nestling mouths gives chicks a competitive advantage, changing the outcome of sibling conflict, but only at nests with sufficient light availability.

Using nestling mouth colour data from the literature, and from our recent comparative analysis (Kilner & Davies, 1998), I tested the prediction that nestling mouth colour should vary with the intensity of family conflicts.

The fitness cost of parental care is notoriously hard to quantify (Clutton-Brock, 1991; Stearns, 1992), so I used % EPY as a measure of family conflict intensity (see Briskie *et al.*, 1994). Between passerine species, there is considerable variation in % EPY, because in some species several eggs per clutch are fertilized by extra-pair males (*e.g.* Dixon *et al.*, 1994; Mulder *et al.*, 1994) while in others virtually none are (Gyllensten *et al.*, 1990, Orell *et al.*, 1997). As average relatedness between nestlings declines, and the genetic stake in siblings becomes increasingly small, selection should favour chicks that are increasingly selfish and that employ begging displays which are more likely to promote victory in sibling conflict. I tested prediction (1), that mouth colour should vary with % EPY; the higher % EPY, the redder the mouth. To control for the potential confounding effects of nest light availability, I split the dataset by nest type and analysed species whose young are reared in darker nests separately from those that rear young in lighter nests.

In experiments with canaries, broods with artificially reddened mouths received more regurgitations than broods with unmanipulated mouths (Kilner, 1997). A parental preference such as this for absolute, rather than relative, differences in mouth colour may pave the way for parent-offspring conflict (*cf.* Lyon *et al.*, 1994). I investigated this possibility by considering the mouth colours of nestling cuckoos, the Cuculinae. I focused exclusively on species that eject host eggs and young from the nest and so are reared alone in the host nest. Because these species dispense with sibling conflict, they provide an excellent opportunity to examine the effects of parent-offspring conflict on nestling mouth colour in isolation. Their lack of relatedness to hosts, and hence entirely selfish interests, means that these cuckoos should exhibit the reddest mouths of all. Ideally, a comparison of the mouth colours of brood parasites and their closest non-brood parasite relatives would reveal any adaptive function of mouth colour for brood parasitism. Unfortunately, I could find data for only three species of non-brood parasitic cuckoos. Instead, I compared the mouth colours of brood parasitic cuckoo nestlings with those of their hosts' own young. Explicitly, I tested prediction (2): that the Cuculinae nestlings that evict host young should have redder mouths than the young of their hosts.

Methods

Scoring nestling mouth colour

In 1996, I compiled video-images of nestling mouths from 31 different British species, which I had filmed under constant lighting conditions as part of a separate experiment. I quantified mouth hue using the Macintosh application Adobe Photoshop which effectively scores mouth colours from red to yellow on a continuous scale of redness (for details of methods see Kilner & Davies, 1998). Adobe Photoshop depicts hue as a circular variable expressed in terms of degrees on a colour wheel. Red is at 0°, green at 180°. Nestling mouth colour hues fall within such a small sector of the colour wheel (see Table 1) that they can be treated as linear rather than circular variables. Since % EPY data were available for only 11 of the species I had filmed, I was unable to use these data to test prediction (1) directly. Instead, I used the database as a yard stick to develop a mouth colour scoring system. I gathered nestling mouth colour descriptions from Harrison & Castell (1998) for each of the 31 species measured in the Kilner & Davies (1998) study. By matching the description (red, orange, yellow, *etc.*) with the numerical score of mouth hue which I had obtained for each species, I derived mean hue scores for a range of colours from crimson to yellow (Table 1). Hence descriptions of the nestling mouth colours of other species, which were drawn from the literature, were converted into arbitary numerical scores. In the comparative analysis described here, mouth colour scores were derived for 30 species using Table 1. For the remaining 11, I used the hue scores that we had measured directly in our previous study.

This crude method of converting literature descriptions into numerical values takes no account of the way that birds perceive colour. Unlike humans, birds have UV photoreceptors that may alter their perception of colours that we see as red, orange or yellow (Bennett *et al.*, 1994). There is a small risk that the difference between human and avian vision may introduce artefacts into this analysis, but as yet the seriousness of these dangers is not known (Hill, 1991; Bennett *et al.*, 1994). Given our current uncertainty about the hazards of relating human vision to avian vision, and the fact that there was no reason to expect the data to contain any systematic bias, it seems reasonable to use this dataset in a preliminary analysis to account for variation in nestling mouth colour between species.

TABLE 1. *Mouth colour descriptions from the literature and their corresponding hue scores derived from Adobe Photoshop*

literature mouth colour description	mouth hue score
crimson/carmine/vermillion	8.3
deep pink/pinkish red	9.8
pink	10.1
red/blood red/bright red/flesh red/pale red/scarlet	16.1
orange/pale orange/rich orange/bright orange/bright orange brick	18.1
flesh/pale flesh/reddish-yellow/pale yellowish flesh	19.6
orange-yellow/bright orange-yellow	20.9
yellow/deep yellow/lemon yellow/bright yellow/yellow ochre/ yellowish/yellow-pink	29.9

Note that redder mouths have lower scores than yellower mouths.

