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Begging blue tit nestlings discriminate between the odour of familiar and unfamiliar conspecifics

Marta Rossi^{1,2}, Reinaldo Marfull³, Sarah Golüke¹, Jan Komdeur³, Peter Korsten^{*†}¹ and Barbara A. Caspers^{*†}¹ 

¹Department of Animal Behaviour, Bielefeld University, Bielefeld, Germany; ²School of Life Sciences, University of Sussex, Falmer, Brighton, UK; and ³Behavioural Physiology and Ecology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

Summary

1. Offspring often solicit, and compete for, limited parental care by elaborate begging behaviour. Kin selection theory predicts that competing offspring should modify the intensity of their begging depending on the degree of relatedness to their nest- or litter-mates.
2. Empirical evidence in birds, which are a key model in the study of parent-offspring interactions, indeed indicates that a lower level of relatedness between offspring in the nest correlates with more intense begging (i.e. more ‘selfish’ behaviour). This implies that competing nestlings can recognize kin, but the mechanism underlying such discrimination is unclear. Birds have long been thought to mainly rely on visual and auditory cues in their social communication, but there is now growing evidence for the importance of olfactory cues too.
3. To assess the potential importance of olfactory cues in modulating nestling begging behaviour, we experimentally tested in a free-living bird, the blue tit *Cyanistes caeruleus*, if nestlings discriminate and adjust their begging behaviour depending on their familiarity with a conspecific nestling odour stimulus.
4. We found that individuals responded with longer and more intense begging bouts to an unfamiliar compared with a familiar odour stimulus.
5. Our findings provide first evidence for a role of olfaction in modulating offspring begging behaviour in a wild bird population. Although our experiment cannot differentiate between the effects of familiarity and relatedness, it raises the interesting possibility that blue tit nestlings may also discriminate between odours of close kin and less related individuals, and adjust their begging behaviour accordingly. This hypothesis requires further testing.

Key-words: avian olfaction, chemical signalling, *Cyanistes caeruleus*, kin recognition, sibling competition

Introduction

In many animals, the offspring are dependent on parental care in the form of food, shelter or protection from predators. Dependent offspring often solicit and compete for limited care through begging behaviour. Begging comes along with costs (e.g. Rodríguez-Gironés, Zúñiga & Redondo 2001; Magrath *et al.* 2010; Andrews & Smiseth 2013; but see Chappell & Bachman 2002), and is thought to signal offspring need (‘hunger’), as begging generally intensifies when offspring are food deprived (e.g. Birds: Marques *et al.* 2011; Mammals: Bell 2008; Insects: Smiseth

& Moore 2007). However, begging intensity is not only influenced by the hunger level of the offspring (Boncoraglio, Caprioli & Saino 2009; Lucass *et al.* 2016), but also by their sex, age and size (Lotem 1998; von Engelhardt *et al.* 2006; Bonisoli-Alquati *et al.* 2011), as well as the degree of relatedness among competing offspring (Briske, Naugler & Leech 1994; Boncoraglio & Saino 2008; Boncoraglio, Caprioli & Saino 2009).

In accordance with predictions from kin selection theory (Hamilton 1964), a comparative study across different bird species has shown that begging intensities of competing offspring are increased in species that have higher rates of extra-pair paternity and consequently lower levels of average relatedness within their broods (Briske, Naugler & Leech 1994). The interpretation of this finding is that

*Correspondence authors. E-mail: peter.korsten@uni-bielefeld.de, barbara.caspers@uni-bielefeld.de

†Shared last authorship.

competing offspring in the nest are selected to behave more 'selfishly' and consequently beg more intensely when the average degree of relatedness among nest-mates is lower. In line with this, two recent studies on barn swallows (*Hirundo rustica*) have found that offspring begging intensities increase when relatedness among nest-mates is reduced as a result of experimental cross-fostering (Boncoraglio & Saino 2008; Boncoraglio, Caprioli & Saino 2009). Both of these studies showed that nestlings beg louder in the presence of unrelated nest-mates, independent of whether cross-fostering had been carried out pre- (Boncoraglio & Saino 2008) or post-hatching (Boncoraglio, Caprioli & Saino 2009). These results suggest that nestlings are capable of kin recognition in the nest. But the mechanisms underlying this capability to recognise kin are as yet unclear (Boncoraglio & Saino 2008; Boncoraglio, Caprioli & Saino 2009).

Most work on kin recognition in birds has focused on the importance of acoustic cues (Komdeur & Hatchwell 1999; Nakagawa & Waas 2004; Sharp *et al.* 2005; Boncoraglio & Saino 2008). So far, the potential role of olfactory cues in bird social communication and particularly kin recognition has been little studied (Nakagawa & Waas 2004), even though olfaction is known to play a crucial role in kin recognition in other vertebrate taxa, including fish, amphibians, reptiles and mammals (Hepper 1991). Although long underappreciated, birds, including passerines, have a well-developed sense of smell. Birds use their sense of smell to navigate and orientate (Gagliardo 2013), locate food (Nevitt, Veit & Kareiva 1995; Amo *et al.* 2013), avoid predators (Amo *et al.* 2008; Eichholz *et al.* 2012; Zidar & Løvlie 2012) and recognise their nest (Minguez 1997; Bonadonna *et al.* 2003; Caspers & Krause 2011). Furthermore, birds have been documented to manipulate the olfactory nest environment by adding aromatic plants that may act as a courtship signal (Brouwer & Komdeur 2004) or reduce nest microbes (Gwinner & Berger 2005; Mennerat *et al.* 2009a) and parasites (Lafuma, Lambrechts & Raymond 2001).

