

Begging duration as a potential indicator of nestling condition in first
and second broods of European starlings
(*Sturnus vulgaris*)

By
Katherine Dorey

A Thesis Submitted to
Saint Mary's University, Halifax Nova Scotia
In Partial Fulfillment of the Requirements for
the Degree of B.Sc. Double Honours
Biology and Environmental Science.

April 2014, Halifax, Nova Scotia

© Katherine Alice Dorey, 2014

Dr. Colleen Barber
Supervisor

Dr. Jennifer Foote
Co-Supervisor

Dr. Jeremy Lundholm
Reader

Table of Contents

	Page
Abstract	i
List of Tables and Figures	ii
Acknowledgements	iii
Introduction	1
Methods	
Study Species	9
Fieldwork	9
Experimental Analysis	11
Statistical Analysis	12
Results	
Begging Duration	19
Brood Condition & Fledging Success	19
Discussion	
Begging Duration	26
Brood Condition & Fledging Success	30
Conclusion	34
Literature Cited	35

Begging duration as a potential indicator of nestling condition in first
and second broods of European starlings
(*Sturnus vulgaris*)

By Katherine Dorey

Abstract

Begging in passerine birds is an honest signal of nestling hunger to the parents. Over the breeding season a decrease in food availability and parental provisioning and an increase in parasite abundance occur suggestive of a decline in brood condition. The purpose of this study was to examine if there is a relationship between begging duration and nestling condition in European starlings (*Sturnus vulgaris*). Females lay two clutches over the breeding season, and both males and females incubate the eggs and provision the offspring. Nestboxes were checked daily for eggs. Upon hatching, a microphone was placed within the nestbox to record begging vocalizations. Begging was analyzed when nestlings were 11 days of age, which is mid-way through the nestling period. Begging duration did not differ between first and second broods. Second broods were in poorer condition than first broods. Second broods with more nestlings were in significantly poorer condition than those with fewer nestlings. Although there was a difference in condition between first and second broods, no difference in fledging success was detected. In summary, no significant relationship was observed between either total duration or mean duration of begging and nestling condition, which suggests that nestlings continue to beg for food regardless of their condition. Duration of a call does not differ with nestling condition; however begging is still an honest signal of nestling need because it is costly to produce.

Date: April 15, 2014

List of Tables and Figures

	Page
Figure 1. Syrinx software display of 11-day old European starling begging calls (Nestbox 1, May 15, 2012).	15
Figure 2. Begging bouts from 11-day old European starling nestlings (Nestbox 1, May 15, 2012).	16
Figure 3. Beg and peeping calls (circled) from 11-day old European starlings. Peeps are characterized by having a duration of $<0.04s$ while begs have a duration $>0.04s$. (Nestbox 1, May 15, 2012).	17
Figure 4. Illustration of the boxes that Syrinx PC Software creates to record start and end times, as well as the 'Beg' annotation that distinguishes each vocalization.	18
Figure 5. Total duration of begging for the 30-minute period for nests containing 1-6 nestlings (n=26 broods).	21
Figure 6. Mean brood condition for first and second broods of European starlings. Error bars represent standard error.	22
Figure 7. Mean brood condition shows a negative correlation with total precipitation (mm) during the first 12 days of the nestling period (Day 0 – Day 11).	23
Figure 8. Mean brood condition in small (1-3 nestlings) versus large (4-6 nestlings) broods within first and second broods of European starlings. Error bars represent standard error.	24
Figure 9. Fledging success in 2011 and 2012. Error bars represent standard error.	25

Acknowledgements

I would like to thank M. Hornsby, M. Latouf, A. Ouedraogo, M. Porter, J. Slade and K. Smith, for collecting the 2011 and 2012 nestlings' data and for their help throughout the year. I would also like to say a special thank you to Hillary Yuill for all of her help and support during the late nights in the lab. Further, I would like to thank my supervisor and co-supervisor, Dr. Colleen Barber of Saint Mary's University and Dr. Jennifer Foote of Algoma University for their encouraging words and their help and support throughout my research especially with research design and statistical analysis.

Introduction:

Communication in animals is an inherent part of every individual's life. It has important fitness consequences and is used during courtship, with offspring and with each other (e.g. to alert of a potential predator)(Kumar, 2003). Various forms of communication include plumage coloration, body movements and acoustic signaling (Kumar, 2003). An important type of acoustic communication is between parents and their offspring (parent-offspring communication), which is critical to the nestling's survival. Such communication involves arrival calls and alarm calls from the parent to the young or begging by the offspring to the parents. This type of communication regulates provisioning and offspring development and ensures that the proper amount of care is provided for daily food and warmth requirements (Leonard & Horn, 2001). In passerine birds, begging for food by the nestlings is an honest signal of hunger to parents (Godfray, 1991 & 1995; Wright & Leonard, 2002; Cotton et al., 1996). Begging mainly occurs when parents are present, but will also occur in their absence (Leonard & Horn, 2001). Nestlings beg by gaping with their beak wide open, standing in the nest, flapping their wings and vocalizing (Leonard et al., 2005). This begging display becomes more intense as nestlings become hungrier and can provide information about nestling body temperature, immunocompetence and body condition from the call characteristics (e.g. pitch, length and posture) (Leonard & Horn, 2001; Maurer et al., 2003). Begging informs parents which nestling should receive the next meal based on their begging intensity (frequency and duration) (Soler & Avilés, 2010; Maurer et al., 2003; Dugas, 2009). Various studies have found that higher begging rates due to hunger influence the parent's

decision to allocate food to a particular nestling over a sibling (e.g. Cotton et al., 1996; Granadeiro et al., 2000; Redondo & Castro, 1992). There is conflict between the allocation of resources parents provide to offspring at each visit to the nest. Each sibling will beg to receive the food, but parents can only feed a certain number of nestlings at each nest visit (Kilner & Johnstone, 1997).

Acoustic communication in urban bird populations, such as the Halifax European starling population is often affected by urban traffic noises and signals may not be received due to ambient noise pollution (McIntyre et al., 2014). Disturbance to communication efficiency as well as decreased foraging sites found in urban settings can reduce overall survival. Anthropogenic noise within the city has the ability to mask the acoustic signals of avian species, which ultimately effects parent-offspring communication. If parents are unable to receive the begging signals properly they may not be able to appropriately allocate the food, affecting nestling survival (Slabbekoorn & Peet, 2003; Leonard & Horn, 2012).

The ultraviolet light (UV) reflectance of the flange (inside of beak) is an important visual cue for nestling food distribution in altricial species. This visual cue could be particularly important for urban bird populations, especially, if acoustic signals are masked. In European starlings (*Sturnus vulgaris*), the colour of the flange will reflect more or less UV over a short- term period based on the nestlings long-term nutritional state, which allows nestlings to signal food deprivation to the parents when gaping (Bize et al., 2006; Jourdie et al., 2004; Mondloch, 1995). A carotenoid-rich diet produces the orange-yellow coloration seen in nestling flange (Thorogood et al., 2008). Because the intensity and reflectance of this signal is

influenced by the diet, nestlings that are in better condition receiving a higher quality (carotenoid-rich) diet will have higher UV reflectance compared to nestlings in poorer condition from a poorer quality (carotenoid-poor) diet (Jacob & Heeb, 2013). Also nestlings in first broods displayed greater reflectance in their flange than nestlings in second broods, which is consistent with a decrease in brood condition as the season progresses (Jacob & Heeb, 2013). It is thought that signal expression should increase with nestling need; however, Bize et al. (2006) have found that parent starlings have high flexibility in their food allocation and can preferentially feed nestlings with a lower signal expression. Perhaps some characteristics of begging indicate condition if they are expressed more and other characteristics indicate condition when they lack in expression such as the flange coloration.

