

Patterns of parent-absent begging in nestling European starlings (*Sturnus vulgaris*)

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Abstract

Parent-offspring communication mediates feeding rates through begging by nestlings, which is energetically expensive and may alert predators to the nest's location, but benefits the nestlings by increasing body condition. Parent-absent begging is a behaviour that has the same risks as parent-present begging, but lacks the immediate benefits. This behaviour is prevalent in many passerine bird species, including European starlings (*Sturnus vulgaris*). During the European starling's annual breeding season (May-July) I recorded nestling begging vocalizations at 18 broods located on the campus of Saint Mary's University, Halifax, N.S., Canada, to examine parent-absent begging. Nestling vocalizations were recorded on days two, seven, 12, 17 and the day before fledging to monitor changes over the nestling period. I predicted that parent-absent begging would increase in European starling nestlings throughout the nestling period, because multiple studies on cavity-nesting species have found that parent-absent begging increases with age. Recordings were analyzed using Syrinx sound analysis software examining the first seven parent-absent intervals occurring after 10:00 am. It was found that there were significant differences in percentage of time spent begging in the absence of parents across the nestling period with it increasing from Days two to Day 17 followed by a decrease in parent-absent begging on the day before fledging. When examining the earlier and later broods separately there were no significant differences found. This study has implications in understanding avian behaviour and will provide insight to the nature of begging, and should guide future studies on European starlings and parent-offspring communication and Saint Mary's University.

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I. Introduction

I.I Avian vocalizations and communication

Millions of years of evolution have transformed birds into some of the most vocally adept animals on the planet, producing intricate acoustic signals to attract mates and scare off predators and rival males, for species recognition, and for communication with offspring (Catchpole & Slater 2008; Podos & Moseley 2009). Some living birds have even evolved a unique trait known as vocal learning; they have the ability to imitate other animals. These birds include parrots, hummingbirds, and songbirds, such as European starlings (*Sturnus vulgaris*) (Brusatte et al. 2015). Vocalizations are a key component in the complex forms of communication found throughout many avian species; these vocalizations are comprised of a network of multiple signals which are vital for reproductive success and nestling survival (Bulmer et al. 2008).

Parent-offspring communication in birds is comprised of various physical and acoustic interactions, the most vital being acoustic. The parent and the offspring must communicate, which will ideally result in the maximized fitness of both the parent and the offspring. Such a network of signalling is adaptive because it results in more effective parental reactions to cues for nest protection and it mediates feeding rates, which occurs through the parents responding to the nestlings' vocalizations (Hinde et al. 2010; Godfray 1995). This parental investment is ultimately converted into offspring fitness (Grodzinski et al. 2009). Whenever circumstances change and the costs and benefits associated with specific behaviours of the offspring are altered, the parent and/or the offspring are selected to alter the behaviour of the offspring accordingly (Litovich and Power 1992). For example, an appropriate reaction to parental alarm calling is particularly valuable to nestlings because of their vulnerability to predation and inability to identify predators at early stages of the nestling period (Magrath et al. 2006).

I.II Begging

The evolution of complex begging displays in various avian species is a significant factor in the success of many species, although it is a costly act in terms of both energetic expenditure and the possibility of attracting predators (Godfray 1995). Like most evolved behaviours, begging is adaptive; in order to receive food, nestlings will perform a begging display in response to parental visits (Leonard et al. 2005). Nestlings that beg in the presence of a parent with food will receive the food as a result, increasing the nestlings body condition and the genetic fitness of the parents. It has been shown in numerous studies on various species that enhanced begging increases the number of parental provisioning visits (e.g. Corney & Barber 2018; Kilner & Johnstone 1997). And so, begging signals are generally thought to function as signals of need (Wright & Leonard 2002), representing an honest signal of the level of hunger of the nestling. However, motives behind the begging displays of some bird species also stem from sibling-sibling competition, resulting in “dishonest” begging (Dawkins & Guilford 1991). Dishonest begging generally occurs in species where the parents do not have the energy or resources to satisfy the needs of their entire brood (Caro et al. 2016).

The act of begging is especially critical in bird species with altricial (rather than precocial) development: nestlings with high rates of growth and a low degree of development at the time of hatching (Jongsomjit et al. 2007). These altricial nestlings depend on their parents for feeding, as they are their connection to the world outside of the nest, and begging is the key to success. Components of these begging displays can be both physical, assuming different begging postures and flashing a brightly coloured gape, as well as acoustic, whereby they transmit high-pitched vocalizations (Sacchi et al. 2002). This study will focus on the acoustic aspects only.