There is now also growing evidence that birds use olfactory cues in social communication (reviewed in Hagelin & Jones 2007; Caro, Balthazart & Bonadonna 2015). These olfactory cues may mainly originate from preen gland secretions (reviewed in Campagna *et al.* 2012), of which the chemical profiles can hold information about species (Soini *et al.* 2013; Krause *et al.* 2014) and sex (Whittaker *et al.* 2010; Amo *et al.* 2012), as well as individual identity (Whittaker *et al.* 2010; Leclaire *et al.* 2011), including information about genetic variability and relatedness (Leclaire *et al.* 2012, 2014). Birds may use such olfactory information in partner recognition and mate choice (Bonadonna & Nevitt 2004; Whittaker *et al.* 2013; Leclaire *et al.* 2014), and for recognising kin (Bonadonna & Sanz-Aguilar 2012; Krause *et al.* 2012; Caspers, Gagliardo & Krause 2015a). However, whether olfactory cues from nest-mates can also influence the intensity of sibling

competition depending on the relatedness of competing nest-mates is unknown.

The present study aims to investigate whether olfactory cues from nest-mates have the potential to influence the begging behaviour of competing nestlings by testing the begging response of blue tit nestlings to an olfactory stimulus originating from familiar vs. unfamiliar conspecifics. Very recently, a study on captive zebra finches (*Taeniopygia guttata*) has demonstrated that begging duration in response to different odour stimuli can be used to investigate odour discrimination in 1-day old nestlings (Caspers *et al.* 2015b). Previously, it has also been reported that 1-day old domestic chicks (*Gallus gallus domesticus*) differ in their behavioural responses to different artificial odour stimuli (Porter *et al.* 1999).

We performed our study on a natural population of blue tits (*Cyanistes caeruleus*). Blue tits appear well-suited for investigating the influence of olfactory cues on offspring begging behaviour and the potential importance of olfaction in modulating sibling competition. Blue tits have a well-developed sense of smell, as has been revealed from behavioural (foraging: Mennerat *et al.* 2005; nest building: Petit *et al.* 2002; Mennerat *et al.* 2009a,b; predator avoidance: Amo *et al.* 2008) and molecular genetic studies (Steiger *et al.* 2008). These molecular genetic studies indicate the presence of functional olfactory receptor genes in blue tits (Steiger *et al.* 2008). To test for the potential importance of olfactory cues from nest-mates in modulating nestling begging behaviour, we presented two conspecific odour stimuli differing in familiarity to 7-day-old blue tit nestlings in a standard test procedure and measured the nestlings' subsequent begging responses.

Materials and methods

EXPERIMENTAL APPROACH

The two odours presented to the 7-day-old blue tit nestlings originated either from themselves plus another chick of their own nest (i.e. a familiar odour), or from two unfamiliar chicks of another nest (for a schematic representation of the experimental design see Fig. 1). Note that the nestlings' odours may not only consist of their own body odour, but also of the odour of their nest. Tests in which we presented each of the two odours consecutively were conducted three times per nestling, while increasing the duration of food deprivation to increase the likelihood that the nestlings showed a begging response (Fig. 1). Nestlings may differ in their begging responses to the two odour stimuli, if they are able to discriminate between them.

STUDY POPULATION AND GENERAL FIELD METHODS

We carried out the odour discrimination experiment in a nestbox population of blue tits at the estate 'De Vosbergen' (53°08'N, 06°35'E) near Groningen, the Netherlands, during the breeding season of 2015. The area contains 210 nestboxes which we visited regularly from March onwards to record lay date of the first egg, clutch size, onset of incubation, and hatching day of the first chick. For a more detailed description of general field procedures see Korsten *et al.* (2006). Odour discrimination test trials were

