



Intensity of mouth coloration in Blackcap *Sylvia atricapilla* nestlings affects food distribution among siblings but not provisioning of the whole brood

EWA WĘGRZYN*

Department of Zoology, University of Rzeszow, Rzeszow, Poland

Among various begging stimuli, mouth coloration has received increasing attention in recent years, and previous research has demonstrated that mouths of nestling Canaries *Serinus canaria* get redder with the extent of food deprivation and that parents preferentially feed nestlings of redder gapes. This study assesses whether the intensity of red mouth colour in nestling Blackcaps *Sylvia atricapilla* is a signal in parent–offspring communication. This is one of the few species with a naturally red gape in which the function of mouth redness has been tested. Three predictions were experimentally tested: (1) reddening the gape of a single nestling within a brood increases its provisioning in relation to other siblings; (2) reddening the gapes of all nestlings within a brood increases parental feeding rate; and (3) food deprivation increases nestling mouth redness. The effect of nestling quality on mouth redness was also assessed. The intensity of gape coloration affected food distribution, but in a way opposite to that expected: an increase in mouth redness of the nestling caused reduced feeding by parents. However, reddening the gapes of all nestlings had no effect on provisioning of the whole brood, suggesting that Blackcap parents use different cues for provisioning particular nestlings and the whole brood. Intensity of mouth redness in Blackcap nestlings was not affected either by food deprivation or by nestling quality in terms of mass and rank in the nest.

Keywords: begging, gape colour, parent–offspring communication, *Sylvia atricapilla*.

Bird parents are presented with a number of sources of information from their nestlings when arriving at a nest with food. The level of parental care may be shaped by parent–offspring conflict (reviewed by Godfray & Johnstone 2000), which is resolved through nestling begging and the parental response (Wright & Leonard 2002, Hinde *et al.* 2010). It has been demonstrated that parental response to begging displays is adaptive, as it may help to adjust provisioning to brood demands and ensure proper distribution of food among nestlings (Grodzinski & Lotem 2007, Grodzinski *et al.* 2009). Both vocal and visual signals have been shown to affect the feeding decisions of parent

birds (e.g. Gottlander 1987, Smith & Montgomerie 1991, Redondo & Castro 1992, Whittingham *et al.* 2003). Begging displays may act separately or as a combination of different begging components in multimodal sensory channels (Jacob *et al.* 2011).

Two general models of nestling behaviour that predict patterns of allocation of food to individual offspring within a brood have been proposed. The first, called ‘scramble competition’ (Parker *et al.* 1989, 2002), assumes that distribution of food is controlled by the offspring and does not require any signaling system. The other model proposes begging as an ‘honest signal’ of an offspring’s true need, hunger or quality (reviewed in Mock *et al.* 2011). In such a scenario, parents are assumed to control food allocation according to the begging displays of their young and, as a result, parental choice can select for ornamental traits in offspring (Lyon *et al.* 1994).

*Present address: Department of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Pozna, Poland. Email: wegrzyn@amu.edu.pl, songbird.ewa@gmail.com

Among various begging displays, mouth coloration has received increasing attention in recent years (reviewed by Kilner 2006). Gape and flange colour have been demonstrated to be condition-dependent (Ewen *et al.* 2008, Dugas & McGraw 2011) and to act as a signal of nestling quality (Saino *et al.* 2000, Loiseau *et al.* 2008) or hunger (Kilner 1997) for bird parents. Several studies have demonstrated parental preferences towards more intensely coloured gapes (Loiseau *et al.* 2008, Dugas 2009). In Canary *Serinus canaria* nestlings, mouths became redder with increasing food deprivation and parents adjusted food allocation among the brood in relation to mouth colour (Kilner 1997). As a mechanism maintaining signal reliability, the author proposed the possible cost incurred by diverting blood from a full gut to the mouth (redness appears due to a rapid blood flush to mouth tissues). Other examples of the signalling function of mouth coloration come from studies on Great Tit *Parus major* (Götmark & Ahlström 1997, Heeb *et al.* 2003) and Barn Swallow *Hirundo rustica* (Saino *et al.* 2000, 2003). In both species, artificial reddening of nestling gapes increased feeding rates by parents, although the chicks in these species have naturally yellow, not red, mouths. Also, experiments on Hihi *Notiomystis cincta* demonstrated increased parental provisioning rate for offspring whose gape colour became intensified after carotenoid supplementation (Ewen *et al.* 2008, Thorogood *et al.* 2011). All of these studies indicate parental selection for redder gapes, irrespective of whether the redness is a natural or artificial gape colour for a given species, and suggest gape coloration as an important factor in parent-offspring communication in food provisioning and distribution. In contrast, experimental reddening of the mouths of Robin *Erithacus rubecula*, Dunnock *Prunella modularis* and Reed Warbler *Acrocephalus scirpaceus* nestlings did not result in an increase in food provisioning by bird parents (Noble *et al.* 1999). Experiments by Clotfelter *et al.* (2003) showed that intensity of red mouth colour in Dark-eyed Juncos *Junco hyemalis* does not indicate the level of hunger but rather the thermal state of nestlings. However, the reaction of Junco parents to changes in nestling mouth redness intensity was not tested, and thus the function of gape coloration in parent-offspring communication in this species remains unresolved.