If a parent comes to the nest with food and there is no begging, parents will often vocalize an arrival call to stimulate the nestlings to beg so the most needy of the nestlings can receive the food (Leonard et al., 2005). Bize et al. (2006) found that when food was abundant parents allocated food to all nestlings begging at various rates. However, in poor ecological conditions those who begged at high rates received the food over nestlings begging at lower rates. This finding indicates that parents use begging rate to determine nestling need.

With all honest signals there must be a cost incurred to displaying it (Maynard Smith & Harper, 2003). The most prominent cost associated with begging is the actual energetic cost of vocalizing, standing and wing movements. Nestlings use up to 28% of metabolized energy for growth so using even a small portion of

overall energy on begging could have growth implications (Verhulst & Wiersma, 1997; Schwagmeyer & Mock, 2008). Continuous begging in a nest can attract predators to the nest location and consequently decrease nestling survival (Redondo & Castro, 1992). When a predator is nearby, the parent will often give an alarm call to signal the nestlings to be quiet (Halupka, 1998; Tarwater et al., 2009).

Some avian species, including European starlings, raise two broods over a breeding season and both parents provide parental care by incubating the eggs and provisioning the offspring (Freitag, 1937). Due to this double brooding and biparental care, European starlings are ideal for examining whether nestling condition and fledging success decrease over the season. Females lay 3-7 eggs per clutch (Higgins et al., 2006). The first and second clutches have an average of 5.8 eggs and 4.6 eggs per nest respectively (Kluijver, 1933; Serra et al., 2012). Christians et al. (2001) suggested that the costs of laying the first clutch and the lower food availability as the season progresses results in lower energy allocation to laying the eggs in second clutches and provisioning the offspring, resulting in smaller second clutches being laid (e.g. Lack, 1947; Cody, 1966). Subsequently, offspring from second broods are also smaller than those in first broods (Cramp 1998; Kessel, 1957). These brood variations are likely influenced by environmental conditions throughout the season (Krementz et al., 1989).

European starlings lay their first clutch in late April and early May and their second clutch near the end of June (Lack, 1947). Parents do not have as much time to dedicate to provisioning due to decreased daylight hours occurring after the summer solstice (June 20th-22nd) (Lack, 1947). Nestlings in the second brood are

typically in poorer condition than those in first broods; some are 19% lighter at nine days of age with a considerably shorter tarsus length than nestlings in first broods (Serra et al., 2012). At the time of fledging, second brood nestlings are also, on average, lighter than those in first broods (Kessel, 1957). Many previous studies on European starlings have found reduced nestling condition in second broods (Jourdie et al., 2004; Bize et al., 2006; Serra et al., 2012).

Nestling condition could be affected by differences in ecological variables such as food availability and weather conditions. Temperature and precipitation have strongly influenced availability and accessibility of important food supplies for birds (Krementz et al., 1989; McCarty & Winkler, 1999; Lack, 1947). Airborne insect numbers decrease in the months from July to September, which is important for insectivorous birds (e.g. Martin, 1987). Gruebler (2007) also found that insects during the post-fledging period was significantly reduced for second broods. However, Christe et al. (2001) found that heavy precipitation in the spring during the first nestling period delayed the emergence of insects, leading to an unusual abundance of insects during the second nestling period.

European starlings are ground foragers that feed on insects, invertebrates, berries and seeds (Kaufman, 1996). During the first brood parents provision the offspring with larvae of true flies from the order Diptera, including the larval stages of snipe flies (*Rhagio mystaceus*) and dung flies (*Scathophaga stercoraria*). The most abundant species in the European starlings diet are larval crane flies (*Tipula oleracea*) known as leatherjackets (Kluijver, 1933). The diet in the second brood consists mainly of grasshopper and cricket larvae (Order *Orthoptera*) and wasp, bee

and ant larvae (order *Hymenoptera*) (Kluijver, 1933). Invertebrate larvae are a finite resource and through predator depletion (Weins, 1989) and emergence of adult flies (Coulson, 1962), the abundance of invertebrates becomes scarce over time. As the season progresses, the starling diet switches from mostly high quality feeding sites with preferred invertebrates to less preferred feeding sites with lower nutritional invertebrates (Feare, 1984) and towards low quality, high fiber fruit berries (Martin et al., 1951; Berthold, 1976).

Warmer temperatures that occur during the second nestling period are associated with an increased abundance of avian parasites (Marshall, 1981). A study conducted on barn owls (*Tyto alba*) found an increase in *Carnus hematerus* during later breeding periods (Roulin, 1999; Hornsby et al., 2013). This ectoparasite commonly affects the European starling nestlings in the Halifax population (Hornsby et al., 2013) and is found to have a negative correlation to nestling spotless starling (*Sturnus unicolor*) condition (Avilés et al., 2009). Merino & Pottie (1995) also found reduced tarsus length and mass linked to high ectoparasite abundance in pied flycatchers (*Ficedula hypoleuca*).

Nestlings that consume fewer or smaller meals have reduced immune responsiveness and are more likely to be affected by bacteria or parasites (Christe et al., 2001; Møller & Saino, 2004). Nestlings with a diet consisting of smaller prey with reduced feeding times do not receive the proper nutrients to defend against parasites and replenish their nutrient levels, resulting in nestlings being in poorer condition and having reduced growth and decreased body mass (O'Brien & Dawson, 2000; Simon et al., 2004; Bize et al., 2003; Richner et al., 1993). Studies have also

shown that first brood nestlings have a higher immunocompetence level than those in second broods, which is suggestive of a seasonal decrease in offspring fitness (López-Rull et al., 2011; Wilk et al., 2006).

Overall, changing weather and ecological conditions over the breeding season can directly and indirectly affect nestling condition by causing adverse changes in food availability (Krementz et al., 1989), parental provisioning (Finlay, 1976) and parasite abundance (Marshall, 1981).

Reduced nestling condition in second broods may also be due to the energetic costs involved in feeding and fledging a brood. Parents of second broods are more often exhausted and cannot increase provisioning to offset the nutritional deficiencies due to parasites (Gustaffson & Sutherland, 1988). This nutrient deficit can lead to nestling mortality and reduced fledging success (Simon et al., 2004). In this situation, parents can evaluate the quality (size and parasite load) of their young and can choose to allocate food to the higher quality nestlings that will have more reproductive success (e.g. Serra et al., 2012; Linden & Møller, 1989). Similarly, parents may decide that the additional provisioning energy requirements from parasites in a food-scarce environment during the second brood will be better spent preparing for winter so they can reproduce again the following year (Christie et al., 1996; Møller, 1997; Haig, 1990; Davis et al., 1999).

As the season proceeds, it is beneficial to lay the second brood as early as possible to ensure food availability (Webb et al., 2002). Females may need to build up energy reserves over a period of time to get ready for the second brood (Thompson, 1992). To get an earlier start on the second brood, maternal care and

sometimes both maternal and paternal care will end sooner in first broods than in second broods. In barn swallows (*Hirundo rustica*) post-fledging care was reduced in the first brood to initiate second broods earlier (Grüebler & Naef-Daenzer, 2008b).

