

Signature page

Do parents listen to their children?: Begging does not go unanswered in European Starlings (*Sturnus vulgaris*)

By
Hannah Beth Corney

A Thesis Submitted to
Saint Mary's University, Halifax, Nova Scotia
in Partial Fulfillment of the Requirements for
the Degree of Bachelor of Science.

March, 2017, Halifax, Nova Scotia

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Abstract

Begging by nestling passerines is an important method of communicating to parents their state of hunger. I examined whether experimentally increased nestling begging in a brood can quickly alter parental provisioning rates in European Starlings (*Sturnus vulgaris*). I predicted that an increased begging level heard by parents during the experimental treatment would result in a significantly higher number of parental provisioning visits compared to the control through a matched pairs design. Twenty nestbox broods were studied to compare the total number of parental provisioning visits during natural (control) and experimentally increased begging conditions. Begging calls of each brood were recorded when nestlings were 13 days old, and the loudest calls from each brood were made into a three-minute loop that ran continuously for one hour during the experimental treatment. On day 14, the total number of provisioning trips made by parents was first determined over a one-hour control watch (natural begging conditions), and then over a one-hour experimental watch (when the begging audio loop playback was projected). As predicted, parents provisioned at a significantly higher rate during the experimental treatment than the control. This finding suggests that European starlings are very sensitive to begging calls made by their offspring, and respond quickly to any changes in begging.

April 20, 2017

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Introduction

Vocal signals are a widespread form of communication in animal taxa that can convey a large amount of information over long distances. For example, alarm calls in social species alert conspecifics of danger (e.g. Dunford, 1977; Leavesley, 2005; Soltis, 2014). Vocal communication can also be used during courtship to signal an animal's species, sex, availability to mate, age, and quality (Mountjoy & Lemon, 1996; Yahner, 2011). Similarly, in species with parental care, offspring often vocalize to parents to indicate their needs for food and/or warmth (birds: e.g. Leonard & Horn 2001, reptiles: e.g. Chabert, 2015; mammals: e.g. Kober, 2007).

Parent-offspring vocal communication can increase the survival rate of the young (e.g. Kumar, 2003). For example, the Nile crocodile's (*Crocodylus niloticus*) young emit calls from within the egg just prior to hatch (Vergne, 2009). These pre-hatch calls elicit maternal behaviours such as nest defense and guiding the mother to the location where her young are buried (Somaweera, 2012). Pre-hatch calls also mediate hatching coordination among siblings (Vergne, 2008) and encourage group cohesion (Vergne, 2011). Mother crocodiles can determine the relative size of the individuals within her brood based on their calls (Chabert, 2015), and respond defensively more often to the higher pitch cries of smaller offspring, as they suffer a higher risk of predation (Somaweera, 2013).

Acoustic parent-offspring communication is found within most avian species. Birds are well known for their vocalizations which are usually classified as calls and songs. Calls are short in length, and have a simple acoustic structure (Kumar 2003), yet contain enough information to transmit the identity of the sender to conspecifics

(Catchpole, 1986). Examples of parental calls to offspring are alarm calls (Randler, 2013) and arrival calls (Raihani, 2007). Nestlings use calls when begging to signal hunger (Kilner, 1999), or as a response to sibling rivalry (nestlings are begging for food, inciting siblings to competitively beg for food as well) (Harper, 1986). Avian songs are more complex, longer in duration than calls, and are used by temperate-breeding passerines in courtship and territory maintenance (Mountjoy & Lemon, 1996).

Altricial bird species are those in which the young are hatched blind, naked and completely dependent upon their parents (Nilsson, & Svensson, 1993). These nestlings (birds too young to leave the nest) and fledglings (birds that have flown from the nest) rely on begging calls to convey their need for food to provisioning parents (e.g. Harper, 1986; Cotton et al., 1996; Maurer et al., 2003). The intensity of begging has been shown to signal the degree of hunger in food-deprived nestlings (e.g. von Haartman, 1953; Leonard & Horn, 2001). Begging behaviour influences the number of provisioning visits by parents (Bengtsson & Rydén, 1983), and the amount of food received, with nestlings that begged more intensely receiving a larger portion of the food (Stamps et al., 1989; Smith & Montgomerie, 1991).