These equivocal results concerning parental preference towards redder-mouthed nestlings

require further investigation. It seems reasonable to test the above preference in the first place using species with naturally red mouths. As shown by previous studies, mouth colour in some species can signal hunger or quality. Here, I use experiments to assess whether Blackcap *Sylvia atricapilla* parents use variation in mouth redness as a signal, and whether mouth colour in Blackcap nestlings reflects their hunger. I also test the relation between gape colour and nestling quality.

The Blackcap is a small, open-nesting, migratory passerine widespread in Central Europe. It breeds in habitats characterized by dense tree and shrub vegetation (Glutz Von Blotzheim & Bauer 1991). It builds thin-walled, open-cup nests of 10 cm diameter and 5 cm height in the shrub and herbaceous layers of forests (Storch 1998). The clutch size is four to five eggs, laid on consecutive days. Incubation lasts 12 days and nestlings stay in the nest for another 12 days, but they are able to leave the nest when 9 days old. It is a model species for research on begging signals for two reasons. First, Blackcap nestlings display bright red gapes while begging, and there is natural variation in redness intensity among nest mates (Fig. 1), which might suggest its signalling function. The nature of the coloration seems similar to a 'canary-like' flush, because the gapes opened mechanically were

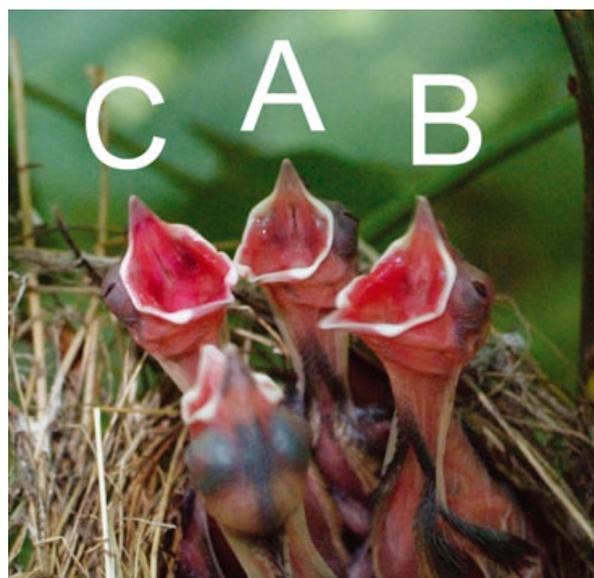


Figure 1. Individual differences in the intensity of mouth redness in Blackcap nestlings: (A) naturally pale, (B) naturally red, (C) artificially reddened with food colouring.

much paler than those presented during active begging. Secondly, Blackcap is a species under high nest predation pressure. On average, only 30% of nests survive (Weidinger 2000, 2002, 2007, Remeš 2003a,b, Scheafer 2004, Węgrzyn Leniowski 2011). In addition, the ability of the parents to defend a nest is limited. Videos by Scheafer (2004) showed that in the majority of predation attempts, parents did not defend their nests. As the amplitude of begging calls is known to increase predation (Briskie *et al.* 1999, Dearborn 1999, Haskell 1999, McDonald *et al.* 2009), we may expect the evolution of visual signalling of hunger instead of costly vocalization.

METHODS

Study area

The study was conducted in 2010 and 2011 in the deciduous forest of the Fox Hill Reserve, south-east Poland (50°6'0"N, 21°59'24"E). The nests were searched by careful inspection of potential nest-sites after mapping males' breeding territories early in the spring. Nests were checked every 3–5 days until predated, or were filmed.