The purpose of this study was to examine begging by first and second broods of nestling European starlings when soliciting food. The objectives of this study were to determine if nestling begging duration (total duration and mean duration), mean brood condition and fledging success differ between first and second broods. I hypothesized that due to the difference in environmental conditions as the breeding season progresses, nestling survival (condition and fledging success), and begging behaviour will be affected. I predicted if brood condition and/or fledging success are reduced in second broods when compared to first broods, then begging duration in second broods would be greater than first broods.

Methods:

Study Species

European starlings were introduced to North America from Europe and Asia in 1890 and 1891. They first inhabited New York City but have since made a westward expansion and established large populations on the continent (Kessel, 1957). This species is highly adaptable and intelligent which has led to established populations on five continents. They are often referred to as a pest due to their large flock formation and negative effects on agriculture (Kaufman, 1996). Starling habitat ranges from urban cities to countryside and open fields. As ground foragers they feed on insects, invertebrates, berries and seeds (Kaufman, 1996). They are secondary cavity-nesters and lay 3-7 blue-green eggs (Higgins et al., 2006; Kaufman, 1996). Females lay two clutches per year and both parents provide care during the twelve days of incubation until nestlings fledge 21 days to 24 days after hatch (Kaufman, 1996). Adults molt once a year at the end of the breeding season and can be sexed by the base colour of their beaks – blue for males and pink for females during the breeding season (Floyd, 2008). Some northern starlings migrate; however, the European starling population in Halifax, Nova Scotia does not appear to do so.

Fieldwork

The fieldwork for this study was completed 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 of 2011 and 2012. There are 45 nest boxes located approximately two-three meters high on trees throughout the campus. Nest boxes were checked daily

until all eggs were laid to determine egg dates and clutch size after which they were checked every other day until all eggs had hatched. Every nest box was then monitored daily and the number of nestlings was recorded and used to determine fledging success (total number of nestlings fledged out of the total nestlings that hatched) in both first and second broods. The day the eggs hatched was assigned to be day zero.

On the first day of the nestling period, Handy Recorders (Zoom H1 Handy Recorder settings, 44.1kHz/16-bit, WAV format, volume 100) were secured directly under nest boxes and a lapel microphone was inserted 12cm into the box. Microphone setup began approximately two hours after sunrise. Recordings were made for five hours (approximately 7:30 am – 12:30pm) each day from day one of the nestling period until the day of fledging. Fledging success was noted when all nestlings had left the nest. At the start of each recording, the nest box number, date and start time were stated while the end time was stated at the end of the recording. When nestlings were 11 days old, they were banded with Canadian Wildlife Service bands on their right tarsus and a light blue (2011) or dark green (2012) band on the left tarsus. Nestlings were also weighed to the nearest 0.5g with a Pesola Spring Scale and their tarsus length was measured with digital calipers to the nearest 0.1mm. Five tarsal measurements were taken and an average length was calculated and used for analysis. Sunrise times for Halifax, N.S were retrieved from the Environment Canada website (www.ec.gc.ca).

Experimental Analysis

For this study, the first 30 minutes of recordings made on the third hour after sunrise was analyzed on day 11 of the nestling period. This specific time period was used to ensure that all recordings would be analyzed from the same time of day so as to be comparable. Day 11 was chosen for vocalization analysis because tarsus and mass measurements were taken for each nestling at this age and were used to estimate nestling condition. Fifteen first broods and eleven second broods were followed. First broods hatched between May 13th - 15th in 2011 and May 5th - 15th in 2012. Second broods hatched between June 22nd - 27th in 2011 and June 19th - 22nd in 2012. Intermediate broods that hatched between May 16th-June 21st, 2011 (n=2) and May 16th-June 18th, 2012 (n=0) were not included in this study because I was most interested in examining begging duration and condition in first and second broods. Also, for statistical purposes, excluding intermediate broods ensured a clear differentiation between first and second broods. Intermediate broods result when first clutches fail early, from late nesting first broods as well as polygynous males (Kessel, 1957; Pinxten et al., 1990). It is unlikely that these intermediate broods will lay a second clutch due to the lateness of the season; also a study reviewing the breeding biology of European starlings only recognizes first, intermediate and second broods (Pinxten et al., 1990).

Spectrograms of vocal recordings were visualized in the Syrinx PC software program vocal record (John Burt, Seattle, Washington). Syrinx is a software program specifically designed to play back animal vocalizations from digital sound recordings. This program allows a person to view microphone input as a

spectrogram display, facilitating analysis of vocal calls (e.g. total duration of begs over a 30-minute period) and specific characteristics such as frequency, duration and type (Figures 1-3) (e.g. Mennill & Ratcliffe, 2000).

Any vocalization on the spectrogram that was longer than 0.04s was deemed to be a beg (Figure 1 & 3) as the nestlings begged both in the presence and absence of the parents. Vocalizations less than 0.04s in duration were annotated as peeps (Figure 3). Peeps are not considered an honest signal of need and differ from begs by the nestling vocalizing with its beak closed. When vocalizations become louder and more frequent, the spectrogram illustrates the vocalizations as darker shades of black and begs become less distinguishable from one another (Figure 2). When begs overlapped with less than 0.001s between them, the vocalizations were annotated as one begging bout. Each vocalization was annotated by manually drawing a box around the length of the vocalization, which then automatically records the start and end time of a particular vocal, giving its duration (Figure 4).

After the box was created, I made an annotation noting whether the vocalization was a beg, begging bout or a peep. Syrinx outputs the time and frequency measurements of the box to a text file. The text file showing the start and end times of the specific vocalizations was then opened in Microsoft Excel (V14.3.9) (Redmond, Washington) file and converted to a .xsl file.

Statistical Analysis

To determine the duration of each vocalization, I calculated the total duration spent begging (begs and begging bouts) in each nest during the 30-minute time period, and the average length of begs (including begging bouts) per nest.

To determine if weather conditions affected begging behavior, nestling condition, or fledging success, the average daily temperatures and total daily precipitation amounts for Halifax, N.S. were retrieved from the Environment Canada website (www.ec.gc.ca). Each nest had a different hatch day and the temperature and precipitation data was collected for each nest from day 0 to day 11. The 12 daily average temperatures were then averaged again to obtain one overall mean temperature for each nest. Precipitation amounts for each day were summed over the same twelve days to determine the total amount of precipitation.

To assess nestling condition of first and second broods, a linear regression between body mass and tarsal length was run on nestlings from 2011 and 2012 using GraphPad Prism 5.04 (La Jolla California, USA). The residuals were used as the index for condition. Any nestlings above zero would be in good condition and those below zero would be in poor condition. To avoid pseudoreplication, residuals for nestlings in each brood were averaged to provide one index of brood condition.

For further analyses, a backward stepwise linear regression using JMP (V11) (SAS Institute Inc. Cary, North Carolina, USA) was run to determine the best linear models. Begging duration was the dependent variable and the independent variables of brood (first or second), condition, total precipitation, average temperature, year and number of nestlings were included along with all two-way interactions among effects. We also used backwards stepwise linear regression to determine differences in brood condition and fledging success. Results were considered significant when $P \leq 0.05$. Using a backwards selection process allowed us to eliminate variables based on their level of interaction and effect on the dependent variable. Doing so allowed

the best linear model to only show relevant variables (Stephens et al., 2007). This type of statistical method has been previously used to analyze similar begging and condition characteristics (e.g. Jacob et al., 2011).