Extra-pair paternity

Data for nestling mouth colour and % EPY were found for 41 passerine species (Table 2). Following previous studies (*e.g.* Briskie *et al.*, 1994), I defined % EPY as the proportion of all nestlings sampled who were not in the nest of their genetic father. For dunnocks and alpine accentors, % EPY was calculated as the proportion of all offspring whose genetic father was not the alpha male rearing them, while for tree swallows (*Tachycineta bicolor*) I calculated the mean of the four measurements of % EPY presented in Table 1 of Barber *et al.* (1996). Where more than one study had measured % EPY for a particular species, I calculated the mean. To meet the statistical assumptions of the comparative method used (see below), the % EPY data were arcsine transformed and then logarithmically transformed.

Nest light availability

I assigned a description of the nest type used by each species in this analysis (see Table 2), and the dataset used by Kilner & Davies (1998), using two field guides (Baicich & Harrison, 1997; Harrison & Castell, 1998). In our previous study, we quantified nest light availability using a photographic light meter (see Kilner & Davies, 1998 for details of methods). For each nest type in the Kilner & Davies (1998) dataset, I calculated a mean score of nest light availability. Thirty of the species in the analysis described here were thus assigned a light meter score in relation to nest type (see Table 2). For the remaining 11, I used the measurements that we had made directly.

To meet the assumptions of the comparative method used (see below), the light meter scores were logarithmically transformed. The transformed scores followed a bimodal distribution, with typically 'dark' nests, such as those placed in cavities or crevices, and domed nests, clearly separated from remaining 'light' cup nests (Fig. 1). I used this distribution to split the dataset into species with 'light' and 'dark' nests, reasoning that prediction (1) was more likely to be upheld in 'light' than 'dark' nests where parents could more easily perceive visual displays. To investigate whether nest light availability influenced mouth colour, I used two types of analyses. In the first, nest light availability was a dichotomous variable ('light' or 'dark') in the second, I used the continuous light availability scores shown in Table 2.

Comparative analyses

There are problems with treating individual species as independent data points (Harvey & Pagel, 1991), which I 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, here % EPY, 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. I measured the degree of association between the two by regressing contrasts in nestling mouth colour on contrasts in % EPY, forcing the regression through the origin as recommended (Purvis & Rambaut, 1994).

Since the outcome of a comparative analysis by independent contrasts may depend on the phylogeny used, I repeated each CAIC analysis three times, with three different phylogenies:

TABLE 2. *Mouth colour and % EPY data for 41 passerine species*

Species	nest type	light	%EPY	mouth colour	Reference
Superfamily Corvoidea					
*Corvus monedula**	nest in cavity[a]	2.3	1.6	blood red[1]	Cezilly & Nager, 1995
*Malurus splendens**	domed nest[c]	1.2	65.0§	orange-yellow[3]	Brooker *et al.*, 1990
Superfamily Muscicapoidea					
*Sialia mexicanus**	nest in cavity[b]	1.2	19.0	orange[2]	Dickinson & Akre, 1998
*Sialia sialis**	nest in cavity[b]	1.2	8.4	yellow[2]	Meek *et al.*, 1994
*Ficedula albicollis**	nest in cavity[a]	1.2	20.8	orange-yellow[1]	Alatalo *et al.*, 1989
*Ficedula hypoleuca**	nest in cavity[a]	0.5	11.0	orange-yellow[1]	Rätti *et al.*, 1995
Luscinia svecica	cup nest on ground[a]	33.0	20.0	orange[1]	Krokene *et al.*, 1996
*Oenanthe oenanthe**	nest in crevice[a]	4.1	11.0	pale orange[1]	Currie *et al.*, 1998
*Sturnus vulgaris**	nest in cavity[a]	3.4	9.7	bright yellow[1]	Pinxten *et al.*, 1993
Superfamily Sylvioidea					
*Troglodytes aedon**	domed nest[b]	1.2	8.4	pale yellow[2]	Soukup & Thompson, 1997
*Remiz pendulinus**	domed nest[a]	1.2	6.9	orange-yellow[1]	Schleicher *et al.*, 1997
*Parus atricapillus**	nest in cavity[b]	1.2	17.0	yellow[2]	Otter *et al.*, 1994
*Parus caeruleus**	nest in cavity[a]	0.3	10.5	yellow[1]	Kempenaers *et al.*, 1992
*Parus major**	nest in cavity[a]	0.5	15.7	bright yellow[1]	Gullberg *et al.*, 1992
*Parus montanus**	nest in cavity[a]	1.2	0.9	orange-yellow[1]	Orell *et al.*, 1997
*Delichon urbica**	mud bowl[a]	0.9	19.0	yellow[1]	Whittingham & Lifjeld, 1995
*Hirundo pyrrohonata**	mud bowl[b]	0.9	23.7	flesh[2]	Brown & Brown, 1988
*Hirundo rustica**	mud cup[a]	0.9	20.3	lemon yellow[1]	Birkhead & Møller, 1995
*Tachycineta bicolor**	nest in cavity[b]	1.2	57.0	yellow[2]	Barber *et al.*, 1996
Acrocephalus arundinaceus	woven cup in reeds[a]	21.3	3.1	yellow[1]	Hasselquist *et al.*, 1995
Acrocephalus paludicola	cup nest in grass[a]	31.3	36.0	reddish-yellow[1]	Schulzehagen *et al.*, 1993