Filming procedure

The nests were filmed using a thumbnail sized micro-camera (Sony ¼-inch LC-S742 C55P4) that was placed at a distance of about 25 cm from the nest and left for a sufficient time to allow the parents to resume their natural feeding activity. Feeding rate at each nest was estimated before mounting the camera by watching the nest from a distance, using binoculars or a telescope, for half an hour. The experiments were conducted when feeding rate after mounting the camera did not differ by more than 10% from the feeding rate before mounting the camera. Some parents did not resume feeding at all, or fed the nestlings at much lower rates even up to 3 h after the camera was mounted. In these cases I removed the camera and stopped filming the nests. In all such instances, parents resumed feeding after the removal of the camera and none of the nests was abandoned. I made an attempt to film 15 nests in 2010, but in six of them the parents did not resume their natural feeding activity. The experiments involving filming (1 and 2) were conducted in the nine remaining nests. The experimental nests contained

from one to five nestlings (one nest with one nestling, two nests with three nestlings, three nests with four nestlings and three nests with five nestlings). Experiments 1 and 2 were conducted on the same nests but in different days. Experiment 1 preceded experiment 2 in all nests.

Experiments

The aim of experiment 1 was to test whether an artificial increase in mouth redness of a single nestling results in it receiving a higher rate of provisioning in comparison with other nest mates. The nests in which parents resumed their natural feeding activity after mounting a camera were filmed for 1 h without any changes in nestling mouth coloration. These films were later treated as controls. One randomly chosen nestling within a brood was marked with a tiny dot on its beak to allow the comparison of its provisioning before and after the change in mouth coloration. After the control film for a given nest was finished, I increased mouth redness of the previously marked nestling using non-toxic food colouring (Kilner 1997). This increased nestling mouth redness for 2–3 h (depending on feeding rate). To dye the mouth of the experimental nestling, I tapped the rim of the nest, which induced gaping, and gently put a small paintbrush with red food colouring into the nestling mouth. The nestling was not handled or removed from the nest. The same procedure was applied to the rest of the brood using a paintbrush dipped in water to ensure that all nestlings were subject to the same treatment. This method proved to be fast and did not affect the later behaviour of the nestlings, which readily begged for food as soon as parents arrived at the nest. To make sure that the experimental procedure was effective, after the painting was finished I asked a naive observer to point out the reddest gape of the brood. At each nest the observer pointed out the dyed nestling. Next the brood was filmed for another hour. After the experiment was finished, I again asked a naive observer to point out the reddest gape and again, each time the observer identified the dyed nestling, which proved that colour enhancement was effective until the end of the experiment.

To examine parental preference for a redder mouth, I conducted two analyses. First, I tested whether parental choice of reddened nestlings during the first visit after treatment in eight nests

differed from random. I assumed that parents would instantly recognize and feed the experimental nestling with the reddest mouth if this trait is favoured. Secondly, I calculated relative food share (RFS) of the experimental nestling before and after the treatment and compared the obtained values to see whether RFS increased after the reddening of the mouth. The RFS was calculated as:

$$\frac{\text{number of feeds to experimental nestling}}{\text{number of all feeds to the brood}} \times \text{number of nestlings in the brood}$$

The first part of the formula is simply a proportion of the feeds obtained by the experimental nestling. Multiplying this by the number of nestlings in the brood enables an assessment of whether frequency of feeding of the experimental nestling was higher (RFS > 1) or lower (RFS < 1) than average (RFS = 1). As the experimental nestling was randomly chosen in each nest, and I was interested in whether the effect of mouth reddening was dependent on nestling position in the brood hierarchy, I used the RFS obtained in a control film as a measure of nestling dominance. I chose this approach rather than comparing the direct number of feeds of the coloured nestling during 1 h of control and experimental treatment, as RFS indicated whether the chick was preferred or not in relation to its nest mates. The number of parental visits at the nest per hour naturally varies to some degree, and thus simple counting of the number of feeds received by the experimental chick before and after the treatment may be misleading. For example, if parents increase feeding to the whole brood for any reason not connected with the experiment, the chick of redder gape will also get more food. However, in the described case it does not result from parental preference towards a redder gape. As using RFS requires at least two nestlings in a brood, I had to exclude one nest with only one nestling from this analysis. Thus experiment 1 was conducted in eight nests, containing from three to five nestlings.