Avian begging also involves behaviours other than vocalizations such as standing in the nest with necks outstretched, gaping with beaks wide open, and wing-flapping (Briskie, 1999). Begging nestlings increase their vocalization pitch, and jostle each other for position by the nest entrance, to increase their chances of being fed first by the incoming parent (Kacelnik et al., 1995). Begging primarily occurs when a parent arrives at the nest, but can also occur while parents are absent (Leonard & Horn, 2001). In some species, the intensity of begging signals the degree of hunger in food-deprived nestlings (e.g. von Haartman, 1953; Leonard & Horn, 2001).

Begging is central to parent-offspring communication in avian species and is accompanied by costs, which aid in keeping the nestlings honest in communicating their needs to parents, thereby setting begging to be a reliable signal (Harper, 1986; Godfray, 1991 & 1995). The effort of displaying and vocalizing hunger requires an energetic expenditure, albeit a fairly minor one (e.g. McCarty, 1996; Verhulst & Wiersma, 1997; Weathers et al., 1997). Parents adjust how often to feed the young based on the intensity of their begging (Leonard & Horne, 2001). The predominant cost of begging, however, is that it can reveal the nest location to potential predators (Leech & Leonard, 1996). Playbacks of recorded begging calls subsequently increased the rate of predation on both artificial cup nesters and artificial cavity nesters (Haskell, 1994; Leech & Leonard, 1997; Haff & Magrath, 2011). Despite the danger begging presents to nestlings, and therefore, current parental reproductive success, conspicuous solicitation (loud and long-duration begging calls) has persisted. With these costs in mind, well-fed nestlings should beg less intensely, as the benefit of receiving food may be outweighed by the potential risk of predation associated with loud begging calls (Leonard & Horn, 1998). However, when nestlings are starving, the risk of possible predation is outweighed by the need for food (Redondo & Castro, 1992).

Alternatively, conspicuous begging may not have arisen through honest signalling, but through sibling rivalry. Godfray's (1995) research provides support for the existence of sibling competition, also known as the competitive begging model. This model predicts that individual nestlings are influenced by the behaviour of their siblings within the nest, begging more intensely when competing with others for food delivered by parents (Godfray, 1995; Price & Ydenberg, 1995; Price, 1996). Nestling vocalizations in competitive begging are explained not as an honest indicator of need, but instead are a

means for nestlings to obtain more resources from parents through encouraging increased provisioning visits, at the expense of other current and future siblings (Trivers, 1974; Smith & Montgomerie, 1991). With increased brood size, each chick receives less food as parents have a lower per-chick provisioning rate (Wright & Cuthill, 1990). Consequently, larger brood sizes create increased sibling rivalry (Price, 1996). Alternatively, honest signalling and sibling rivalry may not be mutually exclusive with conspicuous begging arising from both honest signalling and sibling competition. Begging by nestling European robins (*Turdus migratorius*; Smith and Montgomerie, 1991) and Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*; Price 1996) was attributed to nestling hunger as well as sibling rivalry.

Parental provisioning rates are affected not only by individual nestling begging, but also by the behaviour of the entire brood (Bengtsson & Rydén, 1983). Higher feeding rates were observed in species such as the Great Tit (*Parus major*; Bengtsson & Rydén), and Red-winged Blackbirds (*Agelaius phoeniceus*; Burford et al., 1998), when begging call playbacks were artificially added to the natural begging calls (but see Clark & Lee 1998). An increase in parental provisioning rates may therefore be explained by the overall intensity of begging by the brood rather than by the number of individuals within the brood (Bengtsson & Rydén, 1983). In playback studies, projections of previously recorded nestling begging playbacks is typically chosen over amplifying the naturally occurring begging calls in real time, as the playbacks project consistently over the experimental trial, even when the nestlings themselves are not begging. This is important as begging primarily occurs when a parent arrives at the nest, and studies testing the effects begging has on provisioning adults need begging to occur constantly and consistently (Leonard & Horn, 2001).

Two studies on European starlings (*Sturnus vulgaris*) manipulated hunger levels of nestlings, and found support for the honest signalling hypothesis for begging, but not for that of sibling competition (Kacelnik et al., 1995; Cotton et al. 1996). However, not much work has been done concerning the effects of experimentally increased begging on parental behaviour in the North American populations of European starlings. European starlings are an excellent model species, as they are the third most prevalent bird species in North America. Additionally, they are easy to work with since they breed in nestboxes, and are hardy passerines that easily withstand handling by humans. Starlings also raise two broods in one breeding season (Feare, 1984), effectively doubling the potential sample size for my experiment.