TABLE 2. *(Continued)*

Species	nest type	light	%EPY	mouth colour	Reference
Phylloscopus sibilatrix	domed nest on ground[a]	29.2	0	deep yellow[1]	Gyllensten *et al.*, 1990
Phylloscopus trochilus	domed nest on ground[a]	29.2	20.3	orange-yellow[1]	Gyllensten *et al.*, 1990; Bjornstad & Lifjeld, 1997; Fridolfsson *et al.*, 1997
Superfamily Passeroidea					
*Passer domesticus**	nest in cavity[a]	2.0	13.6	pale flesh[1]	Wetton & Parkin, 1991
*Prunella collaris**	nest in crevice[a]	4.1	37.3	bright red[1]	Hartley *et al.*, 1995
Prunella modularis	cup nest in shrub[a]	13.9	22.6	orange[1]	Burke *et al.*, 1989
Fringilla coelebs	cup nest in shrub[a]	46.8	17.0	carmine[1]	Sheldon & Burke, 1994
Carduelis tristis	cup nest in tree[b]	167.0	14.3	pinkish red[2]	Gissing *et al.*, 1998
Passerculus sandwichensis	cup nest on ground[b]	33.0	33.7	pink[2]	Freeman Gallant, 1997
Junco hyemalis	cup nest on ground[b]	33.0	16.0	deep pink[2]	S. Raouf, pers. comm.
Spizella pusilus	cup nest on ground[b]	33.0	19.2	red[2]	Petter *et al.*, 1990
Calcarius lapponicus	cup nest on ground[b]	33.0	7.4	red[2]	Briskie *et al.*, 1997
Calcarius pictus	cup nest on ground[b]	33.0	33.0	red[2]	Briskie *et al.*, 1998
Miliaria calandra	cup nest in grass[a]	31.3	4.5	flesh[1]	Hartley *et al.*, 1993
Emberiza citrinella	cup nest in grass[a]	31.3	37.0	flesh red[1]	Sundberg & Dixon, 1994
Emberiza schoeniclus	cup nest in grass[a]	33.9	55.0	pale red[1]	Dixon *et al.*, 1994
Dendroica petechia	cup nest in tree[b]	167.0	33.06	red[2]	Yezerinac *et al.*, 1996
Setophaga ruticilla	cup nest in tree[b]	167.0	40.0	red[2]	Perreault *et al.*, 1997
Agelaius phoeniceus	woven cup in reeds[b]	21.3	27.9	red[2]	Gibbs *et al.*, 1990
Cardinalis cardinalis	cup nest in shrub[b]	26.7	13.5	red[2]	Ritchison & Platt, 1994
Passerina cyanea	cup nest in shrub[b]	26.7	35.0	red[2]	Westneat, 1990

Species are arranged in the clades identified by Sibley & Ahlquist's (1990) molecular phylogeny. Species marked with a * rear their young in 'dark' nests; all others rear young in 'light' nests. Letters denote the source of the nest type data, a = Harrison & Castell, 1998; b = Baicich & Harrison, 1997; c = Brooker & Brooker, 1987. The 'light' column shows mean photographic light meter readings recorded from each nest type or each species (see text for details). Numbers indicate the source of the mouth colour data, 1 = Harrison & Castell, 1998; 2 = Baicich & Harrison, 1997; 3 = Brooker & Brooker, 1987. § denotes minimum estimate of EPY. % EPY sources are shown in the end column.

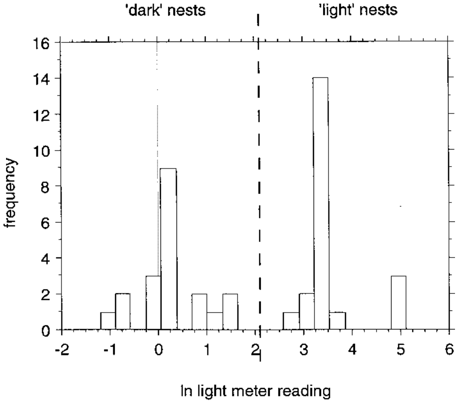

Fig. 1. The frequency distribution of nest light availability. The data have a bimodal distribution and so nests can be readily classified as ‘dark’ and ‘light’.