The aim of experiment 2 was to assess whether an artificial increase in mouth redness of all nestlings within a nest resulted in a higher feeding rate. The procedure was similar to that of experiment 1, with a difference being that I reddened the mouths of all nestlings in a brood. After the treatment, the nest was filmed for 1 h and the observed feeding rate was compared with the con-

trol (feeding rate obtained from a 1-h film before the treatment). Experiment 2 was conducted at nine nests (including one nest with one chick which was treated as the whole brood).

I did not observe any adverse effect of colouring nestlings' mouths on their behaviour or survival. Immediately after the treatment, the begging behaviour of the chicks was no different from that recorded in the control videos. Nests were monitored in the following days after the experiments. One of the nests was predated 3 days after the experiment, but the remaining broods successfully fledged. The interval between the experiments and the predation event as well as a high predation rate in the studied species suggest no connection between these two events.

The aim of experiment 3 was to assess whether the intensity of mouth coloration changes (increases) with the level of hunger in Blackcap nestlings. The experiment was conducted in six nests in 2010, at nests in which parents did not respond well to a camera, and in eight nests in 2011. One randomly chosen nestling from each nest was removed and its mouth was photographed using a Fuji S5-Pro SLR camera. I did not conduct spectrophotometric measurements of gape coloration for two reasons. First, the tiny size of the gape in the studied species raised problems with placing a measuring probe inside the mouth (the probe has to be placed at a 90° angle to the measured surface and in Blackcap nestlings this was impossible). Secondly, gape redness in Blackcap nestlings is a dynamic trait, which means that the gape becomes intensely red during begging for food. This is probably due to blood flush to the open gape, similar to the process described in Canaries (Kilner 1997). Nestling gapes opened mechanically by a researcher are much paler than those presented during begging (E. Węgrzyn pers. obs.). Thus spectrophotometric measurement of gape colour in Blackcap nestlings seemed inappropriate. I therefore used photos of open mouths taken during induced begging displays. After the first photograph was taken, each nestling was kept for 1 h in an artificial nest placed in a warmed box to prevent cooling. The box was warmed by a small warming cushion fixed at its bottom and connected to a cigarette lighter socket in a car. The temperature in the box was maintained between 34 and 36 °C. After 1 h of food deprivation, the nestling's mouth was photographed for the second time. For each photograph, the nestling

was placed on a black background (using a small box lined with black fabric). Begging posture and an open nestling mouth were induced by tapping the rim of the box. All photographs were taken on sunny days between 08:00 and 09:00 h. I controlled the light environment by placing a box in a lightly shadowed area of illuminance 1500 lux (± 10 lux), which was measured using a portable TES-1332 photometer. This approach enabled repeatable light conditions during the taking of photographs without the need to transport the nestlings to a laboratory. Nestlings used in the experiment were between 4 and 6 days old (11 nestlings were 4 days old, two were 5 days old and one was 6 days old). The differences in nestling age were caused by unfavourable weather conditions when three of 14 nestlings were 4 days old. To quantify nestling gape colour, the photographs were imported into Adobe PHOTOSHOP CS (following Kilner 1997). In this program, hue represents the position across the spectrum and is measured in degrees, 0° being the reddest measure; saturation represents colour density, from the least dense (0%) to the most dense (100%); and brightness is the greyscale value of the colour, where 0% is white and 100% is black. Hue, saturation and brightness of nestling mouth were measured at five points (each including 25 pixels), placed inwards from the flanges (the reddest area of the Blackcap nestling mouth).

Nestling mass and rank in the nest

All nestlings used in experiment 3 and their siblings were weighed using an electronic jewellery balance to the nearest 0.01 g. Nestling rank within a brood was estimated on the basis of its weight in relation to the weight of its siblings (the heaviest nestling in the nest was given rank 1, the subsequent rank 2 and so on). Mass and rank of nestlings from 11 nests photographed and measured at the age of 4 days were used to analyse whether intensity of mouth coloration was related to nestling quality.

Data analysis

All analyses were conducted using SPSS 20 software (SPSS Inc., Chicago, IL, USA). Due to the sample size and variable distribution in experiments 1 and 2, non-parametric statistics (related-samples sign test) were used. In experiment 3, mouth colours of food-deprived chicks were compared with their

mouth colours before food deprivation using a paired *t*-test. To compare expected and observed numbers of feeding of the reddened nestling during the first parental visit, the binominal test was used. To analyse the relationship between mouth redness and nestling condition, I used general linear models with brightness, saturation and hue as dependent variables, nestling rank as a random effect, and mass as a covariate.