European starlings are a medium-sized passerine weighing 75-100g and approximately 20cm in length. They are cavity-nesters with females laying 3-7 pale greenish-blue eggs per clutch (Feare, 1984). Eggs are incubated for an average of 12 days after the last egg is laid (Au et al., 2010). The nestling period lasts approximately 21 days (Feare, 1984). Starlings raise two broods over a single breeding season, with both parents providing care in the form of egg incubation and offspring provisioning (Kessel, 1957; Feare, 1984). Parental food provisioning in starlings is mediated through nestling calls, colouration of skin (UV) and mouth (carotenoids), posture and position within the nest (Jacob & Heeb, 2013). The effect that begging calls, skin and mouth colouration have on provisioning rates is mediated through parental assessment of nestling state (Jourdie et al., 2004; Bize et al., 2006). Posture and position within the nest (standing upright and close to nest entrance) is dependent upon on sibling-sibling interactions, as the biggest nestlings generally gain the prime position for feeding (Kacelnik et al., 1995).

The main objective of my study was to examine parental provisioning responses of European starlings when the volume of nestling begging was experimentally increased. No one has yet examined this question in European starlings, and it is important to determine how flexible parental responses are to changes in offspring signals, and how quickly parents can alter their behaviour. I examined whether provisioning by parents was affected by the continuous playing of additional nestling begging calls, by comparing that to their natural, baseline behaviour. I test the hypothesis that if conspicuous begging is a reliable form of parent-offspring communication, provisioning rates by parents can be quickly altered through increased nestling begging. I predict that an increase in the amount and volume of nestling begging through playbacks during the experimental begging period will correspond with an immediate significant increase in parental provisioning visits made to the offspring as compared to the preceding natural conditions occurring during the control period (with no additional begging).

Methods:

2.1 Field site & study species

This study was conducted on the campus of Saint Mary's University, located in Halifax, Nova Scotia (44°37'54.07" N, 63° 34' 47.09" W), during April-July 2016. Starlings that nested in 45 wooden nestboxes (Figure 1) located across the campus of Saint Mary's University (Figure 2) were observed. These boxes are attached to trees at a height of between 3 to 4 metres off the ground, and have been the focus of prior behavioural studies in starlings (e.g. Dorey, 2014; Walthers, 2016). In this study, 88 starling nestlings from 20 nestboxes over two different broods [8 nests in the first brood (April-May) and 12 nests in the second brood (June-July)] were used to study parent-offspring communication in relation to begging and provisioning rates. Each nestbox was checked daily for new eggs during the laying period until no new eggs were detected over two successive days. After egg laying was complete, each nest was monitored during the incubation period for hatch (typically 12 days after incubation begins (Kessel, 1957)). Hatch day was defined as the day the first nestling hatched. Typically, more than half the nestlings hatch on this first day, which was assigned as Day 0.

