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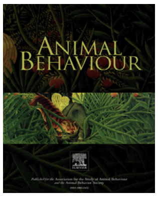

Blue tits do not return faster to the nest in response to either short- or long-term begging playbacks

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In species with parental care, offspring often solicit food through elaborate begging displays. Begging is thought to be a reflection of offspring need, but short-term fluctuations in begging do not necessarily provide reliable information. Parents thus have to adjust their provisioning behaviour to the changing demands of their offspring, while minimizing the costs of responding to unreliable information. We conducted two experiments with blue tits, *Cyanistes caeruleus*, in which we tested how parents respond to short-term and long-term changes in begging intensity. In the first experiment we investigated how parents respond to increased begging during a single nest visit. In the second experiment we investigated how parents respond to increased begging during every nest visit for 1 h. Parents did not return faster to the nest during the short-term manipulation. Contrary to our expectations, however, parents also did not return faster to the nest in response to long-term manipulation. Instead, parents spent more time in the nestbox during both the short-term and the long-term manipulation. Our results highlight that the general pattern of a positive parental response to increased begging may not be a universal one. Comparisons across species and populations may help reveal the factors underlying variation in parental responsiveness to begging.

In many animals, offspring solicit food from their parents by using elaborate begging displays, often including loud begging calls. Such begging is thought to be costly because it attracts predators and is energetically demanding (Godfray, 1991; Roulin, 2001, but see e.g. Glassey, Gunson, & Muir, 2014). Only those offspring for whom the benefits of receiving additional food outweigh the costs of begging should therefore display these signals, such that begging can provide parents with a reliable indicator of need (Godfray, 1991; Kilner & Hinde, 2008; Parker, Royle, & Hartley, 2002). Parents are then expected to benefit from attending to begging displays of their offspring and empirical work seems to support this (but see Caro, Griffin, Hinde, & West, 2016). For instance, house sparrow, *Passer domesticus*, parents that modify the provisioning of food in response to chick begging produce higher quality offspring than those that provide the same amount of food at random (Grodzinski & Lotem, 2007). Moreover, begging playback experiments typically find that adults adjust their provisioning behaviour to changes in begging intensity (reviewed in Budden & Wright, 2001; Kilner & Johnstone, 1997). For instance, yellow-headed blackbird, *Xanthocephalus xanthocephalus*, parents that were exposed to begging playbacks for 2 h doubled their rate of nest provisioning (Price, 1998), and both parents and helpers in the cooperatively breeding Arabian babbler, *Turdoides squamiceps*, substantially increased their rate of provisioning in response to 2–3 h begging playback periods (Wright, 1998). The general conclusion of these studies is that parents respond to increased begging calls by increasing their rate of provisioning (but see e.g. Clark & Lee, 1998; Ricklefs, 1987).

Although parents are expected to benefit from adjusting their provisioning behaviour to changes in the demands of their offspring, it may not be advantageous to indiscriminately respond to any short-term fluctuations in begging behaviour. First, because of the inherent risk of error in any communication system (Godfray & Johnstone, 2000; Wiley, 1994), parents that base their provisioning behaviour on limited information may fail to provide the amount of care with the greatest fitness payoff (Godfray & Johnstone, 2000; Kitamura, Fujita, & Higuchi, 2011). To minimize the probability of such errors, it may be beneficial for parents to use not only current, but also past information. This may especially be relevant in species in which nest visits are frequent and short such that reliable information is more likely to be gained from information gathered over longer time spans or from other sources (Hinde & Kilner, 2007; Kitamura et al., 2011). Indeed, when information gathered at the nest is incomplete or inaccurate, parents have been shown to rely on other cues, such as the behaviour of their partner, to adjust their provisioning behaviour

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(Hinde & Kilner, 2007; Johnstone & Hinde, 2006). Second, while the costs of begging may to some extent ensure its reliability, chicks that succeed in manipulating their parents into providing more care by exaggerating their level of need will nevertheless be at an advantage (Kilner & Hinde, 2008; Kölliker, Richner, Werner, & Heeb, 1998; Neuenschwander, Brinkhof, Kölliker, & Richner, 2003; Trivers, 1974). Indeed, observational studies and supplementary feeding experiments show that increased food intake does not always lead to reduced begging, and that begging intensity is therefore not necessarily a direct reflection of need (Grodzinski & Johnstone, 2012; Krebs, 2001; Lee, Choi, & Choe, 2011; Mock, Schwagmeyer, & Parker, 2005). Moreover, while long periods of begging may be costly, it has been shown that short-term begging may not necessarily be costly (Glassey et al., 2014; Moreno-Rueda, 2007a, Soler et al., 2014) and could therefore easily be exaggerated.