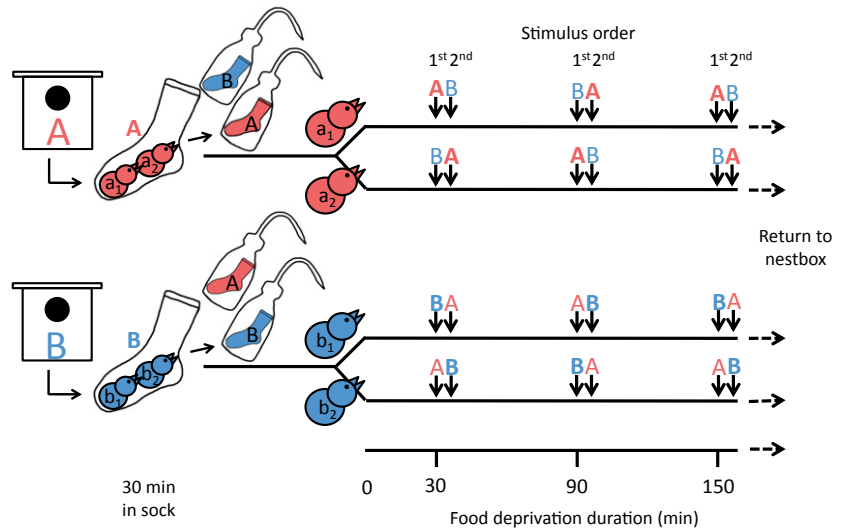


Fig. 1. Schematic representation of the experimental procedure. The order of odour stimulus presentation was alternated among nestlings and test runs (i.e. at 30, 90, 150 min). Capital letters indicate the brood identity of the odour sample. Lower-case letters indicate the brood identity of the tested nestlings; subscripts indicate the individual nestlings.

carried out in the centrally located field station to which we transported the nestlings for olfactory testing. The nestlings were brought back to their own nest after the trials.

As part of another study running at the same time, brood size manipulations were carried out when broods were 4 days old (day of hatching of the first chick = day 0). By moving three nestlings from one brood to another, we created reduced and enlarged broods, respectively. In addition, equally aged broods were randomly assigned to a control treatment, in which no chicks were removed or added. All 4-day-old nestlings were weighed with electronic scales (0.01 g precision) before the brood size manipulations took place. For the odour discrimination experiment, we only included nestlings from reduced ($n = 14$), control-treated broods ($n = 15$) and unmanipulated broods ($n = 17$) that were not part of the brood size manipulation experiment, to ensure that the test nestlings had only experienced their own original brood's odour before the odour discrimination experiment (mean natural brood size, before manipulation: 10.30 ± 1.88 SD, $n = 46$).

ODOUR DISCRIMINATION EXPERIMENT: SELECTING CHICKS FOR OLFACTORY TESTING AND OBTAINING ODOUR SAMPLES

To run the odour discrimination trials we created sets of two 7-day-old broods (dyads) from which we selected nestlings for olfactory testing (Fig. 1). For this, we only included nestlings from broods with six or more chicks to avoid brood desertion by the parents (mean brood size after manipulation: control broods, 10.40 chicks ± 1.36 SD, $n = 15$; reduced broods, 8.43 chicks ± 1.40 SD, $n = 14$, unmanipulated broods, 9.29 chicks ± 2.06 SD, $n = 17$). From each of the two broods in the dyads, we selected the two nestlings with the lowest body mass (as when weighed on day 4), which had their eyes still closed, for olfactory testing. We chose to test the lightest nestlings of the brood, because smaller, more junior nestlings tend to be more responsive when stimulated to beg than the relatively heavier and older ones (Bonisoli-Alquati *et al.* 2011; R. Marfull, J. Komdeur and P. Korsten, unpubl. data). Furthermore, the lightest nestlings of the brood are likely to originate from the last-laid eggs which are known to have low levels of extra-pair paternity in our study population (Magrath *et al.* 2009; Vedder *et al.* 2013). Within each of the brood dyads, test nestlings were individually tested and confronted with two different conspecific stimulus odours, one of which was familiar, i.e. of themselves plus their sibling, and one was unfamiliar, i.e. of the two nestlings of the other brood in the

dyad (Fig. 1). For two of the 46 tested broods, we used two nestlings of an enlarged brood to obtain the unfamiliar stimulus odour, as in these two cases it was not possible to create a dyad with a control, reduced or unmanipulated nest. These two enlarged broods did not contain additional nestlings originating from either one of the two tested broods.

To obtain odour samples of the nestlings, we transported each pair of siblings to the field station in a nylon sock (63% polyamide, 37% cotton, Söckchen Naturelle 60, NUR DIE, DBA Deutschland, GmbH, Rheine, Germany; for details see Krause *et al.* (2014). During the transport, each sock containing a pair of nestlings was placed separately in a closed plastic container (still permitting flow of fresh air through holes in the lid) lined with fresh cotton wool. The containers with the chicks were kept warm with a hot-water bottle during transport. After arrival at the field station, the nestlings were kept in the sock until they had stayed there for a total time of 30 min to standardize the time of odour impregnation (Fig. 1). After 30 min, the nestlings were removed from the socks, weighed (0.01 g precision), and individually placed in a warmed and insulated test chamber for the duration of the test trial. Using containers with warm water, we kept the temperatures of the test chambers between 26 and 33 °C.