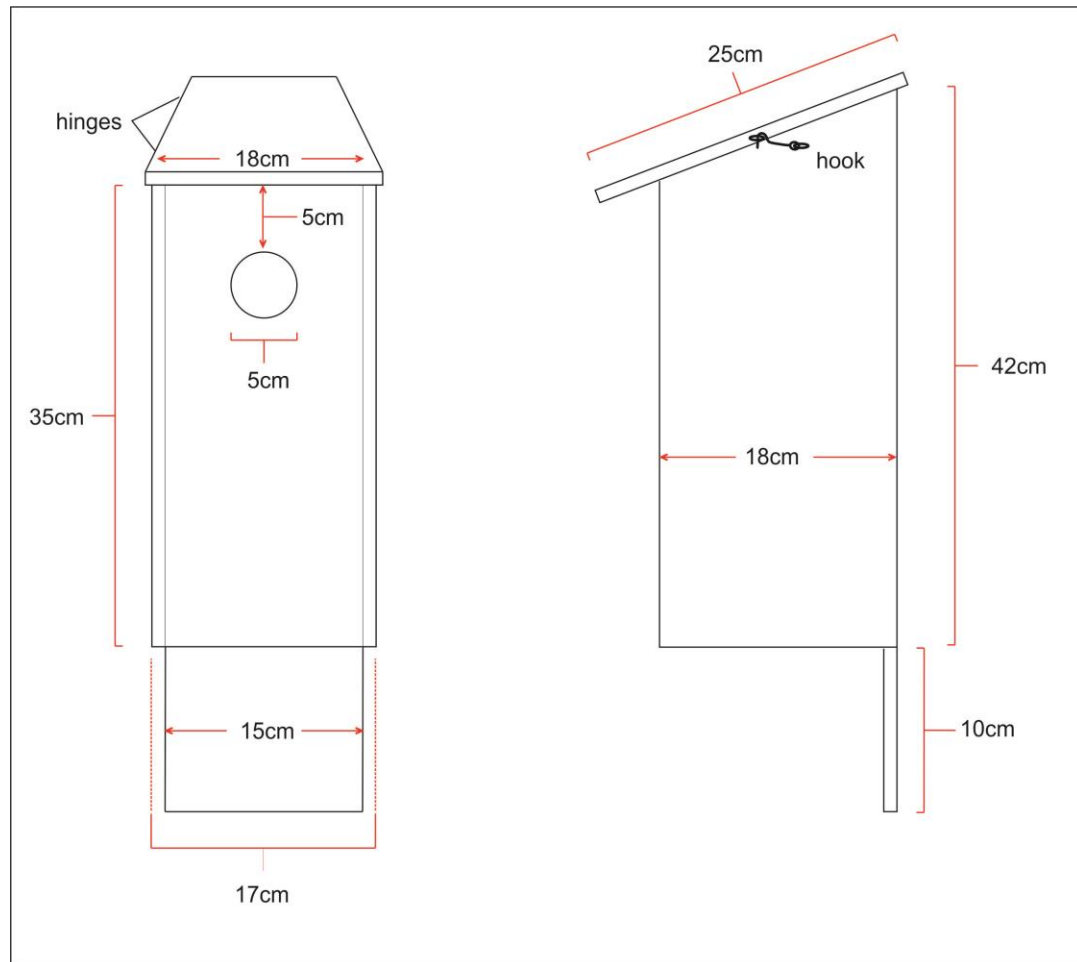


Figure 1: Design and measurements of nestboxes located on Saint Mary's University campus.