I.III Parent-absent begging

Aves, as a class, have undergone many structural and behavioural adaptations to become an extremely successful group. However, there is one unusual behaviour that remains prevalent in the early life cycle stages of many avian species: parent-absent begging (Dor et al. 2007; Bulmer et al. 2007). An increase in begging increases predation risk (McDonald et al. 2009), and begging in the absence of parents might be considered maladaptive because it makes nestlings more susceptible to predation by notifying predators of the location of the nest when no parental protection is present. Therefore, parent-absent begging endures the same energetic and predation costs as parent-present begging, without the immediate benefits of feeding by the parents. The origin of this behaviour is unknown.

It has been proposed that parent-absent begging is caused by increased responsiveness of the nestlings, in their attempt to decrease the risk of missed detections (Leonard & Horn 2001; Dor et al. 2007). This, in turn, would cause increased response to inappropriate cues with age due to an increased readiness to beg. In 2001, Budden and Wright found that 15% of the total begging events in Southern Gray shrikes (*Lanius meridionalis*) were parent-absent. Parent-absent begging is also a common occurrence in Spotless starlings (*Sturnus unicolor*), and recent research on this species has shown that on average the signal intensity of parent-absent begging is lower than that of parent-present begging, showing lower maximum frequencies, lower frequency ranges, and fewer frequency modulations per call (Bulmer et al. 2008). This suggests that there may be a different function for the two methods of begging.

The results of Bulmer et al.'s (2008) study showed that Spotless starling nestlings increased parent-absent begging with age and brood size, as well as with decreasing body condition. The results of Leonard and Horn's (2001) study using tree swallows (*Tachycineta bicolor*) showed that

older nestlings begged more in response to inappropriate cues than younger nestlings, and this caused parent-absent begging to increase through the nestling period. One study with conflicting results is Budden and Wright (2001)'s experiment utilizing southern grey shrikes. They found that Southern grey shrike nestlings decreased parent-absent begging with age.

I.IV This study

European starlings, are cavity-nesting passerines that are non-native to North America, and are the study species of my Honours study. They are medium-sized cavity-nesting birds which undergo altricial development, exhibit biparental care, can lay two clutches each season (early and late), and nestlings fledge after 21-24 days (Feare 1984). They belong to the clade Passeri of the order Passeriformes, meaning they are a songbird with highly complex vocal structures and acoustic abilities. As vocal learners, vocalizations play a major role in the success of these birds as a species. They have the ability to mimic a diverse range of sounds as well as a limitless capacity for vocal learning (Smith, et al. 2005). They do not have a set of pre-determined innate songs as do suboscine birds (Liu et al. 2013). It was proposed by Yoon et al. (2016) that parent-absent begging is more prevalent in cavity nesters due to limited predator access; cavity nesters experience relatively lower risks of nest predation than open-cup nesters. European starling nestlings beg honestly, as their begging intensity directly reflects their level of hunger (Bradley 2018; Cotton et al. 1996).

I.V Objectives

The first objective of this study is to assess the prevalence of parent-absent begging in European starlings. My second objective is to examine the changes in the patterns of parent-absent begging in relation to nestling age. I will examine the percentage of time that nestling European starlings

spent begging in the absence of a parent in relation to the total time spent in the absence of a parent, between parent-present intervals. I had initially assumed that parent-absent begging would decrease, due to my interactions with the nestlings throughout the nestling period and their gradual reduction in begging in my presence. But, upon review of the literature I predicted that parent-absent begging in European starling nestlings would increase with age. Results are expected to support the findings of Bulmer et al.'s (2008) study on the sister species to the European starling, the Spotless starling. The results of this study are also expected to agree with those found by Leonard and Horn (2001) on tree swallows. My research study seeks to better understand the complex patterns of parent-offspring communication in European starlings, and guide future studies at Saint Mary's University involving parent-offspring communication and parent-absent begging. This study will add to the baseline data for the study population and guide future studies of avian behaviour.

II. Methods

II. I. Fieldwork

This study was conducted through May, June, and July of 2018, on the grounds of Saint Mary's University in the south end of Halifax, Nova Scotia, Canada (44°37'54.07"N 63°34'47.09"W - refer to Figure 1). Saint Mary's University has been a research site for various experimental studies on European Starlings for the past 12 years (since 2007), under the supervision of Dr. Colleen Barber (Ph.D.).