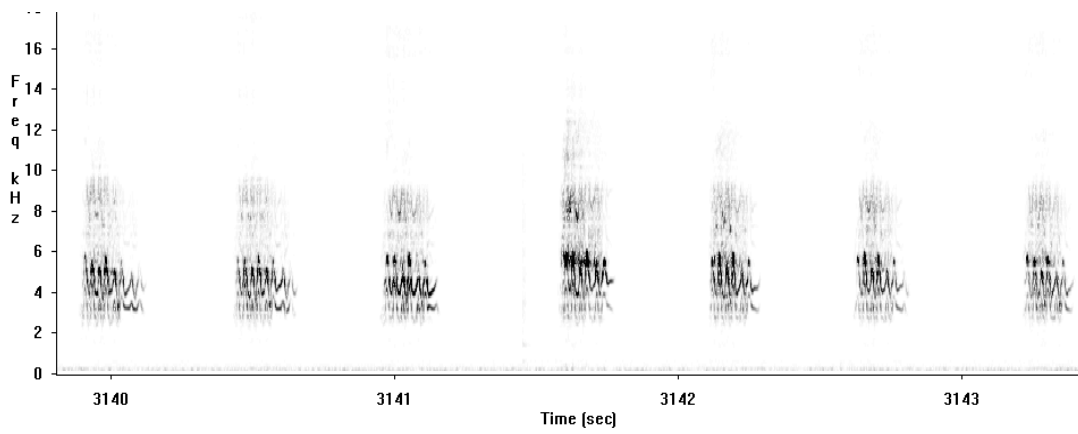


Figure 1: Syrinx software display of 11-day old European starling begging calls (Nestbox 1, May 15, 2012).

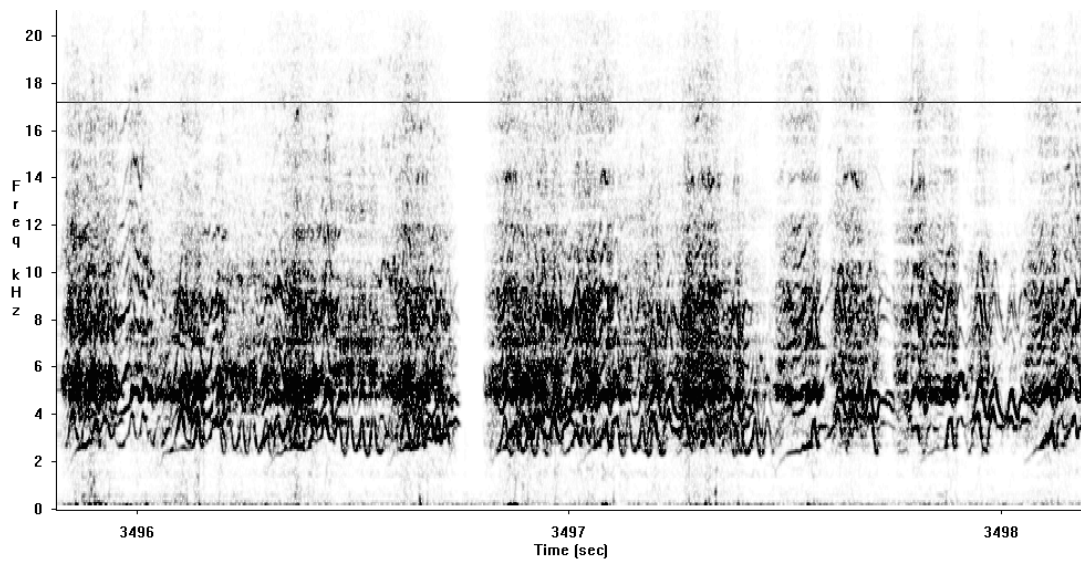


Figure 2: Begging bouts from 11-day old European starling nestlings (Nestbox 1, May 15, 2012)

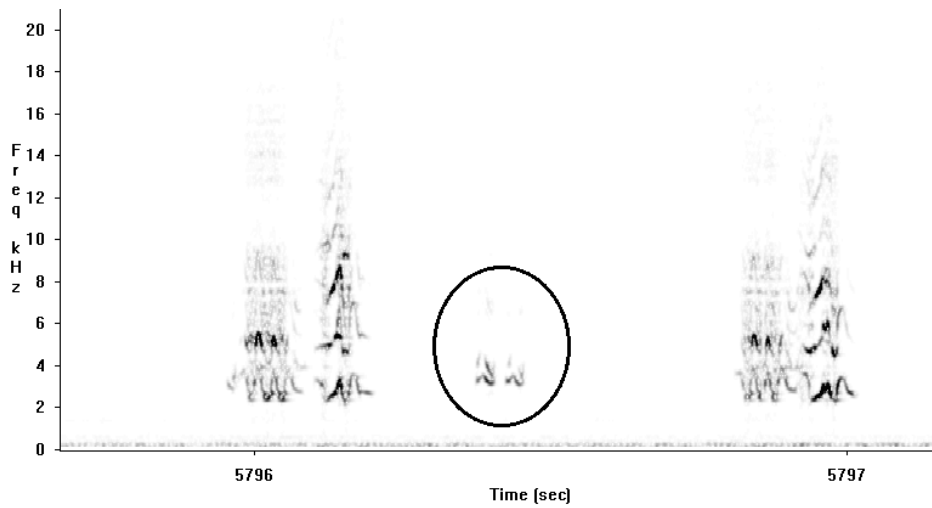


Figure 3: Beg and peeping calls (circled) from 11-day old European starlings. Peeps are characterized by having a duration of $<0.04s$ while begs have a duration $>0.04s$. (Nestbox 1, May 15, 2012).

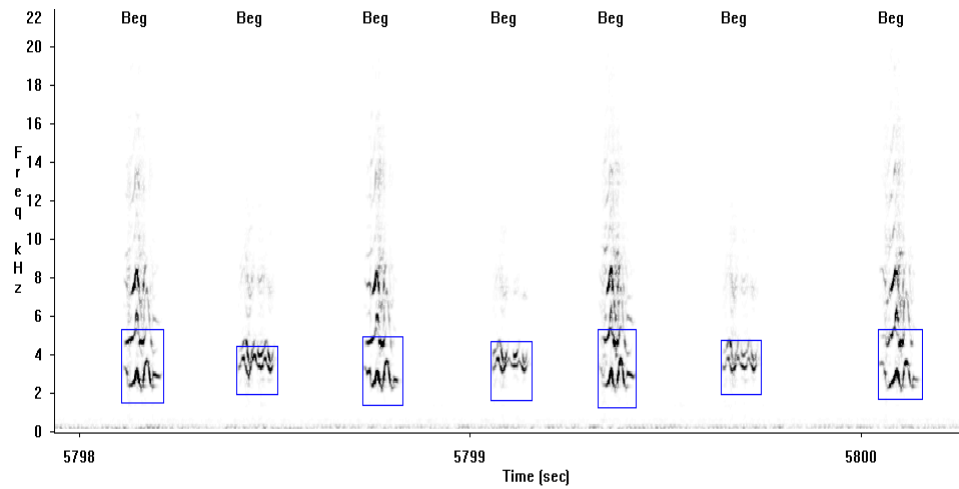


Figure 4: Illustration of the boxes that Syrinx PC Software creates to record start and end times, as well as the 'Beg' annotation that distinguishes each vocalization.