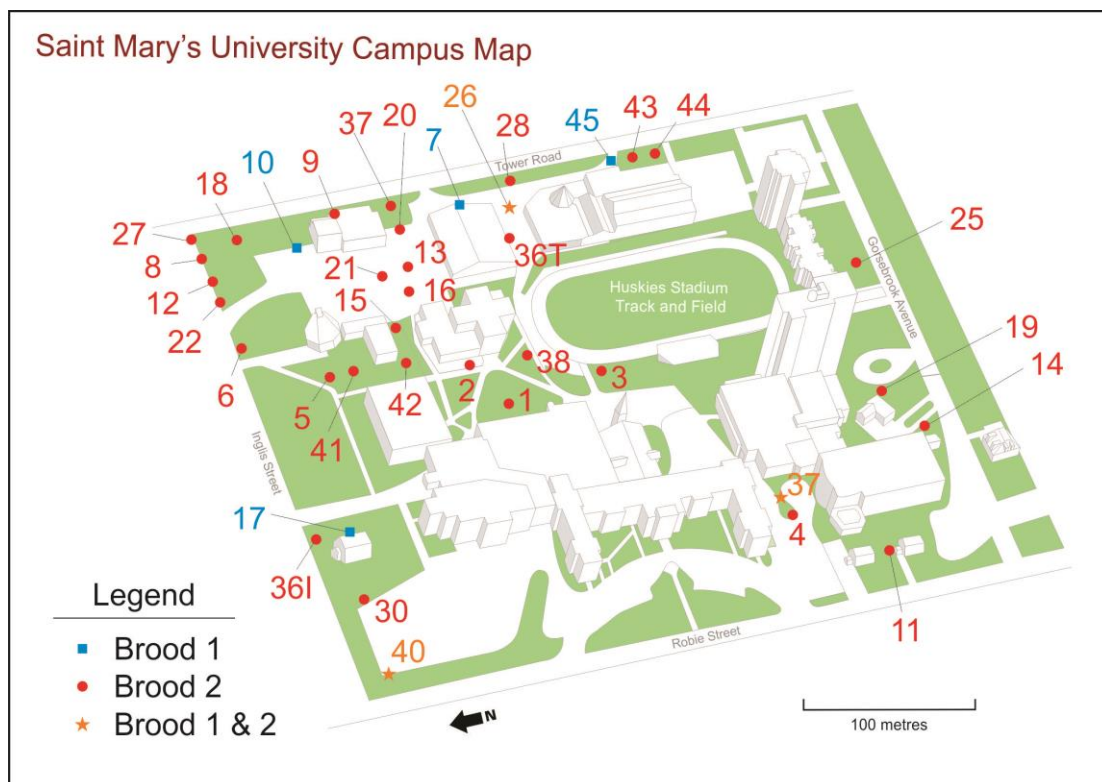


Figure 2: Location of nestboxes on Saint Mary's University campus.

2.2 Recording

Augmentation of nestling begging was achieved by first recording natural nestling begging vocalizations from each nestbox so that when begging calls were played back to the parents, they would be from their own offspring. To record begging calls, Zoom H1 Handy recorders were set up at individual nestboxes on Day 13 of the nestling period (13 days post-hatch of the first nestling). Nexxtech Omidirectional tie-clip microphones were attached to the recorders and set up in nestboxes such that they were suspended 12 centimeters from the top of the box, in the inside left corner, closest to the tree. Both the recorder and the microphone cable were protected from the rain and wind in a plastic bag secured underneath each nestbox.

On Day 13, recording of nestling vocalizations was initiated between 0800 and 0900 h, and stopped between 1300 and 1400 h, which spans the time of day when parents are feeding at a maximal rate (Kessel, 1957). At the start of each recording period, the nestbox number, date, and initiation time were stated. Similarly, at the end of each recording period, the termination time was stated. The microphones remained in the plastic bag for the next day's trials, while the recorders were removed. Microphones and recorders provided minimal disturbance to the birds, with no visible reaction to their placement.

After this five-hour recording period, the Zoom Recorders were taken down and the Day 13 begging recordings were downloaded (only those recorded between 0900 h and 1200 h were used, for consistency amongst nests). Recordings were examined using the digital audio editing program Audacity (Version 3.0, Mazzoni, 2016). From these recordings, three minutes of the highest amplitude begging vocalizations were selected for each session and saved as a new audio file in Audacity. Only the highest amplitude begging calls were selected to ensure parents would hear the recorded begging over the natural nestling vocalizations during the experimental treatment (the enhanced begging trials). Next, the three-minute audio files were converted from wav to MP3 format using iTunes, to enable them to be played on a 4GB Hipstreet Prism MP3 player. The audio files, each specific to one nestbox, were then downloaded onto a MP3 player to be used for playback the following day (Day 14). The MP3 players were set on 'loop' to constantly replay the three-minute audio file for the entire duration of the experimental treatment.

2.3 Experimental Design

On Day 14 of the nestling period prior to conducting the control period (natural conditions with no additional begging calls projected), and experimental treatment (with additional begging calls projected), Zoom Recorders were returned to the nestboxes, attached to the microphones and secured in the bag underneath the nestbox. Sony Stereo Headphones were then draped to a depth of 27 centimeters into each nestbox, with earbuds taped into the top right and left corners. The MP3 players, connected to the headphones, were secured within the bag as well, hidden from view of the parents to ensure no alteration in parental behaviour.

I used a matched pairs experimental design. For each nestbox, I first conducted a one-hour control period (no begging playbacks projected) to obtain baseline parental provisioning rates under natural conditions, and I then conducted a one-hour experimental treatment (with begging playbacks projected) at the same nestbox. The control period always immediately preceded the experimental treatment to ensure that baseline provisioning levels were accurately quantified, and that no carry-over effects from the experiment were observed. All trials were conducted between 0730 and 1200 h. Nestboxes were observed at a range of 5-10 meters away with binoculars so as not to interfere with normal parental provisioning efforts. The same observational vantage position was maintained over both one-hour periods for each nestbox. Each one-hour period (control and enhanced begging) began with the first observed visit of a provisioning parent and provisioning visits were then counted over the next hour. Response variables documented during the control periods and experimental treatments were the a) initial start time of first provisioning visit, b) number of visits, c) duration of

visits, and d) sex of provisioning parent. The total number of provisioning visits were tallied for both the control period and the experimental treatment. Begging by nestlings were also recorded during both one-hour periods for a separate study.