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. Pairs of closely related species were virtual identical in each phylogeny.

Cuckoo mouth colour

To test prediction (2), nestling mouth colour data were compiled for 14 cuckoo species and their most common hosts (Table 3). For the common cuckoo (*Cuculus canorus*) and reed warbler (*Acrocephalus scirpaceus*), I used the hue scores measured directly in Kilner & Davies (1998). All other mouth colour descriptions were converted in numerical scores using Table 1. With this dataset, it was not possible to analyse mouth colour using the Comparative Analysis by Independent Contrasts method. Instead, I compared cuckoo nestling mouth colour with host nestling mouth colour using a Spearman’s rank correlation, both as a means of avoiding confounding phylogenetic effects, and to detect any adaptation on the part of individual cuckoo species in response to their particular hosts. There was no *a priori* reason to expect cuckoos and their hosts to have correlated mouth colours simply as a result of their phylogenies. For cuckoo species that parasitize more than one host, I used the most common host, as described by the bird atlas, for which a description of nestling mouth colour was available.

Results

Effect of nest light availability of nestling mouth colour

(i) using species as independent datapoints

Chicks from ‘dark’ nests had significantly less red mouths than those from ‘light’ nests ($t_{19,20} = 3.63$, $p = 0.0008$; Fig. 2). With continuous

TABLE 3. *Mouth colours of 14 evicting cuckoo species and their most common hosts (for which mouth colour data could be found)*

Cuckoo	species	mouth colour	common host	species	mouth colour
Thickbilled cuckoo	*Pachycoccyx audiberti*	orange[5]	Redbilled helmet shrike	*Prionops retzii*	pink[5]
Hawk cuckoo	*Cuculus varius*	yellow[3]	Common babbler	*Turdoides caudatus*	yellow[4]
Red-chested cuckoo	*Cuculus solitarius*	rich orange[1]	Cape robin	*Cossyphra caffra*	yellow ochre[2]
Black cuckoo	*Cuculus clamosus*	pink[1]	shrike	*Laniarius aethiopicus*	yellow[2]
Indian cuckoo	*Cuculus micropterus*	yellow-pink[3]	Nepal streaked laughing thrush	*Garrulax lineatus*	pale yellowish flesh[3]
Common cuckoo	*Cuculus canorus*	red[6]	Reed warbler	*Acrocephalus scirpaceus*	orange-yellow[4]
Fantailed cuckoo	*Cuculus pyrrhophanus*	yellow[7]	thornbill	*Acanthiza apicalis*§	orange-yellow[8]
Oriental cuckoo	*Cuculus saturatus*	vermillion[6]	Arctic warbler	*Phylloscopus borealis*	yellow[4]
Plaintive cuckoo	*Cacomantis merulinus*	bright orange brick[3]	Southern ashy wren	*Prinia socialis*§	bright orange-yellow[3]
Shining bronze cuckoo	*Chrysococcyx lucidus*	orange-yellow[9]	Yellow-rumped thornbill	*Acanthiza chrysorrhoa*§	yellow[7]
Horsfield's bronze cuckoo	*Chrysococcyx basilus*	orange-yellow[9]	Splendid fairy wren	*Malurus splendens*§	orange-yellow[8]
Klaas' cuckoo	*Chrysococcyx klaas*	bright orange[1]	warblers	*Sylvietta rufescens*§	yellowish[10]
African emerald cuckoo	*Chrysococcyx cupreus*	orange[1]	Common bulbul	*Pycnonotus barbatus*	yellow-pink[2]
Didric cuckoo	*Chrysococcyx caprius*	vermillion[1]	Masked weaver	*Ploceus velatus*§	yellow[2]

§ denotes host species with relatively dark nests. Sources: 1 Fry, 1988; 2 Keith *et al.*, 1992; 3 Ali & Ripley, 1981; 4 Harrison & Castell, 1998; 5 Vernon, 1984; 6 Cramp, 1985; 7 Brooker & Brooker, 1989; 8 Brooker & Brooker, 1987; 9 Brooker & Brooker, 1986; 10 Jensen & Clinning, 1974.