Results

Begging Duration:

Total begging duration and mean beg duration for each nest were tested against six effects. In the best linear model, only the number of nestlings in the nest at day 11 remained. There was a positive correlation between the total begging duration and the number of nestlings which controls for the variations in brood size ($r^2=0.27$, $F_{1,24}=8.74$, $P=0.007$, Figure 5). A positive correlation was also found between the mean begging duration and the number of nestlings ($r^2=0.15$, $F_{1,24}=4.25$, $P=0.05$). However, there were no significant relationships found between begging duration or mean begging duration and the condition of the nestlings, average temperature or total precipitation. There were also no differences found between broods (first vs. second) or years (2011 vs. 2012).

Nestling Condition and Fledging Success:

Nestling condition was tested against five effects and the best linear model contained two-way interactions with the number of nestlings at day 11, brood, year, total precipitation and brood by number of nestling (whole model: $r^2=0.49$, $F_{5,20}=3.89$, $P=0.013$). First broods were in significantly better condition than second broods ($F=12.71$, $P=0.0019$; Figure 6). Total precipitation (x-axis) was negatively correlated with nestling condition (y-axis) ($F=5.7621$, $P=0.0262$; Figure 7). Nestling condition tended to be higher in 2012 than 2011 ($F=4.17$, $P=0.055$). The number of nestlings in a brood, generally, did not affect the nestling's condition ($F=2.87$, $P=0.1060$). However, the number of nestlings was related to brood condition in second broods (brood by number of nestlings interaction) ($F=7.95$, $P=0.011$). Second

broods that had more nestlings were in poorer condition than second broods with fewer nestlings (Figure 8). In first broods, the condition stayed fairly constant with an increase in nestling number, while second broods had decreased condition with an increased number of nestlings (Figure 8).

The best linear model for fledging success contained only year as a significant predictor. Fledging success did not differ between first and second broods, as it was not included in the final model. The year 2012 had significantly higher fledging success ($r^2 = 0.24$, $F_{1,24} = 7.39$, $p = 0.012$; Figure 9).

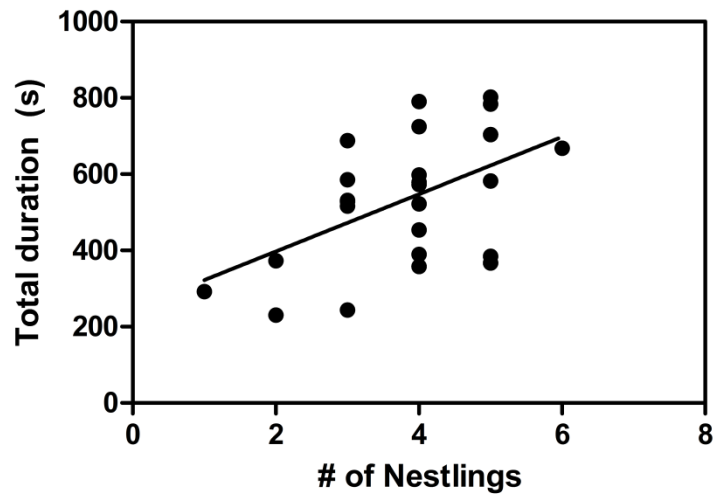


Figure 5: Total duration of begging for the 30-minute period for nests containing 1-6 nestlings (n=26 broods).

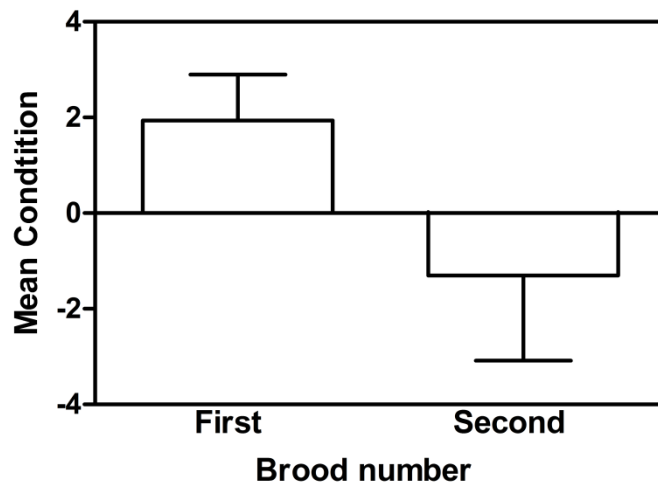


Figure 6: Mean brood condition for first and second broods of European starlings. Error bars represent standard error.

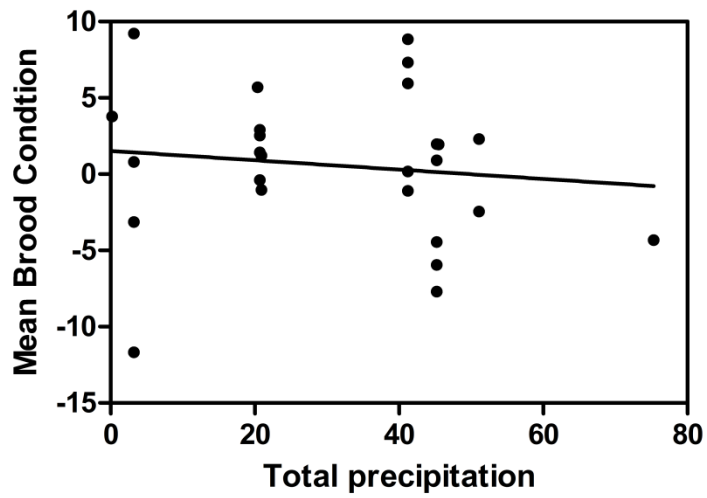


Figure 7: Mean brood condition shows a negative correlation with total precipitation (mm) during the first 12 days of the nestling period (Day 0 – Day 11).

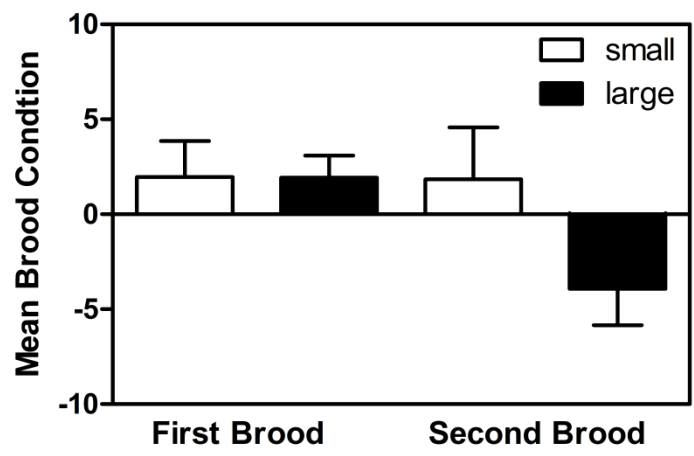


Figure 8: Mean brood condition in small (1-3 nestlings) versus large (4-6 nestlings) broods within first and second broods of European starlings. Error bars represent standard error.