European starlings are an invasive species, first brought over from Europe to North America in 1890, mainly as a method of insect reduction (Linz et al. 2007), as well as an attempt to introduce all bird species mentioned in Shakespeare's plays to America (Homan et al. 2017).

The phenomenal adaptive abilities of *Sturnus vulgaris* have caused thousands to nest in the City of Halifax, Nova Scotia, with a population exceeding 150 million throughout North America (Homan et al. 2017). The large number of starlings, along with relatively large clutch size and high hatching/fledging success, makes them one of the most commonly used passerine species for research (Feenders et al. 2011).

Throughout the breeding season, European starlings have two broods (Linz et al. 2007), referred throughout the paper as the early broods (April 22nd to May 30th) and the later brood (June 6th to July 19th).

II. II. Research setup

To monitor the changes in frequency and duration of nestling begging from hatching to fledging, I selected 15 nest-boxes across the two broods for observation. There were 42 nest boxes on the Saint Mary's University campus as of April 22nd, nine new nest boxes were put up June 13th; all new nest boxes were inactive throughout the later brood. All boxes are located approximately two to three meters off of the ground, secured to the trunk of a tree. The cavity quality was consistent throughout every nest box (6.5 cm diameter circle), and so were the dimensions of every nest-box (16cm x 18cm x 30cm).

Of the nest-boxes selected for analysis, 10 boxes were from the early broods and five were from the late broods, all of which were located within the westernmost region of the University's campus (Figure 1). Three nest-boxes used from the early brood were reused in the later brood either by the same mating pair (n=2) or a different mating pair (n=1). In early May, 10 out of the 29 active nest-boxes were selected for this project, based on similar hatch days and proximity to

one another. In late June, all eight nest-boxes that were active were selected for the study, but only five were analyzed by the time of writing this thesis.

The number of nestlings in each individual brood varied from two ($n=1$) to six ($n=3$); there were also broods of three ($n=2$), four ($n=5$), and five ($n=4$). The mean clutch size of the individual broods used in this study was 4.9 (5.2 from early broods and 4.2 from later broods). The mean hatch success was 91.0% (95.5% for the early broods and 82.0% for the later broods), and mean fledge success was 90.1% (95.8% for the early broods and 78.6% for the later broods).

Nest checks began in late April, to monitor the state of each nest. Each nest-box was checked on the day prior to the expected hatch day and the subsequent days until all eggs had hatched, day zero was the day that hatching started. Hatching is slightly asynchronous (1-2 days). After Day 2, any remaining eggs were considered unlikely to hatch. Data collection began on Day 2 when hatching was assumed to be over.

II. III. Data Collection

On nestling Day 1, each selected nest-box was equipped with a low impedance Nexxtech omnidirectional tie clip microphone, with 70-16,000 Hz frequency sensitivity. The end of the microphone was secured in the back, right corner and descended 12 cm into the nest box. Starting on nestling Day 2 and continuing every day until all nestlings had fledged (at Day 20-23), a Zoom H1 Handy Recorder (handheld audio recorder) was hooked up to the microphone between 8:30 am and 9:30 am and was taken down between 1:00 pm and 2:00 pm. I stated the time of day and nest box number at the beginning of every recording.

Approximately four hours of audio was recorded every day (from Day 2 to fledge day) from each nest-box of both early and later broods; the audio was recorded onto 8GB and 12GB

microSD cards and was then downloaded onto a Seagate® Backup Plus 2TB USB 3.0 drive for storage.

II. IV. Data analysis

First, every recording that was a .MP3 file was converted to a .WAV file, then I analyzed the recordings using Syrinx sound analysis software (J. Burt, 2000, Seattle, Washington). Whenever a new sound file was opened on the software I created an annotation link to the sound file, and then to a metafile. All files created were saved to the same location as the original sound file. The intervals between the first eight parental visits after 10:00 am were identified; the 30 seconds after the parental visit was marked as a ‘dead zone’ because any begging that occurred within this time was likely due to the recent presence of a parent. Annotations were added to indicate when the parent entered the nestbox, exited the nestbox, and at the end of the 30 seconds after the parental visit (Figure 3).

The parent-absent intervals between the dead zones and the next parental visit were searched for begging events, which are referred to as begging bouts. Begging bouts were defined as a display of begging for two seconds or more, bracketed by non-displaying extents of time of two seconds or more, as established by McCarty (1996). The duration and abundance of these parent-absent begging bouts were examined in relation to the amount of time between the end of the 30 second dead zone and the next parental visit to determine average time spent begging per parent-absent interval (over all seven intervals per recording).