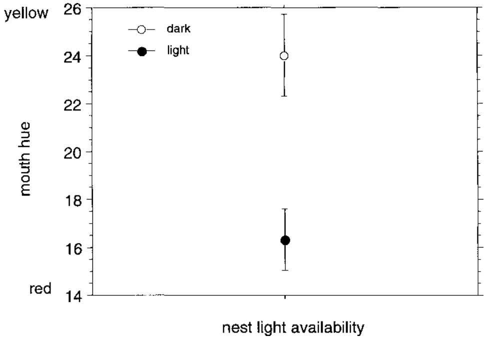

Fig. 2. The effect of nest light availability on nestling mouth colour, treating each species as an independent datapoint ($N = 41$). Chicks from darker nests have yellower mouths than those from lighter nests.

measurements of nest light availability, and including data from both nest types, there was a significant relationship between nest light availability and nestling mouth colour. Chicks from darker nests had yellower mouths than those from lighter nests (Spearman, tied $z = -4.31, p < 0.0001$). However, when the dataset was split by nest type, there was no significant relationship between mouth colour and nest light availability, either for ‘light’ nests ($F_{1,20} = 1.18, p = 0.29$) or ‘dark’ nests ($F_{1,19} = 0.30, p = 0.59$).

(ii) using contrasts an independent datapoints

With light availability as a dichotomous variable, CAIC generated only four contrasts for analysis. For each phylogeny, the trend was the same as the species analysis, bordering on significance with the molecular phylogenies ($t_3 = -2.84, p = 0.066$) but not with the morphological phylogeny ($t_3 = -1.19, p = 0.318$). The bimodal data distribution meant that I could analyse the relationship between the continuous light availibility scores and nestling mouth colour only using datasets that had been split by nest type (Purvis & Rambaut, 1994). There was no significant relationship between nestling mouth colour and light availability for ‘light’ or ‘dark’ nests (Table 4).

Effect of % EPY on nestling mouth colour

(i) using species as independent datapoints

In the first set of analyses, I treated each species as an independent datapoint. With all species included, there was no significant relationship between mouth colour and % EPY ($F_{1,40} = 1.73$, $p = 0.20$; Fig. 3), nor was

TABLE 4. *The results of the comparative analyses, using contrasts generated by the program CAIC 2.0*

phylogeny	dataset	predictor	*F*	*p*
S & A	all nests	% EPY	$F_{1,39} = 0.02$	0.96
S & G	all nests	% EPY	$F_{1,37} = 0.01$	0.92
H & M	all nests	% EPY	$F_{1,32} = 0.27$	0.61
S & A	light nests	% EPY	$F_{1,19} = 14.03$	**0.0015**
S & G	light nests	% EPY	$F_{1,19} = 13.79$	**0.0016**
H & M	light nests	% EPY	$F_{1,18} = 12.41$	**0.0026**
S & A	light nests	light available	$F_{1,19} = 0.15$	0.71
S & G	light nests	light available	$F_{1,19} = 0.17$	0.68
H & M	light nests	light available	$F_{1,18} = 0.04$	0.84
S & A	dark nests	% EPY	$F_{1,19} = 1.76$	0.20
S & G	dark nests	% EPY	$F_{1,17} = 1.81$	0.20
H & M	dark nests	% EPY	$F_{1,14} = 0.44$	0.52
S & A	dark nests	light available	$F_{1,19} = 0.00$	0.99
S & G	dark nests	light available	$F_{1,17} = 0.00$	0.99
H & M	dark nests	light available	$F_{1,14} = 0.00$	0.98

S & A, S & G and H & M refer to Sibley & Ahlquist (1990), Sheldon & Gill (1996) and Howard & Moore (1991) phylogenies respectively. The predictor column describes the main predictor used to generate the set of contrasts produced by CAIC 2.0, and then used in a simple regression to explain the variance in mouth colour contrasts. The results of each regression are shown. Statistically significant *p*-values are shown in bold.

this relationship significant when the analysis was restricted to ‘dark’ nests ($F_{1,20} = 0.033, p = 0.86$; Fig. 3). However, considering ‘light’ nests alone, there was a significant relationship between nestling mouth colour and % EPY ($F_{1,20} = 4.98, p = 0.038$; Fig. 3). Chicks from species with higher % EPY had redder mouths.

(ii) using contrasts an independent datapoints

When I repeated the analysis using CAIC, the same pattern prevailed. Mouth colour and % EPY were not significantly related in analyses that used either the whole dataset, or that were restricted to species with just ‘dark’ nests (Table 4). Using just ‘light’ nests, however, mouth colour and % EPY were significantly related (Table 4; Fig. 4). Again, mouths were significantly redder in species with high levels of %EPY.