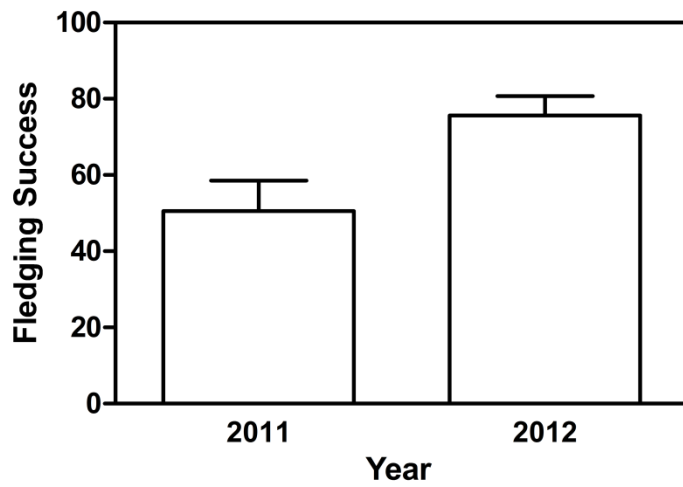


Figure 9: Fledging success in 2011 and 2012. Error bars represent standard error.

Discussion:

Begging Calls

I had predicted that nestling condition and fledging success would be reduced in second broods compared to first broods and as a result, begging duration would be longer in these second broods. However, the results of this study do not support this prediction. Begging duration did not differ between first or second broods despite brood condition being higher in first broods. However, broods having more nestlings, regardless of being a first or a second brood, begged longer and each beg lasted for a longer time. An increase in total length of begging is expected, as more nestlings will typically beg for more time (Wright & Leonard, 2002). However, the increase in mean duration of each beg with more nestlings suggests that with increased sibling competition, each nestling is in more need because each receives fewer meals (Leonard et al., 2000).

Perhaps because nests usually have more than one nestling, competition among nestlings influences begging behavior when the parent is absent. If begging is an honest signal of an individual's need, siblings should not influence it, unless more siblings lead to fewer meals for each individual. However, this study and previous studies have found individual begging differences due to siblings (Kacelnik et al., 1995). A study on tree swallows (*Tachycineta bicolor*) also found an increased begging intensity with increased brood size (Leonard et al., 2000). Other studies, however, have found no difference in begging with brood size (Roulin et al., 2000). Johnstone (2004) suggested that sibling begging might be cooperative. Therefore, the collective begging intensity of the brood influences the total resources that are

provided, ultimately benefiting each sibling. Competitive begging would occur if a nestling changes their begging intensity based on another sibling's begging behavior so as to outcompete them (Parker et al., 2002). Competitive begging is consistent with the parent-offspring conflict hypothesis that suggests there is an imbalance in the amount of food the nestlings will receive and the actual amount of food parents bring back to the nest. Parents are assumed to be equally related to all nestlings and should allocate food evenly. However, European starlings are known to have extrapair paternity, which may increase the parent-offspring conflict (Garcia-Vigon et al., 2009). Regardless of the parent-offspring relatedness each nestling will still value itself more over its siblings and will compete to receive food (Kilner & Johnstone, 1997). A study on pied babbler (*Turdoides bicolor*) fledglings found that siblings did not influence individual begging and that no nestlings incurred extra costs or gained more benefits from changes in begging by their sibling. Pied babbler fledglings did not beg competitively or cooperatively, instead their begging was an honest signal of their individual need (Thompson et al., 2013). Cotton et al (1996) found that begging by nestling European starlings was not affected by the number of siblings, which contrasts with my findings.

In my study, nestlings continued to beg when parents were present as well as when they were absent, which is similar to Leonard et al's (2005) findings for tree swallows. When observing the Syrinx PC spectrogram, it appears that more continuous begging occurred when the parent arrived (Dorey, pers. obs), which you could hear as a scratch or thump on the recording. A previous study observed parent-absent begging and found that this type of begging generally occurs at a

lower pitch and increases with nestling age and brood size while decreasing with better condition (Bulmer et al., 2008).

Contrary to my study, many previous studies have found a significant relationship between begging calls and condition. One study actually found that zebra finch (*Taeniopygia guttata*) nestlings begged more intensely on higher quality diets (Krause et al., 2011). This positive correlation between condition and begging rate is consistent with the positive correlation found by Jacob and Heeb (2013) in the UV reflectance of nestling flange. An increase in signal expression is thought to occur when nestlings are in poorer condition and therefore, these two studies contradict my prediction as well as the results of prior studies (e.g. Cotton et al., 1996; Kilner & Johnstone, 1997). However, findings from Krause et al. (2011) also showed no differences in begging duration between nutritional treatments were detected. A previous study on European starlings examined if the mean frequency, mean duration, mean number of syllables and various other components of call structure reflected nestling condition. They found that lower values for call structure could predict nestlings that were in better condition (Jacob et al., 2011). Therefore, European starling nestlings beg less if they are in better condition, which is consistent with my original prediction but not supported with my findings.

Although no relationship between begging duration and body condition was found in my study, various other studies have found a relation with different call characteristics including pitch, intensity (posture) and UV reflectance of nestling flange. For example, Gladbach et al. (2009) studied Wilson's storm petrels (*Oceanites oceanicus*) and found a relationship amongst the pitch of begs and nestling

condition, with poorer condition nestlings begging at a higher frequency than nestlings in better condition. This characteristic also led to these individuals nestling receiving larger meals. It has also been found that hungrier nestlings will increase their begging intensity by, not only gaping, but standing, moving their wings and trying to get the closest spot to the nest opening. Similarly, begging intensity also increases when there is more sibling competition, which could lead to fewer meals to each individual keeping them hungrier longer (Jacob et al., 2011). European starlings can also indicate their condition by the UV reflectance and coloration of the inside of their beak (flange). Nestlings in better condition reflected a higher amount of UV signaling than nestlings in poorer condition (Jacob & Heeb, 2013). These three aspects of signaling were not examined during my study but future studies may benefit from including acoustic and video data.

The frequency (number) of begs for each nest was also assessed, however, due to lack of video cameras, could not be used as overlapping begs (begging bouts) were not distinguishable and an accurate count could not be obtained. However, Krause et al. (2011) did examine the number of begs made by zebra finch nestlings over a one hour period and found no correlation with nutritional treatments.

There have been various findings that show begging characteristics are signals of nestling condition (i.e. honest signal). The contradiction amongst the compared studies suggests that begging behaviour, as a condition indicator could be a species-specific trait. As well, particular characteristics may indicate condition in one species, but not another, suggesting that individual species may have adapted a more suitable method of signaling nestling need. For example, in European starlings

begging duration may not signal condition but perhaps another acoustic characteristic or combination of acoustic and visual signals together convey need. Conversely, not all of the mentioned results agree with the honest-signaling hypothesis, which suggests begging calls are an honest signal of nestlings need. As cited, zebra finches actually beg more intensely when in better condition (Krasue et al., 2011). My study and some others have found that begging behaviour is influenced by siblings, suggesting that individual begging may not be an honest signal (Parker et al., 2002; Krause et al., 2011). Contrasting, Cotton et al. (1996) and Thompson et al. (2013) found that begging is not influenced by siblings and appears to be a reliable, honest signal of their need.