Annotations were added to all parent-absent begging bouts (Figure 4). The length of each begging bout in each of the seven parent-absent intervals was added up and divided by the total amount of time for which the parent was absent. This gave me the percent of time that the nestlings

spent begging in the absence of parents. An average time for each recording was calculated by adding all percentages (seven) from the same recording and dividing it by seven. These averages were then added together with same day averages calculated from the 15 different nest boxes and were then divided by 15 (the total number of recordings for each nestling day) to find out the average percent of time spent begging in the absence of a parent on that particular day. I only analyzed recordings from Days 2, 7, 12, 17, and the day before fledging.

III.V. Statistical analysis

The average percentages from each recording (across seven parent-absent intervals per recording; 50 recordings from early broods, 25 recordings from later broods) were entered on a spreadsheet and using the GraphPad Prism 6 software, the normality of all the data (n=15) was tested using the d'Agostino-Pearson omnibus normality test. The data were determined to be non-parametric, and a Friedman test was run. A normality test was also performed on the data from the early broods only (n=10); these data were also determined to be non-parametric and a Friedman test was run. A Friedman test was selected in both cases because our data represented a matched design. After the Friedman test a Dunn's post-hoc test was run. There was not enough data to successfully test the data from only the later broods (n=5) to run a separate test. Results were considered significant when $P \leq 0.05$.

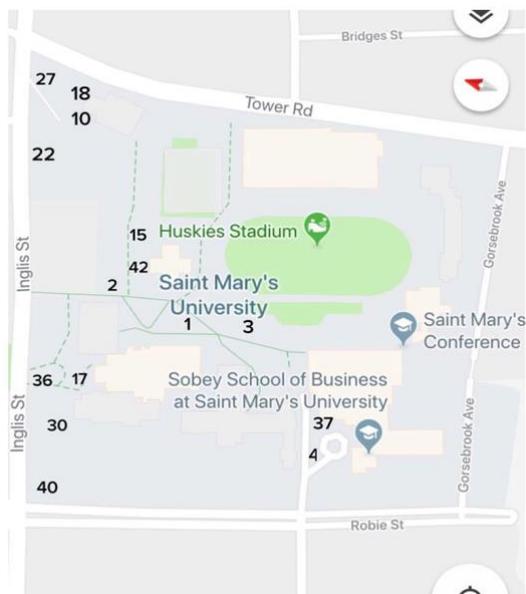


Figure 1. A map of the Saint Mary's University campus (screenshot taken from Google Maps) marked with the identification number of each nest box recorded throughout this study.

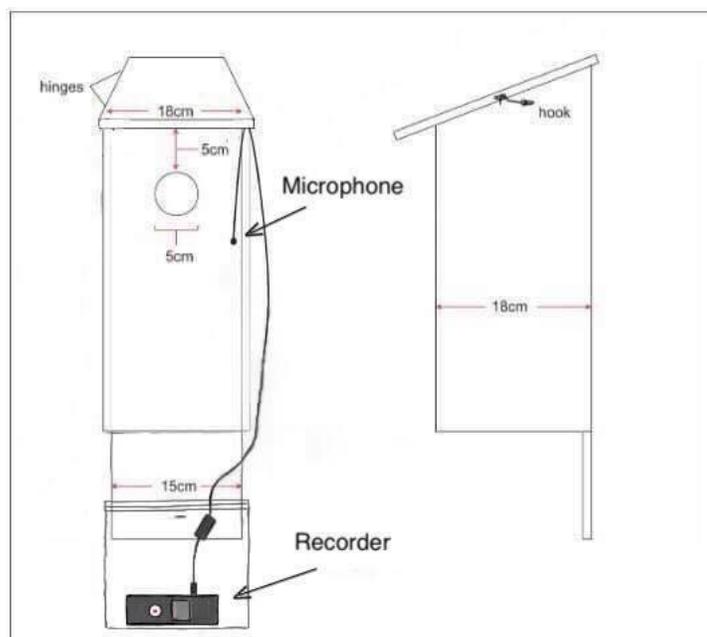


Figure 2. The design of the nest boxes present across the Saint Mary's University campus, Halifax, Nova Scotia. The research set up included an omnidirectional microphone descended 12cm into the back right corner of the nest box, connected to an audio recorder outside of the nest box contained in a Ziploc bag.