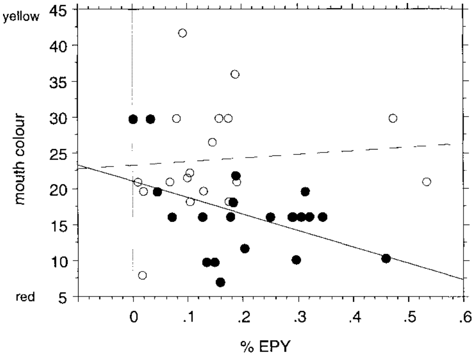

Fig. 3. The relationship between nestling mouth colour and % EPY, where each point represents a different species ($N = 41$). The data for % EPY have been arcsine and logarithmically transformed. Data for 'light' nests are shown with filled circles, with a solid regression line through them, while those for 'dark' nests are shown with open circles, with a dotted regression line through them. The graph shows that in species where % EPY is high, and nests are 'light', nestlings have redder mouths. No equivalent relationship exists for species with 'dark' nests.

Cuckoo nestling mouth colour

Cuckoos had significantly redder mouths than their hosts (Wilcoxon: $z = -2.16$, $N = 14$, $p = 0.03$), but since this analysis does not control for phylogenetic effects, it is impossible to determine the adaptive significance of the result. There was no correlation between host and cuckoo nestling mouth colour (Spearman: $z = -1.42$, $N = 14$, $p = 0.16$), even when cuckoo species raised in relatively dark nests (see Table 3) were excluded (Spearman: $z = -0.74$, $N = 8$, $p = 0.46$).

Discussion

Two selective forces determine nestling mouth colour

Previous attempts to explain the diversity of signal design between species have considered either selection for signal efficacy (the 'tactical' approach *e.g.* Endler, 1991; Wiley, 1994) or the effects of conflicts of interest (the 'strategic' approach *e.g.* Briskie *et al.*, 1994) but seldom address both at once (see Johnstone, 1998). The contention that the enormous variation in animal signal design reflects the diversity of selective forces at work (Guilford & Dawkins, 1991, Johnstone, 1997, Bradbury & Vehrencamp, 1998) therefore

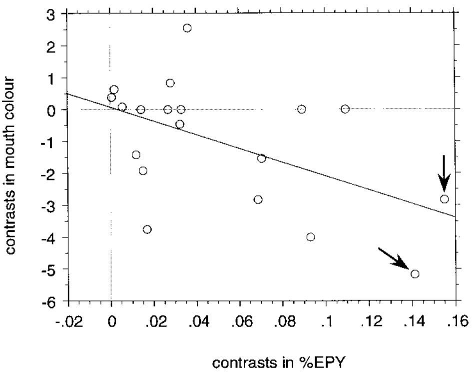

Fig. 4. The relationship between nestling mouth colour and % EPY for species that rear their young in 'light' nests. The independent contrasts shown were calculated by CAIC 2.0 using the Sibley & Ahlquist (1990) phylogeny. The graph shows that, in species where % EPY is high, nestlings have redder mouths. The relationship remains statistically significant if either of the points marked with an arrow are removed. If both are removed, $p = 0.0669$.

remains untested. Here I show that the variety of nestling mouth colour can be explained by at least two different selective pressures.

Despite the less than perfect measurements of colour and light availability, the results indicate that some of the variation in nestling mouth colour between species can be accounted for by the light available in the nest (*cf.* Kilner & Davies, 1998), much as Ficken (1965) speculated some time ago. Species that typically raise young in 'dark' nests have chicks with yellower mouths than those that rear young in 'light' nests, where mouths are generally redder (Fig. 2). It may be that the two types of nest differ in ambient light colour, so that different mouth colours better maximize brightness contrast between the mouth interior and its fleshy white border. Or perhaps in 'dark' nests, yellow mouths function to maximize the contrast between the chick and the dark nest background against which it displays.

The analyses also reveal that family conflicts influence the evolution of nestling mouth colour, but only in conjunction with selection for signal efficacy. In species where sibling conflict is most intense, because % EPY is high, offspring display redder mouths than in species with lower % EPY. But a significant relationship exists only for chicks reared in lighter nests, and not for species reared in darker nests. Presumably, the restricted lighting conditions of 'dark' nests mean that mouth redness is not a useful weapon in sibling conflict. Indeed, the evidence from the light availability analyses suggests that it may even reduce competitive ability. However, the ambient light conditions of more exposed nests confer a use for mouth redness in sibling competition, either because there is sufficient light for parents to exercise a preference for red *per se*, or because it enhances chick detectability (see Introduction).

All analyses of correlated evolution are open to the criticism that any significant relationship may be an artefact of a correlation with a third variable. In this case, for example, it may be that intense sexual selection in species with high % EPY has resulted in more brightly coloured, redder plumage in males (*e.g.* Hill, 1991) and this in turn has caused offspring to accumulate red pigment in their mouths. This particular possibility seems unlikely for two reasons. First, it predicts that all species should have redder mouths with increasing % EPY irrespective of nest type, which is not the case. Second, although males of three of the species in this analysis (*Calcarius pictus*, *Emberiza schoeniclus*, *Passerina cyanea*) have high rates of % EPY and their nestlings have red mouths, males of these species do not have red plumage.