Brood Condition and Fledging Success

As predicted, brood condition was reduced in second broods when compared to first broods. This finding is consistent with those of previous studies also conducted on European starlings that examined the differences in condition between first and second broods (Jourdie et al., 2004; Bize et al., 2006; Serra et al., 2012). We observed that second broods had more parasites than first broods (Barber, pers. comm., 2013). Several studies have found increased temperatures are associated with increased parasite loads. There was tendency, though not significant, for broods in 2012 to be in better condition than broods in 2011 even though a previous study on the same population during the same years found that *C. hemapterus* was greatly reduced in 2011 compared with 2012 (11:117 respectively) (Hornsby et al., 2013). However, these numbers are still significantly lower than those found by other studies examining parasite abundance (Liker et al., 2001). Also,

López-Rull et al., (2010) found an increased abundance of *C. hemapterus* in second broods of Spotless starlings (*Sturnus unicolor*). Though my study did not find a significant positive correlation between nestling condition and temperatures, an increased number of parasites, coupled with reduced food availability could leave second broods at a disadvantage as they can put less energy towards growth.

Several studies have shown a decrease in immune responsiveness between first and second broods (López-Rull et al., 2011; Wilk et al., 2006). Second brood nestlings may not have the ability to defend against parasites, which would reduce the amount of energy allocated to growth and/or vocalizing their need. Although it seems that ectoparasites would have a large effect on nestling condition, it did not seem to affect the nestlings studied in Hornsby et al. (2013). Though, there could have been multiple ectoparasites in the nest, only *C. hemapterus* was assessed. It also appears that *C. hemapterus* did not have an effect on the fledging success of the nestlings as 2011 showed only 11 parasites in the Hornsby et al (2013) study but in the current study, the year 2011 showed significantly reduced fledging success (Figure 9). Although one could assume the differences in fledging success between years could be caused by poor environmental conditions, the differences in mean temperature or total precipitation between years were not analyzed.

Parasites cannot entirely explain the decrease in nestling condition observed in second broods, but perhaps the environmental conditions could negatively affect available resources for growing broods. It is possible that during this study (2011 & 2012), precipitation had an effect on food availability, thermoregulation and/or parent's ability to provision their offspring; all of which would affect nestling's

condition. Total precipitation was negatively correlation with brood condition in this study (Figure 7). It is also known, with the current climate trends that weather events will be less predictable and more extreme, potentially having further consequences on nestling condition and overall survival (Møller, 2011; Bize et al., 2010).

It is apparent that some aspect of the environment or parental ability to provision changes during the second brood as nestlings can only maintain good condition if there are fewer siblings. During the first brood, the condition of the nestlings stays fairly constant regardless of the number of nestlings in a nest. This suggests that parents have enough energy with enough resources to provide almost equal distribution of these resources. The opposite findings are seen in second broods, as larger second broods had a lower brood condition than smaller second broods (Figure 8). There may not be enough food to provide to larger broods later in the season or parents may be physically exhausted from feeding and fledging the first brood and can only allocate enough energy to provide well for a smaller brood. Therefore, the ecological conditions during the time of second broods only supply enough resources (parent energy and food) to meet requirements of up to three nestlings and if there are more nestlings, these resources get spread out reducing condition for longer. Diminished resources would have consequences on the growth and condition of larger second broods. In fact, Gruebler & Naef-Daenzer (2008a) found that even though feeding rates increased in second broods, the food supply was greatly reduced and second broods were not actually receiving more food but instead received smaller meals. Important food supplies are often day length-

dependent and temperature-dependent, meaning that as the season progresses and temperature increases, resources are reduced, as is the amount of time in which to provide them. In a study on barn swallows day length was identified as the variable that most constrained provisioning to larger broods. A large portion of the day is spent provisioning regardless of brood size. Parents would not be able to increase much more time spent foraging for more offspring. (Tinbergen & Verhulst, 2000). However, day length cannot explain the decrease in condition observed in my study for larger second broods as the difference in day length between first and second broods likely only differs by a few minutes. Also, the Halifax population of European starlings laid their second clutch on or near the summer solstice, a month earlier than the second clutch of barn swallows is laid. So it is more likely that first broods of European starlings have a shorter day length.

Conclusion:

In conclusion, there was no evidence that begging duration was an indicator of a nestling's condition in European starlings. Previous studies on European starlings and other altricial species found significant relationships between various call characteristics and condition. Nestling condition was significantly reduced in second broods. Condition was negatively correlated with precipitation. However, condition was unaffected by temperature changes in our population. It is unlikely that day length is significantly reduced from May to June to be the cause of reduced condition in larger second broods. This study found no evidence suggesting why fledging success would be reduced in 2011 but is most likely due to annual differences in ecological conditions. I plan to conduct further research to determine if temperature and precipitation were significantly different between 2011 and 2012, which could explain the differences observed.

My study is a contribution to the evidence for sibling competition affecting begging signaling and brood condition in nestling birds. This is an important relationship, as parents must have the ability to minimize sibling competition in order to maximize reproductive success to produce the highest number of best quality nestlings to ensure recruitment to pass on their genes and maintain the population size.

Attempting to relate certain begging characteristics to life history traits may provide more conclusive and consistent results. Parent-offspring communication is widely studied, however, due to conflicted findings further research is required.

Literature Cited:

- Avilés S.J.M., Pe´ Rez-Contreras T., Navarro C. & Soler J.J. (2009) Male Spotless Starlings Adjust Feeding Effort Based On Egg Spots Revealing Ectoparasite Load. *Animal Behaviour*. Vol.78:993–999
- Berthold P. (1976) The control and significance of animal and vegetable nutrition in omnivorous songbirds. *Ardea*. Vol.64:140–153
- Bize P., Stocker A., Jenni-Eiermann S., Gasparini J. & Roulin A. (2010) Sudden weather deterioration but not brood size affects baseline corticosterone levels in nestling Alpine swifts. *Hormones and Behavior*. Vol.58(4):591-598
- Bize P., Piau R., Moureau B. & Heeb P. (2006) A UV signal of offspring condition mediates context-dependent parental favouritism. *Proceedings of the Royal Society B*. Vol.273:2063–2068
- Bize P., Roulin A., Bersier L.-F., Pfluger D. & Richner H. (2003) Parasitism and developmental plasticity in alpine swift nestlings. *Animal Ecology*. Vol. 72:633–639
- Bulmer E., Celis P. & Gil D. (2008) Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). *Behavioural Ecology*. Vol.19:279–284
- Christe P., Lope F., Gonzalez G., Saino N. & Møller A.P. (2001) The influence of environmental conditions on immune responses, morphology and recapture probability of nestling house martins (*Delichon urbica*). *Oecologia*. Vol.126:333–338
- Christe P., Richner H. & Oppliger A. (1996) Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behavioral Ecology*. Vol.7:127–131
- Christians J.K., Evanson M. & Aiken J.J. (2001) Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *Animal Ecology*. Vol.70:1080-1087
- Cody M.L (1966) A General Theory of Clutch Size. *Evolution*. Vol.20:174-184
- Cotton P.A., Kacelnik A., Wright J. (1996) Chick begging as a signal: are nestlings honest? *Behavioural Ecology*. Vol.7:178–182
- Coulson J.C. (1962) The biology of *Tipula subnodicornis* Zetterstedt, with comparative observations on *Tipula paludosa* Meigen. *Animal Ecology*. Vol 31:1-21