Following the control period, the MP3 player was turned on, projecting the three-minute vocalization loop from the nestbox at the maximum MP3 volume (60-70 decibels) for the experimental treatment. The volume of calls from the MP3 player appeared to be louder than the natural nestling vocalizations as they could be heard from the observation positions. However, to be able to statistically determine whether playback projections were significantly louder when played than when not played, I measured the decibel levels within each nestbox with a Checkmate SPC Meter after the control period and experimental treatments were completed. I took two different sets of readings for each nestbox on Day 14; five readings were taken and averaged for each nestbox during a) the control period (no begging playbacks) b) the experimental treatment (with begging playbacks).

2.4: Statistical analysis

All data were analyzed using Graphpad Prism 6. To determine whether data were normal, I used a D'Agostino-Pearson omnibus normality test. I determined that the sound pressure level data from the experimental treatment were not normally distributed, and I therefore used a Wilcoxon signed rank test for paired, non-normally distributed data. Similarly, the provisioning rate data for controls were not normally distributed, and so I did a Mann-Whitney test to determine if any difference in provisioning rates existed between first and second broods. I did an unpaired t test (provisioning data were normally distributed for the experimental treatments) to test for differences between provisioning rates in first and

second broods of the experimental treatments. As no significant differences were detected in provisioning rates between first and second broods for either the control periods or the experimental treatments, I combined data for both broods for each of the control periods and experimental treatments. I then used a Wilcoxon signed rank test was to detect provisioning rate differences between control periods and experimental treatments. Results were considered significant when $P \leq 0.05$.

Results

Sound pressure level was significantly greater when begging playbacks were projected than without the playbacks (Wilcoxon $W=253$, $n=22$ nestboxes, $P<0.0001$, Figure 3).

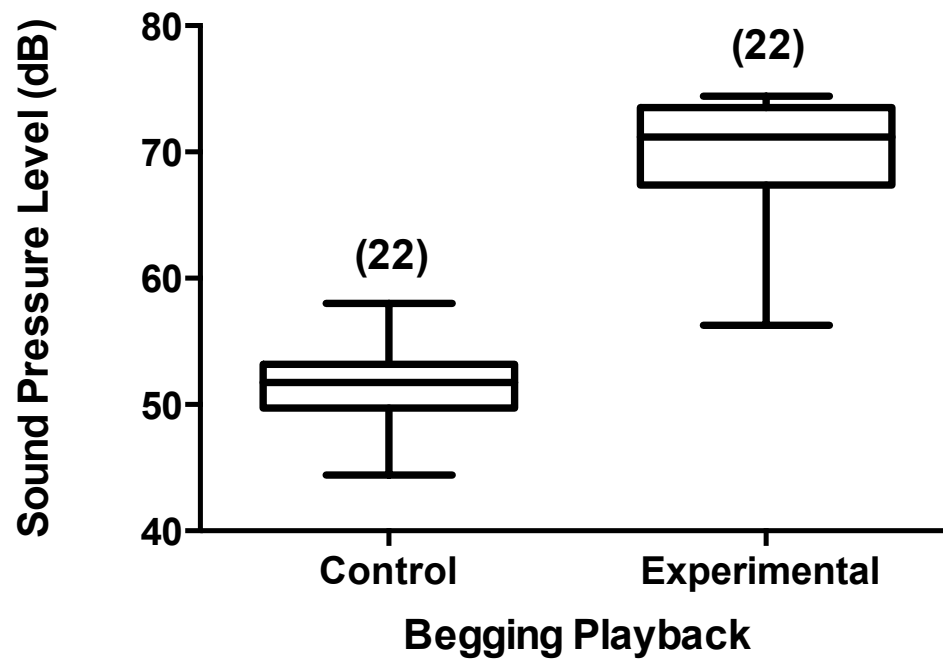


Figure 3: Boxplots showing (median, quartiles and range) sound pressure level (dB) within each nestbox during the Control period (no begging playbacks) and the Experimental treatment (with begging playbacks) on Day 14 of the nestling period (Day 0 is hatch day).