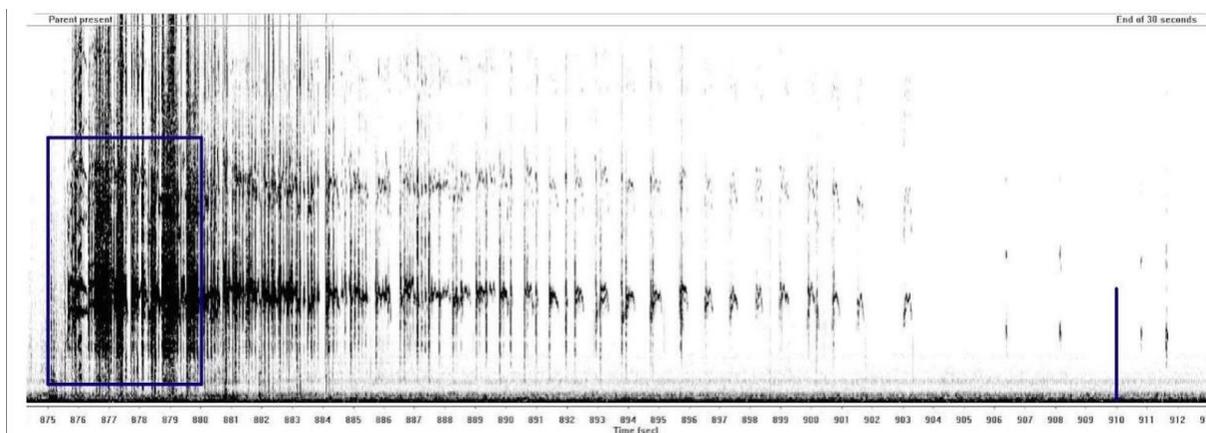


Figure 3. Screenshot of a spectrogram taken during recording analysis on Syrinx software. Image shows the process of marking a parental provisioning visit and setting a delay time of 30 seconds before counting any begging bouts as “Parent-absent begging”. Analysis began at the end of the 30 seconds.

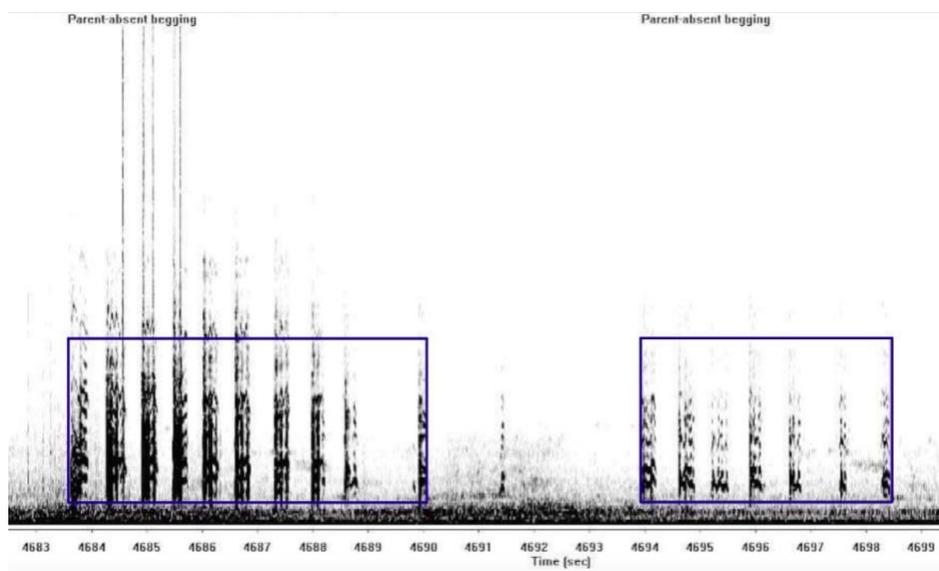


Figure 4. Spectrogram showing the process of the recording analysis with Syrinx sound analysis software; annotations are around two separate parent-absent begging bouts. The definition of begging bouts as established by McCarty (1996) was used throughout this study: displays of begging for two seconds or more, bracketed by non-displaying extents of time of two seconds or more.

III. Results

III.I Analysis of the changes in average time spent parent-absent begging over all broods

There was a significant difference in time spent begging when parents were absent among the five different nestling ages ($F_r = 41.65$, $df = 5, 15$, $P < 0.0001$; Figure 5). Nestlings begged for a significantly shorter percentage of time on the day before they fledged as compared to all other stages in the nestling period except for when they were two days of age. On average nestlings begged for a significantly longer percentage of time when they were in the mid-late stage of the nestling period (Days 12 and 17) than during the beginning (Day 2) and the end (Day before fledge) of the nestling period (Figure 5). The average percent of time spent begging each day increased from Day 2 until Day 17 and suddenly decreased the day before fledging. Most variance occurred on Day 12, with average percent time spent begging ranging from 21.3% to 99.4%. The least variance was observed on Day 17, ranging from 51.1% to 98.2%.