Each sock, which we assumed to contain the nestlings' body odours (Mardon & Bonadonna 2009; Krause *et al.* 2014), was put separately and inside-out into a clean 500-mL wide neck wash bottle (Rotilabo, Carl Roth) for odour stimulus delivery (Caspers, Gagliardo & Krause 2015a). To ensure that the experimenter (MR) was blind with respect to the brood identity of the odour sample, the bottles with the odour stimulus were prepared by a second person. After each experimental session, bottles and socks were washed with odourless soap (Eubos Wasch + Dusch, perfume-free). Thereafter, the bottles were additionally rinsed with ethanol to remove any potentially remaining blue tit odour.

ODOUR DISCRIMINATION EXPERIMENT: TEST PROCEDURE

We developed the odour discrimination test procedure by combining a begging test protocol previously applied to wild blue tits (Lucass *et al.* 2016) and an olfactory test protocol based on individual begging responses previously applied to zebra finches in the laboratory (Caspers *et al.* 2015b). Directly after being placed individually in the test chamber, each nestling was stimulated to beg and fed with a maximum of three defrosted fly larvae (purchased at the local pet shop and normally used as fishing bait), depending

on the nestlings appetite, in order to 'equalise' the nestlings' hunger level at the start of the odour test trials (for details on the feeding protocol see Supporting Information, Data S1). After being fed, each nestling was covered with a dark cloth to reduce heat dissipation and provide a quiet environment, and the test chamber was closed with a carton lid. From this moment onwards the nestlings were food deprived. We provided odour stimuli to the chicks at three different time points, i.e. 30, 90 and 150 min after the onset of food deprivation.

During each test, we gently opened the test chamber, removed the cloth, and once the nestling was motionless again, we started the odour discrimination test procedure (method adapted from Caspers *et al.* 2015b). To provide an odour stimulus and induce the nestling's begging behaviour, we directed soft puffs of air from the wash bottle containing the odour sample, within 2 cm of the nestling's head. This odour stimulus comprised both a chemical and a tactile stimulus caused by the air flow. Each odour sample was presented by pressing the bottle five times (c. 1 puff per second). The two odour samples (familiar and unfamiliar, see above) of each dyad of broods were presented sequentially (Fig. 1) to each of the nestlings, and their immediate begging responses were recorded with a video camera (AIPTEK AHD H500, AIPTEK International Inc., Hsin-Chu, Taiwan). Since the familiar and unfamiliar stimulus odours were presented in sequence, the experimenter waited after the first stimulus until the nestling was motionless again before presenting the second stimulus. To control for a potential stimulus order effect (e.g. nestlings may respond more strongly to the first stimulus presented) the order of the familiar and unfamiliar odour stimuli was alternated both across the two test nestlings of each nest and the different tests (i.e. at 30, 90 and 150 min after the onset of food deprivation). The order of the familiar and unfamiliar odours at the first test of the two nestlings (at 30 min) was randomly assigned (see Fig. 1). After finishing the odour discrimination trial (i.e. after 150 min from the start of the food deprivation), the nestlings were fed until satiation with hand-rearing food for young birds (Orlux Handmix, Versele-Laga, Belgium; following Lucass *et al.* (2016)), before returning them to their nest.

ETHICAL NOTE

None of the nestlings were harmed by the test procedure. Nestlings were on average slightly heavier after they had been fed at the end of the experimental trials than at the start of the trials before the food deprivation (mean body mass at the start of the trials: 5.84 g \pm 0.11 SE; mean body mass after the hand-feeding at the end of the trials: 5.93 g \pm 0.11 SE; paired *t*-test -3.865 , d.f. = 91, $P < 0.001$).

Survival until 15 days of age when nestlings were weighed for the last time before fledging was similar for nestlings included in the odour discrimination test trials and other nestlings in the population that were not tested (tested: 93.5% alive, $n = 92$; non-tested: 95.8% alive, $n = 623$). Mean body mass at 15 days of age was also similar for tested and non-tested nestlings (tested: 10.96 g \pm 0.12 SE, $n = 86$; non-tested: 10.98 g \pm 0.04 SE, $n = 595$). More detailed statistical analyses of the effect of the odour discrimination test trials on nestling survival and body mass at 15 days of age which controlled for nestling body mass at 4 days of age as well as for the brood size manipulation treatment confirmed the absence of negative effects of the odour discrimination test trials on nestling growth and survival (Tables S1 and S2). These analyses showed that survival was not different between tested and untested nestlings (Wald $F = 0.011$, d.f. = 1, 708.0, $P = 0.91$; Table S1) while body mass at 15 days of age of nestlings included in the begging test trials was on average slightly higher (+0.207 g \pm 0.085 SE; Wald $F = 2.621$, d.f. = 1, 630.4, $P = 0.015$; Table S2) compared with nestlings

not included, which may be the result of selection of generally healthy broods with a minimum size of six nestlings for the odour discrimination test trials.

The study was conducted in full compliance with Dutch law and regulations. The experiment was approved by the animal ethics committee of the University of Groningen (Institutional Animal Care and Use Committee, DEC-RUG, Project number: DEC 6981B).