Parents provisioned at a significantly higher rate (number of feeding visits/hour) during the experimental treatment than the control period (Paired $t=2.280$, $df=19$ nestboxes, $P=0.03$, Figure 4). Sample size decreased to 20 nestboxes as provisioning visits for two nestboxes could not be accurately quantified.

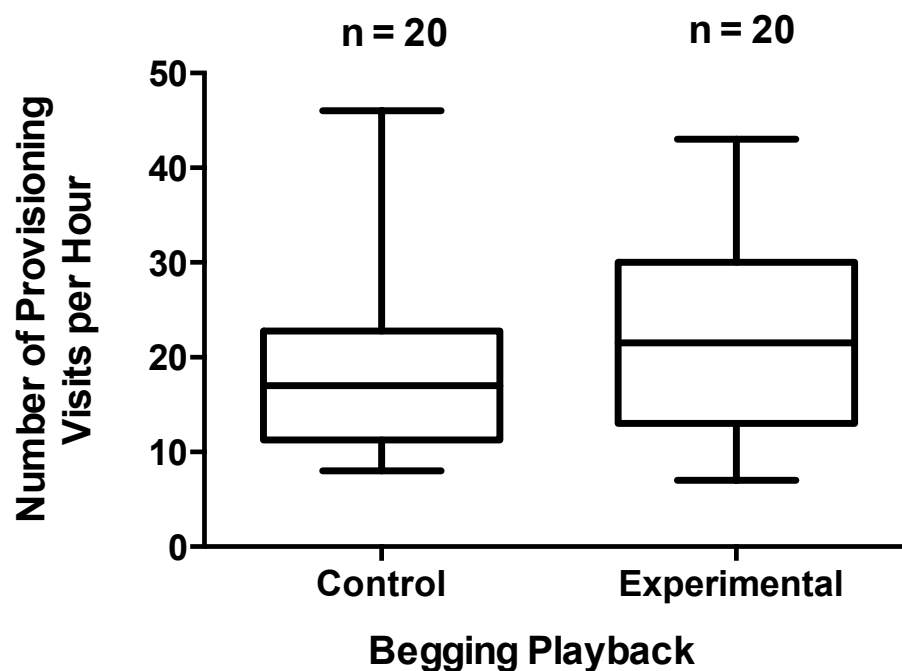


Figure 4: Boxplot illustrating (medians, quartiles, and range) number of parental provisioning visits per hour to the nestboxes during the Control period (no begging playbacks) and the Experimental treatment (with begging playbacks) on Day 14 of the nestling period (Day 0 is hatch day).

Discussion

As the begging call playbacks projected from nestboxes during the experimental treatments were significantly louder than the control periods when no playbacks were projected, parents would have heard them. Results of this study confirm that parents heard the increase in volume of nestling begging, and responded quickly by increasing provisioning rates to offspring. Their ability to respond so quickly to the begging signal illustrates how flexible parents are in provisioning behaviour. This finding supports my prediction that parents would respond to an increase in begging volume during the experimental treatment by increasing their provisioning rate as compared to the natural baseline quantified during the control period (Figure. 4).

In another parent-offspring study on European starlings, Kacelnik et al. (1995), examined the effect on a target chick when placed in varying brood sizes. They found that the target chick changed his/her begging behaviour based on the brood size in which they were placed, but their unmanipulated nestmates showed no such changes in begging. Therefore, chicks did not alter their begging behaviour based on the begging behaviour of their nest mates, but instead their begging was proportional to their individual need i.e. honest signalling (Kacelnik et al. 1995). Results from this study also found that target chicks were more likely to be fed if they increased begging intensity and altered their position to be closer to the nest entrance (Kacelnik et al., 1995). It was postulated by von Haartman (1953) and Kacelnik et al. (1995) that parents feed the nestling closest to the entrance, and that the current begging by other chicks has an effect on future parental provisioning rates.

Cotton et al, (1996) conducted a similar experiment on European starlings to that of Kaclenik et al. (1995) where all chicks within the brood except for the target chick had their hunger levels manipulated, effectively creating a competitive environment. The result was that the begging efforts of the target chicks were also not influenced by changes in the begging behaviour of their siblings. Cotton et al.'s findings (1996) support begging being an honest indicator of need, which remains unaffected by the begging efforts of nest mates. Therefore, the increased provisioning rates by adult European starlings to their offspring during the experimental treatment in my study may be due to parents responding appropriately to what they believe to be very hungry offspring.