Parents thus have to balance responding to the changing needs of their offspring while minimizing the risk of using unreliable information or being exploited by manipulative offspring. Yet, most published studies report a positive response to begging playbacks (reviewed in Budden & Wright, 2001; Kilner & Johnstone, 1997; Tarwater, Kelly, Brawn, 2009), seemingly suggesting that parents indiscriminately respond to elevated begging levels. However, these studies have typically manipulated begging intensity for at least 1 h and sometimes for the entire provisioning period (e.g. Hinde, 2005; Ottoson, Backman, & Smith, 1997). How parents respond to shorter term variation in begging behaviour remains largely unknown. Zebra finches, *Taeniopygia guttata*, exposed to 2 min begging playbacks were more likely to feed during and 1 min after the playback (Muller & Smith, 1978) and red-winged blackbirds, *Agelaius phoeniceus*, exposed to playbacks during a single nest visit returned faster when the calls were all from the same chick than when the calls were from different chicks (Yasukawa, Urish, Her, & Light, 2008). This suggests that parents may be sensitive to short-term changes in begging. No studies, however, have experimentally examined whether parents change provisioning behaviour in response to an increase in begging during a single nest visit.

We conducted two experiments in which we tested the responsiveness of blue tit, *Cyanistes caeruleus*, parents to short-term and long-term changes in begging intensity. Earlier work showed that blue tit chicks increased begging when deprived of food (Dickens, Berridge, & Hartley, 2008), which suggests that parents may benefit if they respond to changes in begging intensity. Moreover, correlational work in blue tits showed that parents spent more time away from the nest following a visit during which the chicks did not beg (Grieco, 2001), suggesting that parents are responsive to immediate cues from their offspring. In the first experiment, we investigated how parents respond to increased begging during a single nest visit. In the second experiment we investigated how parents respond to increased begging during every nest visit for 1 h.

METHODS

Study Population

We studied a population of blue tits in the Westerholz forest near Landsberg am Lech, southern Germany (48°08′26″N, 10°53′29″E), during the 2015 breeding season. The study area is a mixed deciduous forest dominated by mature oak trees and contains 277 nestboxes of which 107 were occupied by blue tits. Blue tits are small (ca. 10–12 g) cavity-nesting passerines that are socially monogamous (although social polygyny sometimes occurs; Kempenaers, 1994). The female alone builds the nest and incubates the eggs, but both parents contribute extensively to nestling provisioning (Cramp & Perrins, 1993). Blue tits in our population produce up to 13 (mean ± SD $= 8.7 \pm 1.7$) offspring per breeding attempt and produce only one brood per year; the few cases where a replacement clutch was produced following the failure of the first attempt were not included in the experiments. Starting mid-March, all nestboxes were monitored at least once every week to determine the start of nest building, the start of laying, clutch size, hatch date and fledging success. For a more detailed description of the study site and general field procedures, see Schlicht, Girg, Loës, Valcu, and Kempenaers (2012).

Nest Visit Monitoring System

Each bird in the study was equipped with a passive integrated transponder (PIT, BIOMARK HPT8 animal tag 134.2 kHz FDXB, 8.4 mm × 1.4 mm, 0.03 g, Biomark, Boise, ID, U.S.A.) which was inserted under the skin on the back (as in Nicolaus, Bouwman, & Dingemanse, 2008). Some adults had been tagged during previous breeding attempts in our population, but most were caught with mist nests before the onset of breeding. Nest visits were recorded continuously at all nests with an automated monitoring system (see Schlicht et al., 2012 for details). Briefly, all nestboxes were equipped with a transponder reading device, a real-time clock, light barriers and a data storage device. Whenever a tagged bird passed through the nest hole, its identity, the associated time and date and the direction of its movement through the nest hole were automatically stored.

Recording of Begging Calls

To obtain chick begging calls for the playback experiments, recordings were made at a nearby blue tit population in Munich. This population has an earlier onset of breeding which allowed us to record the calls before our population had reached the stage that was the focus of our study (i.e. nest containing chicks of 9 or 12 days old). Begging calls were recorded from six nests containing 9-day-old chicks and six nests containing 12-day-old chicks. To standardize the begging recordings with respect to the number of chicks, broods of five chicks were created by temporarily removing any excess chicks. These excess chicks were kept warm and sheltered, and were returned to the nest immediately after the recording. A small microphone was placed against the inside wall of the nestbox, just under the surface of the nesting material, and connected to a Microtrack II (M-Audio, Cumberland, RI, U.S.A.) mobile digital sound recorder. The 1 h recordings were taken in uncompressed WAV format at a sampling rate of 44.1 kHz and bit depth of 24. The input level of the recorder was manually set to a level that yielded a high sound quality but was sufficiently low to prevent clipping. From each recording, we extracted 5–15 begging events with high begging intensity and minimal background noise. Following a burst of intense begging upon arrival of a parent at the nest, chick begging normally quickly diminishes and begging typically ceases within 15 s. Therefore, recordings were cut to include the first 15 s following the arrival of a parent at the nest and thus encompassed one complete begging event (see also Hinde, 2005). The amplitude of each extracted begging event was normalized for each chick age, such that all begging events of day 9 had the same amplitude and all begging events of day 12 had the same amplitude. Using Audacity (v1.2.6, http://audacityteam.org), background noise at frequencies below the range of blue tit calls was attenuated by applying a high pass filter at 1500 Hz (Bijnens & Dhondt, 1984; Doutlerant, Lematrei, & Lambrechts, 2001; McDonald, Te Marvelde, Kazem, & Wright, 2009). Together, we created a total of 50 different begging recordings from six nests with 9-day-old chicks and 50 different recordings from six nests with 12-day-old chicks. Examples of spectrograms of these recordings are provided in the Appendix (Fig. A1).