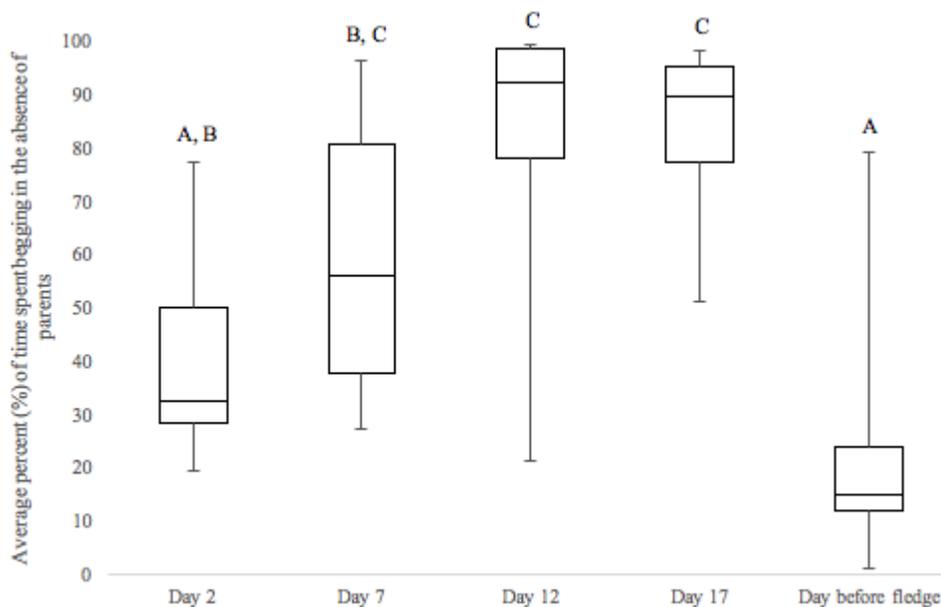


Figure 5. Box plot using quartile distribution quantifying the average percent of time spent begging per parent absent interval annotated over seven parent-absent intervals per day. Data from both

early and later (May-July) broods ($n=15$). The letters above each column represent the significance of the difference between them - the columns that share a letter are not significantly different.

III.II Analysis of the changes in average time spent parent-absent begging over early broods

Analyzing the data from only the early brood (Figure 6), there is an evident increase in average time spent parent-absent begging from Day 2 until Day 17, followed by a significant decrease the day before fledging ($F_T = 28.88$, $df = 5, 10$, $P < 0.0001$). The hatching success for the early broods was 95.5% and the fledge success was 95.8%. The average percent of time spent parent-absent begging each day increased from Day 2 until Day 17 and suddenly decreased the day before fledging. Most variance occurred the day before fledging, with average percent time spent begging ranging from 1.1% to 78.9%. The least variance in parent-absent begging was on Day 17, ranging from 75.8% to 98.2%.