RESULTS

The probability of random feeding of any of eight reddened nestlings (of a total 33 nestlings) during the first visit to the nest of a single parent was 0.24, which produced an expected value of 3.8 reddened nestlings fed by at least one of two parents. The observed number of reddened nestlings fed during the first visit was 1.0, which was significantly less than expected (binominal test: $P = 0.027$).

The analysis of the RFS of the experimental nestlings before and after mouth reddening also revealed no parental preference towards higher intensity of red coloration of offspring gapes. RFS of reddened nestlings (mean \pm sd = 0.98 ± 0.17) was lower than their RFS before mouth painting (1.46 ± 0.80 ; sign test: $P = 0.008$). Without exception, all reddened nestlings received less food in relation to their siblings than the same nestlings during the control (Fig. 2). Unexpectedly, there was no difference between dominant (RFS > 1) and subordinate (RFS ≤ 1) nestlings (sign test: $P = 0.289$); irrespective of whether they received more or less food than their nest mates during the control, their share of food brought by parents decreased after the intensity of their gape redness was increased (Fig. 2).

Feeding rate after artificial reddening of the gapes of the whole brood (mean = 15.49 ± 10.73 , $n = 9$ nests) was not significantly different (sign test: $P = 0.508$) from the feeding rate in the same nests before treatment (mean = 15.05 ± 11.00 , $n = 9$ nests). Changes in brood provisioning in particular nests after an increase in gape redness of all nestlings were inconsistent: in some nests parents increased feeding rate, whereas in others the rate was decreased (Fig. 3).

After 1 h of food deprivation, the intensity of gape redness did not change significantly, in hue, saturation or brightness (Table 1). There were also no visible differences in mouth colour between

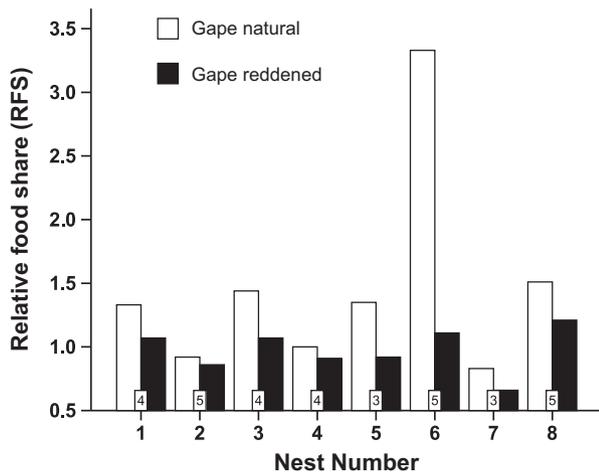


Figure 2. Relative food share of the experimental nestlings before (open bars) and after (filled bars) artificial mouth reddening ($n = 8$ nestlings). RFS = 1 represents the mean food share of the nestling in a given nest, and thus nestlings with RFS > 1 received more food than their nest mates (dominant chicks) and nestlings with RFS < 1 received less food than their nest mates (subordinate chicks). Annotations above nest numbers indicate brood size in each nest.

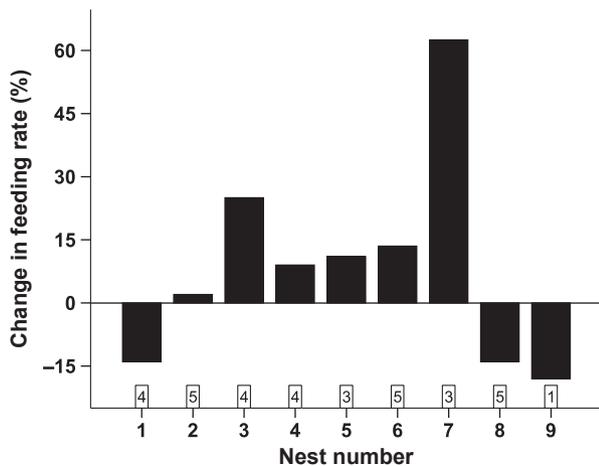


Figure 3. Changes in feeding rate after artificial mouth reddening of whole broods ($n = 9$ broods) in relation to controls. Annotation above nest number indicates brood size in each nest.

satiated and hungry nestlings, at least as perceived by the human eye. The results of GLMs revealed that mouth coloration was not associated with nestling quality. None of the colour parameters (brightness, saturation and hue) was correlated with nestling mass or rank within the nest (Table 2).