Sibling conflict

Instead the analyses presented here suggest that, in well illuminated nests, the redness of nestling mouths is the scar of family battles that have been waged in the past. Where optimal provisioning levels differ greatly between siblings, *i.e.* sibling conflict is highly intense, chicks display redder mouths than in more harmonious broods. Perhaps what we see today reflects the resolution of family conflicts, with nestling mouth colour at its ‘equilibrium’ redness. Since all nestlings in brood display the same mouth colour, it confers no current competitive advantage at all. Chicks nevertheless retain red mouths where appropriate because any yellow-mouthed mutant would immediately lose sibling conflict.

Sexual conflict

Multiple paternity within broods not only intensifies sibling conflict, it also creates a divergence in optimal provisioning rules for male and female parents, causing sexual conflict over resource allocation. Whereas females are selected to divide resources equally among the brood, for example, each male would prefer her to invest preferentially in his offspring. Put in terms of nestling mouth colour, the optimal colour from each father’s perspective is redder than for the mother. The redness of nestling mouths may therefore indicate the outcome of sexual conflict as well as the intensity of sibling conflict.

Sexual conflict over offspring provisioning, as a result of multiple paternity, can manifest itself in a variety of ways. In mice, for example, it has been suggested that the conflict appears as a battle over the level of resources to be extracted from the mother between paternal and maternal genes in the foetus (Haig & Graham, 1991). In birds, where fathers provide care for young, it is harder for males to manipulate levels of maternal care via their offspring without laying themselves open to manipulation. The task would be simpler if fathers could readily identify their own chicks, but there is no evidence so far that such paternity markers exist (Kempanaers & Sheldon, 1996). For mothers and chicks, at least, the costs of discrimination probably outweigh the benefits of nepotism (Davies, 1992; Keller, 1997; see also Lotem, 1993), which favours young that disguise their paternity. Sexual conflict is thus a double-edged sword for avian fathers, simultaneously promoting the manipulative begging required to exploit mothers, and scrambling the kin recognition cues necessary to avoid consequent exploitation themselves.

The best allocation strategy for males that are unable to recognize their own young might be to ensure they feed only high quality chicks, either by selecting larger young to feed (Slagsvold *et al.*, 1994; Slagsvold, 1997) or by exploiting competitive asymmetries within the brood (Slagsvold, 1997; Kölliker *et al.*, 1998). Alternatively, the begging signal equilibria may differ between males and females, with fathers demanding a higher level of solicitation before supplying food (Kölliker *et al.*, 1998). Whether males and females can respond differently to nestling mouth colour is tested in the succeeding paper (Noble *et al.*, this volume).

Parent-offspring conflict

If parents adjust provisioning rates in relation to absolute, rather than relative, mouth redness then nestling mouth colour may reflect the strength of parent-offspring conflict as well. By upholding prediction (2), the analysis of Cuculinae nestling mouth colour appears to support this possibility. The 14 cuckoo species in the analysis had significantly redder mouths than the young of their hosts. However, there was no indication that cuckoos have modified their mouth colours as a specific adaptation for parasitizing a particular host. In fact, it is impossible to tell from the comparative analyses presented here whether the Cuculinae have redder mouths than their hosts as a general adaptation for brood parasitism, or as a phylogenetic artefact. Since the three species of non-brood parasitic cuckoos for which data were found (*Coccyzus americanus*, *C. erythropthalamus*, *Geococcyx californianus*) all have red or pink mouths (Baicich & Harrison, 1997), the most conservative interpretation of the results is that cuckoo nestling mouth colour is not an adaptation for a brood parasitic lifestyle.

A more intriguing possibility is that a red mouth may be part of the trickery used by brood parasites to dupe some, but not all, of their hosts. The common cuckoo, for example, parasitizes three major hosts in Britain: the reed warbler, whose young possess yellow gapes, the dunnock, which has orange-mouthed chicks, and the meadow pipit (*Anthus pratensis*), whose nestlings display flesh-red mouths (Kilner & Davies, 1998). Adult female cuckoos faithfully parasitize one host species and form distinct 'races' or gens, each recognizable by the egg patterning that usually mimics the eggs of the particular host (Brooke & Davies, 1988). By contrast, adult males mate promiscuously across the different female races (Marchetti *et al.*, 1998). Egg mimicry persists, nonetheless, presumably because it is inherited maternally and expressed only by females. Mimicry of host chick appearance, however, is impossible (Marchetti *et al.*, 1998). In reed warbler nests, the cuckoo chick elicits sufficient care from its reed warbler hosts by exploiting the usual communication system between host young and their parents, relying on an exaggerated begging call to compensate for a deficient visual stimulus of a single gape (Davies *et al.*, 1998; Kilner *et al.*, 1999). But different host species vary in the details of their begging display with some more vocal than others (Kilner & Davies, in press). To elicit care successfully from its various hosts, perhaps the cuckoo nestling has to perform a variety of begging tricks, some of which may be essential in one host but quite useless in others. The ambient light in different host nest types may mean that a red mouth is vital in duping meadow pipit hosts, for example, but irrelevant for fooling reed warbler hosts.