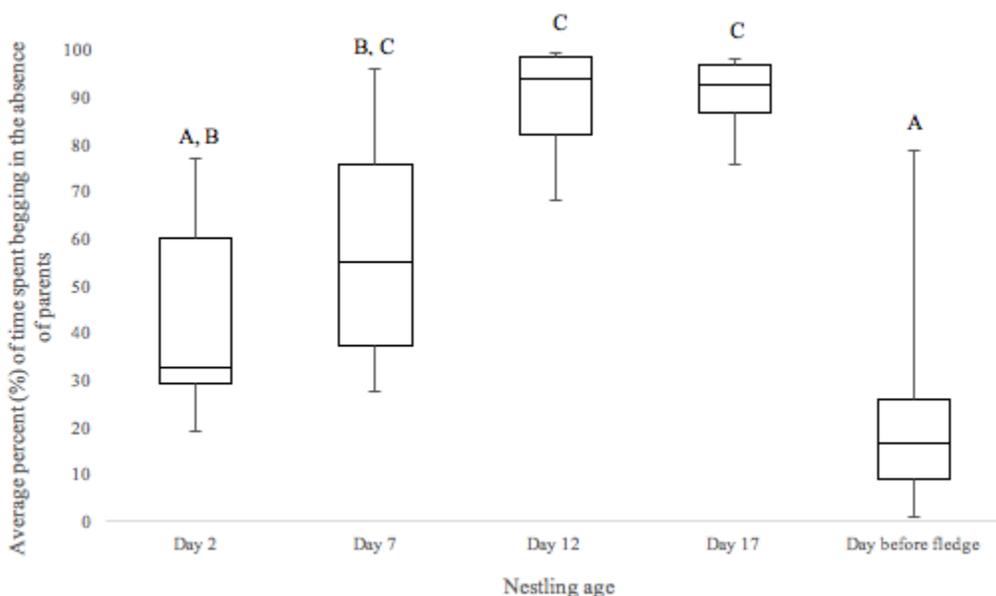


Figure 6. Box plot using quartile distribution quantifying the average percent of time spent begging per parent absent interval annotated over seven parent-absent intervals per day. Data from early (May-June) broods only ($n=10$). The letters above each column represent the significance of the difference between them - the columns that share a letter are not significantly different.

III.III Analysis of the changes in average time spent parent-absent begging over later broods

When the averages from the later broods were graphed exclusively, the data followed the same trend as in the earlier broods, with average time spent begging in the absence of parents increasing until the day before fledging. The hatch success of the later broods was 82.0% and the fledge success was 78.6%. The average percent of time spent begging each day increased from Day 2 until Day 17 and suddenly decreased the day before fledging. Most variance occurred on Day 12, with average percent time spent begging ranging from 21.3% to 99.4%. The least variance occurred on Day 2, ranging from 24.8% to 50.9%.

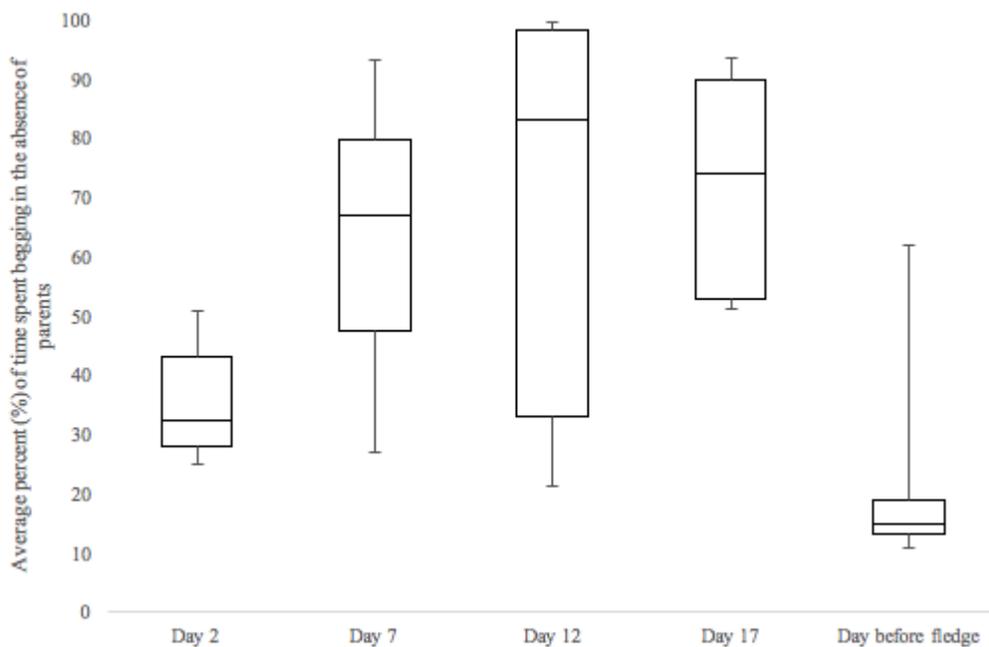


Figure 7. Box plot using quartile distribution quantifying the average percent of time spent begging per parent absent interval annotated over seven parent-absent intervals per day. Data from early (June-July) broods only (n=5).

IV. Discussion

The major finding of this study is that the average percent of time European starling nestlings spent begging in the absence of parents increased throughout the nestling period, excluding the day before fledging when it suddenly decreased significantly. There are several studies examining parent-absent begging on a number of different passerine bird species (Budden & Wright 2008; Bulmer et al. 2008; Dor et al. 2007; Leonard & Horn 2001; Leonard et al. 2005). The time spent parent-absent begging generally increases with age, this was seen with European starlings, Spotless starlings (Budden & Wright 2008), and tree swallows (Leonard & Horn 2001), but there are some exceptions, such as Southern Gray shrikes (Budden & Wright 2001).