Table 1. Mean values of hue, saturation and brightness of nestling gapes measured before (0) and after 1 h (1) of food deprivation ($n = 14$).

	Mean	Min	Max	sd	t	P
Hue 0	-0.36	-3	4	2.02	-0.23	0.818
Hue 1	-0.21	-4	3	1.97		
Saturation 0	74.36	60	81	6.87	-0.81	0.430
Saturation 1	75.29	57	83	7.92		
Brightness 0	76.07	67	80	3.43	-0.06	0.952
Brightness 1	76.14	69	81	3.91		

To test the difference between the variables before and after food deprivation, a paired t -test was used.

Table 2. Results of general linear models testing the effect of nestling mass and rank within the nest on parameters describing mouth colour (hue, saturation and brightness), $n = 11$.

	Mass		Rank	
	$F_{1,4}$	P	$F_{1,4}$	P
Hue	1.921	0.224	3.109	0.123
Saturation	0.126	0.737	0.186	0.936
Brightness	0.020	0.893	0.446	0.773

DISCUSSION

The aim of this study was to test whether the intensity of red gape coloration in Blackcap nestlings affects parental preferences and functions as a signal in parent-offspring communication. Experiment 1, in which the mouth of one nestling in each nest was reddened, demonstrated that chicks with redder mouths received less food in relation to their nest mates than they did before the treatment. In contrast to the results obtained by Kilner (1997) on Canaries, Blackcap parents favoured chicks with less red mouths. Additionally, the nestling with an artificially reddened mouth was chosen by parents during their first visit to the nest after treatment in only one of the eight nests, supporting the view that an increase in mouth redness resulted in a lower probability of being fed. This part of the study provided evidence that Blackcap parents respond negatively to changes in intensity of nestlings' mouth redness, and thus it has a signalling function in the studied species. Although begging has often been interpreted as a signal of need (Kilner 1997, Johnstone & Godfray 2002), other authors have demonstrated that traits presented during begging indi-

cate not need but the quality of nestlings (Saino *et al.* 2000, Ewen *et al.* 2008, Dugas 2009, Mock *et al.* 2011). I addressed both issues in my study by testing whether gape colour was related to nestling hunger or its mass and rank in the nest. Experiment 3 demonstrated that mouth redness in Blackcap nestlings did not change with food deprivation and therefore is unlikely to reflect nestling hunger. Similarly, gape colour was not related to nestling quality, at least in terms of chick size and hierarchy in the nest. Thus, the question of signal content in Blackcap mouth redness remains unanswered.

An unexpected outcome of experiment 1 was that the intensity of mouth redness in Blackcap affected food distribution among nestlings in a way opposite to that expected: reddened chicks received less food than their less red siblings. This suggests that in Blackcaps, there might be a different signalling mechanism from those reported for signals of hunger (Kilner 1997) or quality (Loiseau *et al.* 2008) in other species, where redder offspring were favoured by parents. For example, as the mouth redness comes from vascularized tissue inside the gape, stretching the tissue may change its colour, perhaps in the way in which a balloon gets paler as it is inflated. Thus nestlings that beg for food more intensely, with wider open beaks, may present paler gapes. Although my experiment with food deprivation demonstrated that mouth redness is not related to hunger, it has to be highlighted that, to get comparable images, I induced begging until nestlings fully opened their mouths, and then photographs were taken. In natural situations, more needy nestlings open their gapes wider than their recently fed siblings. Whether this is the case in Blackcaps has to be tested in subsequent studies.

In experiment 2, I revealed that artificial reddening of the mouths of all nestlings within a nest did not affect the provisioning of the whole brood. It might seem contradictory to the results of experiment 1, as one may expect that reduction in feeding of one dyed nestling should result in reduction of feeding of the whole brood when gape redness of all nestlings is increased. However, this expectation may be misleading, because parents may use different cues for food distribution than for provisioning the whole brood (Mas & Kölliker 2011). While differences in gape redness intensity can be easily noticed among nest mates (one nestling is redder than others) and thus effectively used during food

distribution, the assessment of the same feature of the whole brood may prove to be more difficult due to the lack of reference. The feeding rate of the whole brood is likely to be related to such reliable indicators of brood food demand as the number of young and their size. Thus dynamic signals of quality or hunger revealed by particular nestlings (such as changes in mouth colour) may work in food distribution, while static cues (for example total gape area) indicating brood and nestling size may be used for adjusting the feeding rate of the whole brood. The results of experiment 2 may also be explained by strategic responses of parents to colour, based on probabilities of future reproduction. Thorogood *et al.* (2011) recently demonstrated that more colourful broods, consisting of nestlings of higher quality, were better provisioned, but only if parents were not going to breed again that season. This shows that parents may react differently to the same signal depending on other environmental factors. Such flexibility in response to the stimuli may be the case in my study, as in experiment 2 some parents increased feeding rate, whereas others decreased the rate. However, most of the changes in feeding rate fell within the natural fluctuation observed in songbirds, which suggests that the majority of parents simply did not react to the experimental manipulation.