Bengtsson and Rydén (1983) demonstrated in a study similar to Cotton et al (1996), that when recorded begging calls of Great-tits (*Parus major*) were played during parental feeding visits an increase in parental feeding rates was observed. From the results of their study, Bengtsson and Rydén (1983) reason that it is not number of nestlings, or non-vocal components that influence parental feeding rates but is a direct result of the intensity of begging by the brood. It is through an increase in this intensity that parents are influenced to increase their provisioning rates closer to the maximum amount they can achieve. These results align with my hypothesis that conspicuous begging acts as an honest signal of hunger, which results in an increase in parental provisioning rates.

An alternative hypothesis is that the increased offspring provisioning rates are the result of escalated sibling competition, where chicks try to outcompete their siblings by begging louder and longer to obtain potentially limited resources from parents (Rodriguez-Girones, 1999). Other names for this phenomenon are “intra-brood” conflict (Macnair & Parker 1979), and the scramble competition model (Ploger & Mock, 1986)

where nestlings 'scramble' for additional attention from provisioning parents. The central idea is that the level of parental investment is fixed, and each nestling attempts to manipulate the parent into providing more of this investment to them over their siblings (Smith & Montgomerie, 1991). Therefore, the begging behaviour of each chick is dependent upon that of his/her siblings, as they try to beg the loudest to receive the largest portion of food.

Smith and Montgomerie's study (1991) found that food-deprived American robins (*Turdus migratorius*) increased their begging intensity and consequently obtained more food from provisioning parents. They propose that since the probability of being fed is directly related to begging intensity, scramble competition for parental attention is also likely to occur. To test this, certain chicks within broods were food-deprived, while others were fed. The satiated (control) nestlings changed their begging intensity proportionally to match that of their hungry siblings. This result suggests that the begging intensity of one nestling is dependent upon the begging intensity of its siblings. Smith and Montgomerie (1991) concluded that their results supported the model that honest signalling (responding solely based on your own physiological needs), and sibling competition (adjusting begging intensity based on sibling begging intensity) are not mutually exclusive. They proposed that conspicuous begging is an evolutionary stable strategy whereby nestlings beg as an honest indicator of their physiological needs as well as a response to sibling competition.

A third alternative explanation for this increase in provisioning rates is that parents are attempting to silence their offspring, thereby decreasing the risk of nest predation. One of the main costs of begging is that it reveals the nest location to potential

predators, which could enforce honest signalling by offspring (Haskell, 1994). Several studies have shown that an increase in begging results in both an increase in parental provisioning rates, and in nest predation (Bengston & Rydén, 1983; Haskell, 1994; Haff & Magrath, 2011; but see Yasukawa, 2016). It may be that parents increase their provisioning rates to satiate the nestlings, thereby stopping begging, and preventing predators from locating the nest (Briskie et al., 1999; Haskell, 1999; Leech & Leonard, 1997).

Increased provisioning rates may also potentially be due to smaller load sizes (amount of food delivered each time) being brought to nestlings. Load size was unable to be quantified in my study as an appropriate distance needed to be maintained to avoid influencing parental provisioning rates. In a study conducted on Tree swallows (*Tachycineta bicolor*; McCarty, 2002) however, it was found that there was no trade-off between frequency of provisioning visits and load size. This study also found that load size did not vary with age of nestlings, number of nestlings being fed, or with the sex of the provisioning parent.

The increased provisioning rates observed when additional begging was projected clearly illustrate how effective parent-offspring communication is, with parents quickly responding to their young. Future research directions could examine why parents are not already feeding at the maximum rate before the begging playbacks (i.e. is parental survival or future breeding success affected?). The next step for our breeding population is to analyze the begging recordings of Day 14 nestlings before and during the additional begging playbacks to determine if their begging calls vary in pitch, or duration. If nestlings increase their begging rate or pitch during the playbacks, the results would be

suggestive of sibling rivalry.

Conclusion

To summarize, European starlings appear to demonstrate effective parent-offspring communication as increased provisioning rates were observed when additional begging was projected. Parents are sensitive to their offspring's signals, and are extremely flexible in their response to them.

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