ODOUR DISCRIMINATION EXPERIMENT: PROCESSING OF THE RECORDED BEGGING RESPONSES

Video recordings of the nestlings' begging behaviour in response to the odour stimuli were analysed by an observer who was blind to the stimulus odour (familiar/unfamiliar) (MR). The begging responses were quantified both in terms of the duration of the begging bouts and the intensity of the begging behaviour following a scoring method adapted from Lucass *et al.* (2016) (see Data S2, including Fig. S1 and Table S3). The begging bout duration was measured from the moment the nestling opened its beak in response to the odour stimulus till the moment the nestling closed its beak for longer than 1 s. We used VLC media player (www.videolan.org) with the plugin 'Jump to time v2.1' (addons.videolan.org) to measure time in centiseconds (0.01 s). Importantly, the results are qualitatively similar when using begging intensity scores instead of begging duration (Table S4).

STATISTICAL ANALYSIS

To assess whether nestlings differed in their begging responses to the familiar and unfamiliar stimulus odours we carried out a two-step analysis. Briefly, in the first step, we analysed whether the likelihood of a response, i.e. whether a nestling begged or not, was dependent on odour stimulus type (familiar/unfamiliar). In the second step, after excluding all tests without a response, we analysed whether the duration or intensity of the begging responses depended on odour stimulus type. In our statistical models, we controlled for a number of additional variables that may affect the nestlings' begging responses (see below). The total sample consisted of 92 individual nestlings from 46 broods, which were each tested three times (i.e. after 30, 90 and 150 min of food deprivation), each time with both of the stimulus odours (i.e. familiar and unfamiliar). Hence, the total number of tests (observations) was 552 (92 individuals \times 3 replicates \times 2 odours).

The statistical analyses were carried out in R version 3.1.3 (R Core Team, 2015) using the ASREML-R software, version 3 (Gilmour *et al.* 2009). First, to test whether the likelihood of a begging response (yes/no) was dependent on odour stimulus type (familiar/unfamiliar) we implemented generalized linear mixed models (GLMMs) with a binomial error distribution and a logit link function, which included all tests on the 92 nestlings ($n = 552$ observations). In addition to (i) odour stimulus type (familiar/unfamiliar), we also included the following predictor variables to control for their potential influence on the nestlings' begging responses: (ii) food deprivation duration as a factor with three levels (30, 90 and 150 min); (iii) odour stimulus order as a factor (first/second); (iv) focal chick body mass as a continuous variable (in g); and finally, (v) we included the brood size manipulation treatment of the nestling's brood as a factor (reduced/control/unmanipulated). To aid the interpretation of the estimated model coefficients, we mean-centred focal chick body mass before inclusion in the model (Schielzeth 2010). To account for the non-independence of multiple observations on the same individual chicks (in total six olfactory tests per nestling), and of the two chicks of the same brood, we included chick and brood identity (ID) as random effects in the model. Chicks were nested within broods.

Subsequently, to test whether the duration of the begging response depended on the stimulus odour (familiar/unfamiliar), we employed linear mixed models (LMMs), after first excluding all tests (observations) without a begging response. This analysis was carried out on a subset of 177 tests (observations) on 69 nestlings from 42 nests. In addition to odour stimulus type, we included the same set of predictor variables to control for their potential influences on the intensity and duration of the begging responses as in the analysis of the likelihood of a begging response (yes/no) described above. Again, nestling and brood ID were included as random effects, with chicks nested within broods, to account for the non-independence of observations on the same nestlings and of nestlings of the same brood. Nestling body mass was mean-centred again before inclusion in the model as predictor.

All main effects were kept in the models regardless of their significance to avoid inflation of type-I error rates (Mundry & Nunn 2009; Forstmeier *et al.* 2011). We also tested for significant effects of the two- and three-way interaction(s) among food deprivation duration and odour stimulus type and stimulus order. None of the interaction terms were significant and we excluded them from the final model. We confirmed the validity of all statistical models by visual inspection of the residuals for normality, heteroscedasticity and nonlinear patterns. *P* values of the predictors were inferred from conditional Wald *F* tests as implemented in ASR_{EML-R}. We considered *P* values <0.05 to be significant.

Results

LIKELIHOOD OF BEGGING RESPONSE

Nestlings were increasingly likely to beg in response to the odour stimulus with increasing food deprivation duration (Fig. 2a; Table 1A). Nestlings were also more likely to respond to the first compared with the second odour stimulus (Fig. 2a; Table 1A). There was a significant effect of the mass of the focal nestling, with lighter nestlings being more likely to respond (Table 1A). The brood size treatment had no significant effect on the likelihood of begging (Table 1A). Finally, there was no significant difference between the proportion of nestlings responding to the familiar vs. the unfamiliar conspecific odour (Fig. 2b; Table 1A).