Although the sample size in my study was rather small ($n = 8-9$), it is comparable to the sample size in the study by Kilner (1997), in which the author demonstrated that intensity of mouth redness functions as a signal of hunger in Canary nestlings ($n = 7-8$). This suggests that different results obtained in studies on Canary and Blackcap begging behaviour may not be caused by limited sample size in my experiments but could arise from different signalling strategies employed by the two species and/or different physiological mechanisms underlying colour production and change. This discrepancy leaves the question of the function of gape coloration in other species with red-gaped nestlings unanswered. Specifically, it remains unclear why nestlings of some songbird species evolved red gapes without carotenoid-rich integument, whereas the majority have yellow ones (Kilner 2006). Further investigations are needed to understand the role of red mouth coloration in begging displays.

The study was supported by the POL-POSTDOC III grant no. PBZ MNiSW 07/2006/13. I kindly thank two

anonymous referees for helpful comments and suggestions that improved my manuscript.

REFERENCES

- Briskie, J.V., Martin, P.R. & Martin, T.E. 1999. Nest predation and the evolution of nestling begging calls. *Proc. R. Soc. Lond. B* **266**: 2153–2159.
- Clotfelter, E.D., Schubert, K.A., Nolan, V. Jr & Ketterson, E.D. 2003. Mouth color signals thermal state of nestling dark-eyed juncos. *Ethology* **109**: 171–182.
- Dearborn, D.C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk* **116**: 448–452.
- Dugas, M.B. 2009. House sparrow, *Passer domesticus*, parents preferentially feed nestlings with mouth colours that appear carotenoid-rich. *Anim. Behav.* **78**: 767–772.
- Dugas, M.B. & McGraw, K.J. 2011. Nestling mouth coloration: proximate mechanisms, correlates, and constraints in house sparrows *Passer domesticus*. *Condor* **113**: 691–700.
- Ewen, J.G., Thorogood, R., Karadas, F. & Cassey, P. 2008. Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behaviour in the hihi *Notiomystis cincta*. *Oecologia* **157**: 361–368.
- Glutz Von Blotzheim, U. & Bauer, K.M. 1991. *Handbuch der Vögel Mitteleuropas Vol. 12/II*. Wiesbaden: AULA-Verlag.
- Godfray, H.C.J. & Johnstone, R.A. 2000. Begging and bleating: the evolution of parent-offspring signaling. *Proc. R. Soc. Lond. B* **355**: 1581–1591.
- Götmark, F. & Ahlström, M. 1997. Parental preference for red mouth of chicks in a songbird. *Proc. R. Soc. Lond. B* **264**: 959–962.
- Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **18**: 269–276.
- Grodzinski, U. & Lotem, A. 2007. The adaptive value of parental responsiveness to nestling begging. *Proc. R. Soc. Lond. B* **274**: 2449–2456.
- Grodzinski, U., Hauber, M.E. & Lotem, A. 2009. The role of feeding regularity and nestling digestive efficiency in parent-offspring communication: an experimental test. *Funct. Ecol.* **23**: 569–577.
- Haskell, D.G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Anim. Behav.* **57**: 893–901.
- Heeb, P., Schwander, T. & Faoro, S. 2003. Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Anim. Behav.* **66**: 637–642.
- Hinde, C.A., Johnstone, R.A. & Kilner, R.M. 2010. Parent-offspring conflict and coadaptation. *Science* **327**: 1373–1376.
- Jacob, S., Rieucou, G. & Heeb, P. 2011. Multimodal begging signals reflect independent indices of nestling condition in European starlings. *Behav. Ecol.* doi: 10.1093/beheco/arr 121.
- Johnstone, R.A. & Godfray, H.C.J. 2002. Models of begging as a signal of need. In Wright, J. & Leonard, L.M. (eds) *The Evolution of Begging*: 1–20. Dordrecht: Kluwer Academic Publishers.
- Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond. B* **264**: 963–968.