The large decrease in parent-absent begging at the end of the European starlings' nestling period is likely the result of an attempt by the parents to coax the nestlings to leave the nest by decreasing the feeding rates. However, feeding does not stop, and by holding food away from the nest, the parents can encourage the nestlings' decision to leave the nest in order to obtain the food (Martin 2015). But fledging is not the end of the nestlings time spent begging - there is still a post-fledging dependence period where the nestlings are still being fed by parents and are learning to survive outside of the nest. It has been proposed that heavier fledglings have higher rates of survival than the lighter ones (Monrós et al. 2003). As the age of the nestlings increase, and the days until fledging decrease, the observed increase in parent-absent begging until the day before fledging is likely due to the nestlings getting larger and hungrier and the parents increasing their feeding rates as a result. The parents make the decision to expend a lot of energy into feeding up until fledging, because larger nestlings are better off outside the nest than the lighter ones. Feeding is ultimately halted around days 19-21 (the day before fledging) whenever the nestlings are large and have developed enough to survive outside of the nest. Though this is still a perplexing find,

because we would expect lower feeding rates to cause increased nestling hunger, and therefore increased parent-absent begging. It is possible that there is an underlying parent-offspring conflict behind the nestlings' sudden decrease in parent-absent begging. It has been suggested that the nestling day on which the nestlings' fledge is determined by negotiations between the parents and the offspring, in an attempt to balance the dangers of a prolonged nestling period and the dangers of leaving the nest too soon (Martin et al. 2018). If this is true, it is likely that these negotiations would alter the nestlings' begging behaviours later in the nestling period, and could possibly make them more aware of the risks of parent-absent begging causing that sudden decrease right around their transition from nestling to fledgling.

When examining the results of parent-absent begging from the early and later broods separately, I found no significant differences. Although, the average time spent begging in the absence of parents were generally lower in the later broods, it is possibly due to the fact that the parents have less energy to invest than in the earlier broods. There are tradeoffs between the energy expended by the parents and the brood success evident in the mean hatch success (95.5% early brood and 82.0% later brood) and fledge success (95.8% early brood 78.6% later brood). A lower nestling survival rate reflects reduced parental success in delivering sufficient food to the nestlings, resulting in lower body conditions (Grundel 1987). Due to the fact that the nestlings of the later broods are more accustomed to the lower efforts, and ultimately the lower feeding rates of the parents, they likely beg less readily in the absence of parents. Spotless starlings were found to decrease parent-absent begging with decreasing brood size (Budden & Wright 2008), this suggests that the lower rates of parent-absent begging in the European starlings' later broods may also be correlated to the lower brood sizes.

The results of this study agree with those found by Bulmer et al. (2008). These results are likely similar due to the genetic similarity of the two species used: European starlings and Spotless starlings. It has been suggested that this increase in parent-absent begging (with age) that occurs in a number of passerine bird species is caused by the nestlings increasing responsiveness in order to miss fewer parent-present cues with the increasing hunger levels throughout the nestling period. This would cause the nestlings to beg more readily (Leonard & Horn 2001). It has also been proposed that increased parent-absent begging over the nestling period is due to an error in communication, and that the nestlings are responding to inappropriate cues (Clemmons 1995). However, this hypothesis does not explain the increase throughout the nestling period, as the cognitive abilities of altricial species also increase with age as the brain fully develops (Khayutin 1985). Therefore, the increase of parent-absent begging with age suggests that this behavior is not due to nestling errors in differentiating appropriate and inappropriate cues (Budden & Wright 2001; Leonard & Horn 2001).

To conclude, the results of this study supports my prediction that European starling nestlings would increase parent-absent begging throughout the nestling period, similar to what was found in the genetically similar Spotless starlings. However, there was an unexpected decrease in average time spent parent-absent begging the day before fledging. Future studies should focus on what impacts other factors (body condition, brood size, parental investment, etc.) have on the behaviour of parent-absent begging in passerine species. Understanding how the many different factors interconnect can assist in discovering the root cause of this unusual behaviour. Studying the behaviour of parent-absent begging has many implications in the study of animal behaviour, specifically parent-offspring communication. I am completing this study in the hopes that it will help guide future studies on European starlings here at Saint Mary's University on the behaviour

of European starlings as well as parent-offspring communication. These findings may possibly be applied to native passerine bird species, to better understand species behaviour which can then contribute to overall conservation efforts.

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