DURATION OF BEGGING RESPONSE

Next, for the subset of observations where the nestlings responded to the conspecific odour stimulus, we analysed whether the duration of the begging bouts differed depending on the familiarity of the stimulus odour (familiar vs. unfamiliar). Just as with the likelihood of response, the duration of food deprivation had a positive effect on the duration of the nestlings' begging responses (Fig. 2c; Table 1B). There was no significant difference in begging bout duration between the first and second stimulus presented (Fig. 2c; Table 1B). Again, lighter nestlings showed a significantly stronger response, i.e. longer begging bouts (Table 1B). The brood size treatment had no significant effect on the begging duration (Table 1B). Finally, odour stimulus type had a significant effect on begging bout duration. Nestlings begged about 1 s (14.0%) longer when

they were presented the unfamiliar stimulus odour (Fig. 2d; Table 1B). A model solely including odour stimulus type as a predictor (i.e. not controlling for any of the other predictor variables) also showed a significant effect of odour stimulus type (Wald *F* = 6.371, d.f. = 1, 139.5, *P* = 0.013). Note that a substantial part of the variance in begging duration (after controlling for the fixed effects) was explained by the random effect of brood ID (34.3%; Table 1B); nestling ID explained a smaller part of the total variance (3.7%; Table 1B). Results for begging intensity scores were similar (not shown here; for details see Table S4).

Discussion

Our experiments, performed on 7-day-old wild blue tit nestlings, confirmed that offspring solicitation behaviour is influenced by several factors, of which some are well-known to influence begging, such as the duration of food deprivation and the focal individual's body mass. Individuals were more likely to respond and begged longer and more intensely with increasing food deprivation, and also when having lower body mass. Furthermore, nestlings were less likely to respond to the second stimulus odour provided during each of the test trials, which may reflect an effect of short-term habituation to the stimulus. Moreover, our data reveal that the begging responses of blue tit nestlings are influenced by conspecific body odours. Nestlings showed longer and more intense begging bouts when presented with a stimulus odour originating from unfamiliar chicks compared with a familiar stimulus odour. This effect (i.e. on average 1 s longer begging to the unfamiliar odour stimulus) was in the same order of magnitude as the effect of 90–150 min of food deprivation (i.e. 2–2.5 s longer begging; see Table 1B and Fig. 2c,d). This indicates that blue tit nestlings have the capability to discriminate between familiar and unfamiliar conspecific odours. Thus, blue tit nestlings may have the potential to adjust their begging behaviour under natural conditions in response to such conspecific odour cues, including the odours of their nest-mates. This raises the interesting possibility that blue tit nestlings may also discriminate between odours of full-siblings and half-siblings, and adjust their begging behaviour accordingly.

Our finding is consistent with previous empirical work on barn swallows, which found more intense, louder begging by nestlings in the presence of unrelated nest-mates (Boncoraglio & Saino 2008; Boncoraglio, Caprioli & Saino 2009). At first sight, our finding of blue tit chicks begging more in response to the odour of unfamiliar, unrelated chicks may appear to reflect an adaptive behaviour consistent with kin selection theory (Hamilton 1964). However, it is important to note that in our experiment we cannot differentiate between the effects of familiarity and relatedness. Thus, it is as yet an open question what the biological significance of this observation is with regard to the natural situation where nestlings will normally not be