- Kilner, R.M. 2006. Function and evolution of color in young birds. In Hill, G. & McGraw, K. (eds) *Bird Coloration*: 201–232. London: Harvard University Press.
- Loiseau, C., Fellous, S., Haussy, C., Chastel, O. & Sorci, G. 2008. Condition-dependent effects of corticosterone on a carotenoid-based begging signal in house sparrows. *Horm. Behav.* **53**: 266–273.
- Lyon, B.E., Eadie, J.M. & Hamilton, L.D. 1994. Parental choice selects for ornamental plumage in American Coot chicks. *Nature* **371**: 240–243.
- Mas, F. & Kölliker, M. 2011. Differential effects of offspring condition-dependent signals on maternal care regulation in the European Earwig. *Behav. Ecol. Sociobiol.* **65**: 341–349.
- McDonald, P.G., Wilson, D.R. & Evans, C.S. 2009. Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. *Behav. Ecol.* **20**: 821–829.
- Mock, D.W., Dugas, M.B. & Strickler, S.A. 2011. Honest begging: expanding from signal of need. *Behav. Ecol.* **22**: 1–9.
- Noble, D.G., Davies, N.B., Hartley, I.R. & McRae, S.B. 1999. The red gape of the nestling cuckoo (*Cuculus canorus*) is not a supernormal stimulus for three common cuckoo hosts. *Behaviour* **136**: 759–777.
- Parker, G.A., Mock, D.W. & Lamey, T.C. 1989. How selfish should stronger sibs be? *Am. Nat.* **133**: 846–868.
- Parker, G.A., Royle, N.J. & Hartley, I.R. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philos. Trans. R. Soc. B* **357**: 295–307.
- Redondo, T. & Castro, F. 1992. Signalling of nutritional need by magpie nestlings. *Ethology* **92**: 193–204.
- Remes, V. 2003a. Breeding biology of the Blackcap *Sylvia atricapilla* in the Czech Republic: an analysis of nest record cards. *Sylvia* **39**: 25–34.
- Remes, V. 2003b. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap *Sylvia atricapilla*. *Conserv. Biol.* **17**: 1127–1133.
- Saino, N., Calza, S., Martinelli, R., De Bernardi, F., Ninni, P. & Møller, A.P. 2000. Better red than dead: carotenoid-based mouth coloration reveals infection in Barn Swallow nestlings. *Proc. R. Soc. Lond. B* **267**: 57–61.
- Saino, N., Ambrosini, R., Martinelli, R., Ninni, P. & Møller, A.P. 2003. Gape coloration reliably reflects immunocompetence of barn swallow (*Hirundo rustica*) nestlings. *Behav. Ecol.* **14**: 16–22.
- Scheafer, T. 2004. Video monitoring of shrub-nests reveals nest predators. *Bird Study* **51**: 170–177.
- Smith, H.G. & Montgomerie, R. 1991. Nestling American Robins compete with siblings by begging. *Behav. Ecol. Sociobiol.* **29**: 307–312.
- Storch, D. 1998. Densities and territory sizes of birds in two different lowland communities in eastern Bohemia. *Folia Zool.* **47**: 181–188.
- Thorogood, R., Ewen, J.G. & Kilner, R.M. 2011. Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. *Proc. R. Soc. Lond. B* **278**: 2638–2645.

- Węgrzyn, E. & Leniowski, K.** 2011. Nest site preference and nest success in Blackcaps *Sylvia atricapilla* in Poland. *Ardeola* **58**: 113–124.
- Weidinger, K.** 2000. The breeding performance of Blackcap *Sylvia atricapilla* in two types of forest habitat. *Ardea* **88**: 225–233.
- Weidinger, K.** 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *J. Anim. Ecol.* **71**: 424–437.
- Weidinger, K.** 2007. Handling of uncertain nest fates and variation in nest survival estimates. *J. Ornithol.* **148**: 207–213.
- Whittingham, L.A., Dunn, P.O. & Clotfelter, E.D.** 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. *Anim. Behav.* **65**: 1203–1210.
- Wright, J. & Leonard, M.L.** 2002. *The Evolution of Nestling Begging: competition, Cooperation and Communication*. Dordrecht: Kluwer Academic Press.

Received 2 November 2011;
revision accepted 12 September 2012.
Associate Editor: Keith Tarvin.