Whatever the cuckoo species, providing that males and females are often reared by different hosts, there can never be perfect mimicry of host nestling appearance and selection for cuckoo chick visual displays that are functionless with some hosts may result. This might explain why cuckoo nestling mouths are redder, but not correlated with, the mouth colour of most common host's young.

Family differences in the resolution of conflicts of interest?

The argument that mouth colour may be functionless in some nests can be extended to species that rear their own young, providing that the colour of a nestling's gape costs little to maintain. In particular, for species that build cup nests in tussocks, shrubs or trees, there can be enormous variation in the specific nest location selected by parents and consequently the visual environment in which offspring display (R.M. Kilner & N.B. Davies, unpubl. data). In some nests, the light available may mean that nestling mouth colour is vital in enhancing detectability, in others the nest may be so dark that mouth colour is much less important. Providing mouth colour is a cheap signal, each species should display the colour best suited to the average nest location, but from nest to nest its importance may vary considerably.

Unlike males displaying to females (Endler, 1987, 1992; Endler & Théry, 1996), chicks in the nest cannot choose a signalling environment in which to maximize the signal:noise ratio of their visual display. A male cock-of-the-rock (*Rupicola rupicola*), for example, leks in a patch of woodland that maxmizes the visual contrast between the colour of its plumage and the background against which it displays (Endler & Théry, 1996). By contrast, a chick is saddled with a signalling environment selected by its mother when she decided where to build her nest. Within species, the variety in parental choice of the microhabitat in which signals are sent may have profound consequences for the role of visual displays in parent-offspring communication. For a start, it weakens the interdependence between habitat choice and sensory systems in the evolution of visual displays (Endler, 1992), increasing the variance in the correlation between the signal and either of these two variables. Furthermore, the choice of nest site may influence parental vulnerability to exploitation by offspring visual displays and therefore dramatically alter the nature of family conflicts. Just as adult ecology can influence the outcome of sexual conflict within species (Davies, 1992), so nest ecology could affect the resolution of parent-offspring conflict, causing family differences in the settling of disputes. With such a variety of nest locations selected within some species, there may be no universal resolution to family conflicts of interest within species, contrary to theoretical expectations (Godfray, 1995b; Mock & Parker, 1997).

Assumptions to test: a guide to experimenters

The key assumption on which interpretation of these comparative analyses rests is that parents from a variety of taxa within the passerines should favour chicks with redder mouths, either because they possess a sensory bias for red *per se* (Ryan, 1997; Endler & Basolo, 1998; Jones & Hunter, 1998), or perhaps because red enhances chick detectability. Moreover, parents should not only select red-mouthed individuals to feed, they should return to the nest sooner with food if their entire brood's mouths are reddened (see Noble *et al.*, this volume).

At first sight, these assumptions appear simple enough to test with some mouth colour manipulation experiments. Unfortunately, the variety of nest locations used within species, the potentially minor role of nestling mouth colour in securing food, and the significant confounding effects of other components of the begging display (Kilner & Johnstone, 1997) mean that such experiments are far from straightforward to execute. The two studies (Götmark & Ahlström, 1997; Kilner, 1997) that have successfully demonstrated a preference for red circumvented these problems. Both controlled nest light availability either by conducting experiments under laboratory conditions (Kilner, 1997) or regulating the light supplied to nest boxes (Götmark & Ahlström, 1997). By reducing the brood to just two young, both studies eliminated the effects of chick size on nestling provisioning, and one also controlled chick hunger (Kilner, 1997). Despite the best intentions, it may not always be possible to control all these potentially confounding variables at once, and consequently experimental data may prove difficult to interpret (see Noble *et al.*, this volume).

Diversity of other begging signals

In summary, the comparative analyses presented here suggest that nestling mouth colour is correlated with the intensity of family conflicts, but only when chicks display in an environment in which redder mouths can elicit a parental preference. Bright nestling mouth colour is only one component of a suite of solicitation behaviours that make up the begging display. For offspring reared in open nests, two different comparative studies have now shown that the exuberance of different elements of the begging display is correlated with % EPY. Where % EPY is high, displays involve the use of louder calls (Briskie *et al.*, 1994), and redder gapes (this study). Whether family conflicts can influence components of the begging display given by young raised in dark nests remains to be discovered. Since nest type can influence both the cost and efficacy of signal transmission, it is likely that in dark nests different components of the begging display are influenced by the strength of family disputes.

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