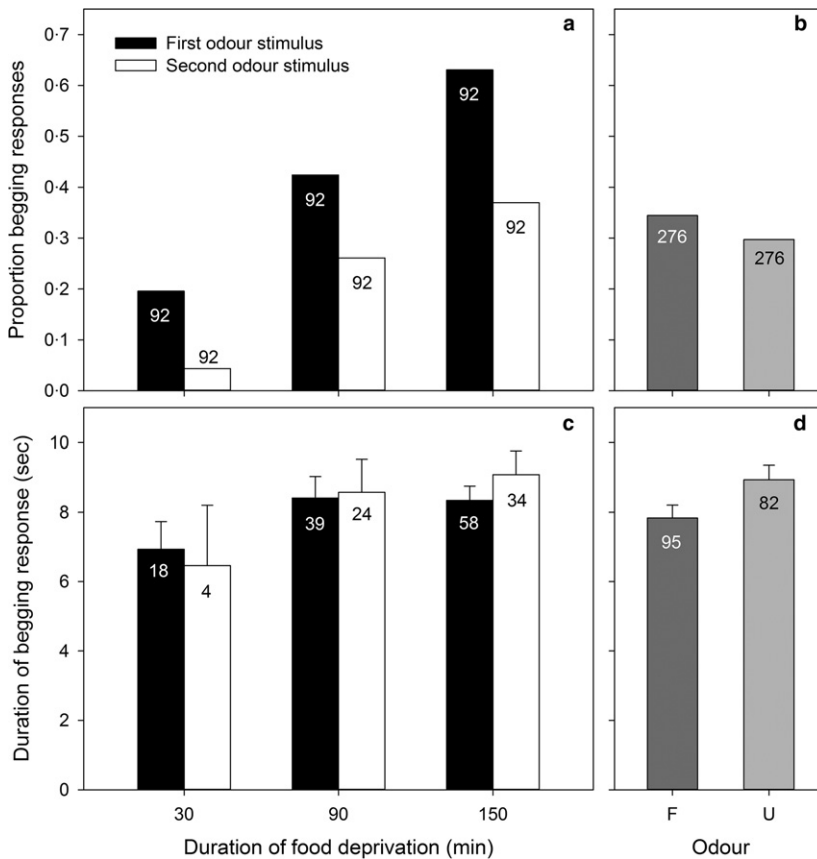


Fig. 2. Begging responses of blue tit nestlings to conspecific odour stimuli. The top panels (a, b) indicate the proportion of nestlings responding as (a) a function of the duration of food deprivation and the first vs. second stimulus presented, (b) as well as the familiarity of the odour stimulus (familiar: F; unfamiliar: U). The bottom panels (c, d) represent the mean (\pm SEs) duration of the begging bouts, as (c) a function of the duration of food deprivation and the first vs. second stimulus presented, (d) as well as the familiarity of the odour stimulus (familiar: F; unfamiliar: U). Plots are based on the raw data and the numbers in the bars provide the number of observations.

confronted with unfamiliar nest-mates, whereas they may encounter less related nest-mates, in case of naturally occurring mixed paternity. It would therefore be important to follow-up on this first finding with further work investigating whether such differential begging responses may also occur in relation to odours of familiar nest-mates varying in relatedness to the focal individual. Clearly, to be able to interpret differential begging behaviour in response to different conspecific odour stimuli as being adaptive, one would for example need to demonstrate that individuals beg more when presented with odour stimuli from paternal half-sibs compared with full-sibs.

Notably, first evidence from other bird species indicates that odour familiarity (i.e. through learning) may not always be required for olfactory kin recognition. For example, adult European storm petrels (*Hydrobates pelagicus*) have been reported to recognise unfamiliar kin based on olfactory cues (Bonadonna & Sanz-Aguilar 2012). Furthermore, barn swallow chicks were found to beg louder when faced with unrelated foster chicks in their nest, no matter whether the latter had been cross-fostered pre- (Boncoraglio & Saino 2008) or post-hatching (Boncoraglio, Caprioli & Saino 2009). Body odours, which have been shown to encode information about relatedness (Leclaire *et al.* 2012, 2014; Stoffel *et al.* 2015) might thus function in olfactory kin recognition, without prior learning. However, at this point, it remains to be investigated whether such olfaction-based kin recognition also occurs in blue tits. Further, we can only speculate on whether

blue tits may also use olfactory cues in other social contexts. However, given accumulating evidence from other bird species (European storm petrels: Bonadonna & Sanz-Aguilar 2012; starlings: Amo *et al.* 2012; dark-eyed juncos: Whittaker *et al.* 2013; zebra finches: Caspers, Gagliardo & Krause 2015a) and the fact that blue tits use olfactory cues in a variety of other situations (Petit *et al.* 2002; Mennerat *et al.* 2005, 2009a, b; Amo *et al.* 2008), it seems not unlikely that in addition to their visual and acoustic senses, blue tits may also use their sense of olfaction in other social situations, including mate choice.

A purely mechanistic explanation for the finding that nestlings begged more when presented with the odour of unfamiliar conspecifics may be the occurrence of long-term habituation to familiar odours of conspecifics to which individuals are continually exposed in the nest. Such habituation to odours is a well-known phenomenon, which is also commonly used in the standard habituation/dishabituation test paradigm (Johnston *et al.* 1993; Arbuckle *et al.* 2015). Individuals that are confronted repeatedly with the same odour habituate and show decreased responses. The presentation of another, distinct and novel odour stimulus can then elicit an increased response again. This phenomenon is widely used as a test paradigm to determine odour discrimination in mammals (Johnston *et al.* 1993; Arbuckle *et al.* 2015), and may also explain why blue tit nestlings show stronger begging responses to the unfamiliar stimulus odour. However, it should be noted that in a previous study on zebra finches, 1-day old chicks begged

Table 1. Summary of the statistical models predicting (A) the likelihood of a begging response (fitting the presence/absence) and (B) the duration (in seconds) of begging responses of blue tit nestlings in relation to the (1) familiarity of a conspecific odour stimulus (familiar/unfamiliar), as well as the level of (2) food deprivation (30, 90, 150 min), (3) odour stimulus order (first, second), (4) nestling mass (in g, mean centred) and (5) brood size manipulation category (unmanipulated, control, reduced). The likelihood of a begging response (A) was fitted by a generalized linear mixed model with a binomial error distribution and logit link function ($n = 552$ begging tests on 92 nestlings from 46 nests). The duration of the begging responses was fitted by a general mixed model with a Gaussian error distribution and identity link function ($n = 177$ tests on 69 nestlings from 42 nests). Brood ID and nestling ID were included as random effects. Significant terms are in bold. Nonsignificant interaction terms were excluded from the final model. For further details see the section on *Statistical analysis* in the Methods

Fixed effects	(A) Likelihood of begging response				(B) Duration of begging response			
	Coefficient (SE)	Wald <i>F</i>	d.f.1, 2	<i>P</i> value	Coefficient (SE)	Wald <i>F</i>	d.f.1, 2	<i>P</i> value
Included in final model								
Intercept	-1.944 (0.469)				4.719 (0.935)			
Odour (ref: familiar)	-0.332 (0.234)	2.021	1, 544.0	0.16	1.149 (0.458)	6.299	1, 134.4	0.013
Food deprivation (ref.: 30 min)	90 min: 1.886 (0.333)	35.230	2, 544.0	<0.001	90 min: 2.028 (0.754)	5.776	2, 134.6	0.004
	150 min: 2.856 (0.340)				150 min: 2.514 (0.740)			
Stimulus order (ref.: first)	-1.405 (0.244)	33.320	1, 544.0	<0.001	0.300 (0.477)	0.395	1, 130.5	0.53
Nestling mass (g)	-0.745 (0.209)	12.660	1, 68.8	<0.001	-0.780 (0.382)	4.173	1, 66.5	0.045
Brood size manipulation (ref.: unmanipulated)	Control: 0.519 (0.562)	1.823	2, 40.9	0.17	Control: 1.680 (1.086)	1.687	2, 41.2	0.20
	Reduced: -0.559 (0.567)				Reduced: -0.118 (1.097)			
Excluded								
Odour × Food deprivation		0.877	2, 539.0	0.42		1.181	2, 132.9	0.31
Odour × St. order		2.855	1, 543.0	0.092		0.285	1, 133.7	0.59
St. order × Food deprivation		1.141	2, 541.0	0.32		0.385	2, 128.1	0.68
Odour × F. deprivation × St. order		0.019	2, 142.9	0.98		0.550	2, 61.7	0.58
Random effects								
	Variance (SE)				Variance (SE)			
Brood ID	0.984 (0.565)				4.495 (1.747)			
Nestling ID	1.188 (0.523)				0.484 (1.060)			
Residual	-				8.126 (1.090)			

longer towards a familiar, albeit artificial, odour stimulus (i.e. orange oil) compared with a non-familiar stimulus (Caspers *et al.* 2015b).

Finally, we also found that a substantial proportion of the variance in begging duration was explained by between-brood variation (34.3% of the variance after controlling for the fixed effects). The causes for the observed similarity in begging behaviour of chicks of the same brood are currently unknown, but are likely due to shared genetic and environmental effects, the latter possibly also including differences in parental provisioning behaviour (Lucass *et al.* 2016) and prenatal maternal effects (reviewed by Müller *et al.* 2007; also see e.g. Hinde, Buchanan & Kilner 2009). A number of studies on different taxa have reported differences in offspring solicitation behaviour between broods or litters (Kölliker *et al.* 2000; Agrawal, Brodie & Brown 2001; Lock, Smiseth & Moore 2004; Lucass *et al.* 2016), which may also be (partly) genetic in origin (Agrawal, Brodie & Brown 2001; Lock, Smiseth & Moore 2004; Dor & Lotem 2009). Theory and empirical evidence suggests offspring solicitation and parental provisioning responses to be co-adapted within families, which will be reflected by (genetic) co-variation between parent

and offspring behaviours (e.g. Wolf & Brodie 1998; Hinde, Johnstone & Kilner 2010; Kölliker, Ridenhour & Gaba 2010). It would be worthwhile to also investigate in our study population whether the observed between-brood variation in offspring begging behaviour relates to parental provisioning responses, as has recently been reported for another blue tit study population (Lucass *et al.* 2016).

In conclusion, this study provides first evidence for a role of conspecific olfactory cues in modulating offspring solicitation behaviour in a natural bird population. Hence, olfaction, which has been previously demonstrated to act as a mechanism for kin recognition in birds, may also influence sibling competition depending on offspring relatedness. However, while our study strongly hints at the importance of olfaction in modulating sibling competition, follow-up work is necessary to test whether competing offspring also vary the level of begging depending on their relatedness per se.

Authors' contributions

B.A.C. and P.K. conceived of the experiment; M.R., P.K. and B.A.C. designed the experiment. M.R. carried out the experiment; R.M. and P.K.

provided assistance in the field to enable the experiment; M.R. analysed the video recordings; M.R., S.G. and P.K. carried out the data analyses; P.K. and J.K. coordinated the long-term blue tit population study; J.K. provided logistic support; M.R., P.K. and B.A.C. wrote the manuscript with input from S.G., R.M. and J.K.

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Data accessibility

The data acquired during this experiment are available on Dryad Digital Repository <https://doi.org/10.5061/dryad.q5b10> (Rossi et al. 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Nestling begging postures.

Table S1. Generalized linear mixed model predicting the survival probability of nestlings until 15 days of age depending on whether or not they were included in the odour discrimination test trials.

Table S2. General linear mixed model fitting the mass of nestlings at 15 days of age depending on whether or not they were included in the odour discrimination test trials.

Table S3. Overview of nestling begging scores.

Table S4. Summary of a general mixed model fitting the intensity score.

Data S1. 'Equalizing' hunger levels of nestlings.

Data S2. Scoring begging intensity.