- Cramp S. (1998) The complete birds of the western Palearctic on CDROM. Oxford University Press, Oxford
- Davis J.N., Todd P.M. & Bullock S. (1999). Environment quality predicts parental provisioning decisions. *Proceedings of the Royal Society B: Biology*. Vol.266: 1791-1797
- Dugas M.B. (2009) House sparrow, *Passer domesticus*, parents preferentially feed nestlings with mouth colours that appear carotenoid-rich. *Animal Behaviour*. Vol.78:767-772
- Environment Canada (2011-2012) Sunrise/Sunset Calculator. Accessed From www.ec.gc.ca
- Feare C.J. (1984) The Starling. Oxford Press, Oxford
- Finlay J.C. (1976) Some effects of weather on Purple Martin activity. *Auk*. Vol.9: 231-244
- Floyd T. (2008) Smithsonian Field Guide to the Birds of North America. Scott & Nix Inc. HarperCollins publishing. pp:364
- Freitag F. (1937) Aus dem Leben beringter Star zur Fortpflanzungszeit II. *Ibid*. Vol 9:43-49
- Garcia-Vigon E., Veiga J.P. & Cordero P.J. (2009) Male feeding rate and extrapair paternity in the facultatively polygynous spotless starling. *Animal Behaviour*. 78:1335-1341
- Gladbach A., Büßer C., Mundry R. & Quillfeldt P. (2009) Acoustic parameters of begging calls indicate chick body condition in Wilson's storm petrels *Oceanites oceanicus*. *Journal of Ethology*. Vol.27:267-274
- Godfray H.C. J. (1991) Signalling of need by offspring to their parents. *Nature*. Vol.352:328-330
- Godfray H.C.J. (1995) Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Animal Nature*. Vol.146:1-24
- GraphPad Prism version 6.00 for Macintosh, GraphPad Software, La Jolla California USA, www.graphpad.com".
- Granadeiro J.P., Bolton M., Silva M.C., Nunes M. & Furness R.W. (2000) Responses of breeding Cory's shearwater, *Calonectris diomedea*, to experimental manipulation of chick condition. *Behavioural Ecology*. Vol.11:274-281

- Grüebler M.U. (2007) Time constraints of breeding twice. On the fitness relevance of timing of reproduction and post-fledging parental investment in the barn swallow (*Hirundo rustica*). Ph.D. thesis, University of Zurich
- Grüebler M.U. & Naef-Daenzer B. (2008a) Postfledging parental effort in barn swallows: evidence for a trade-off in the allocation of time between broods. *Animal Behaviour*. Vol.75:1877-1884
- Grüebler M.U. & Naef-Daenzer B. (2008b) Fitness Consequences of Pre- and Post-Fledging Timing Decisions in a Double-Brooded Passerine. *Ecology*. Vol. 89:2736-2745
- Gustaffson L. & Sutherland W.J. (1988) The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature*. Vol.335:813-815
- Haig D. (1990) Brood reduction and optimal parental investment when offspring differ in quality. *Animal Nature*. Vol.136:550-556
- Halupka K. (1998) Vocal begging by nestlings and vulnerability to nest predation in meadow pipits *Anthus pratensis*: to what extent do predation costs of begging exist? *Ibis*. Vol.140:144-149
- Higgins P.J., Peter J.M. & Cowling S.J. (2006) Handbook of Australian, New Zealand and Antarctic birds. Volume 7: Boatbill to starlings. Melbourne: Oxford University Press.
- Hornsby M.A.W., Fairn E.R. & Barber C.A (2013) Male European starlings do not use egg spots as a cue to adjust investment in nestlings. *The Wilson Journal of Ornithology*. Vol.125:109-115
- Jacob S. & Heeb P. (2013) Mouth color components of begging are dynamic signals of quality in European starling nestlings. *Avian Biology*. Vol.44: 39-44
- Jacob S., Rieucan G. & Heeb P. (2011) Multimodal begging signals reflect independent indices of nestling condition in European starlings. *Behavioural Ecology*. Vol.22:1249-1255
- Johnstone R.A. (2004) Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist*. Vol.163:388-406
- Jourdie V., Moureau B., Bennet A.T.D. & Heeb P. (2004) Ultraviolet reflectance by the skin of nestlings. *Nature*. Vol 431: 262
- Kacelnik A., Cotton P.A., Stirling L. & Wright J. (1995) Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proceedings of the Royal Society B*. Vol.259:259-263.

- Kaufman K. (1996) *Lives of North American Birds*. Houghton Mifflin Company. pp:500.
- Kessel B. (1957) A Study of the Breeding Biology of the European Starling (*Sturnus vulgaris* L.) in North America. *The American Midland Naturalist*. Vol.58(2):257-331
- Kilner R. & Johnstone R.A. (1997) Begging the question: are offspring solicitation behaviours signals of need? *Tree*. Vol.12(1):11-15
- Kluijver H.N. (1933) Bijdrage tot de Biologie en de Ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* Linn.) gedurende zijn Voortplantingstijd. Med.Plantenziektenkundigen. *Dienst te Wagenigen*, no. 69
- Krause T.E., Honarmand M. & Naguib M. (2011) Zebra finch nestlings beg more under better nutritional conditions. *Behaviour*. Vol.148:1239-1255
- Krementz D.G., Nichols J.D. & Hines J.E. (1989) Postfledging survival of European Starlings. *Ecology*. Vol.70:646-655
- Kumar A. (2003) Acoustic communication in birds: differences in songs and calls, their production and biological significance. *Resonance*. Vol.8:44-55
- Lack D. (1947) The Significance of Clutch Size. *Ibis*. Vol.89:302-352
- Leonard M.L., & Horn A.G. (2001) Begging in the absence of parents by nestling tree swallows. *Behavioral Ecology*. Vol.12(4):501-505
- Leonard M.L. & Horn A.G. (2012) Ambient noise increases missed detections in nestling birds. *Biology Letters*. Vol.8:530-532
- Leonard M.L., Horn A.G., Gozna A. & Ramen S. (2000) Brood size and begging intensity in nestling birds. *Behavioural Ecology*. Vol.11:196-201
- Leonard M.L., Horn A.G. & Mukhida A. (2005) False alarms and begging in nestling birds. *Animal Behaviour*. Vol.69:701-708
- Liker A., Ma' Rkus M., Voza' R A., Zemankovics E. & Ro' Zsa L. (2001) Distribution Of *Carnus Hemapterus* In A Starling Colony. *Canadian Journal Of Zoology*. Vol.79:574-580
- Linden M. & Møller A. P. (1989) Cost of reproduction and covariation of life-history traits in birds. *Trends in Ecology & Evolution*. Vol.4:367-371
- López-Rull I., Celis P., Salaberria C., Puerta M. & Gil D. (2011) Postfledging recruitment in relation to nestling plasma testosterone and

- immunocompetence in the spotless starling. *Functional Ecology*. Vol.25:500–508
- López-Rull I., Salaberria C. & Gil D. (2010) Seasonal Decline In Yolk Size And Seasonal Androgen Concentration In A Double-Brooded Passerine. *Ardeola*. Vol.57:321–332
- Marshall A.G. (1981) The ecology of ectoparasites insects. *Academic Press*, London
- Martin A.C., Zim H.S. & Nelson A.L. (1951) American Wild- life and Plants: A Guide to Wildlife Food Habits. Dover, New York.
- Martin T.E. (1987) Food as a limit on breeding birds: a lifehistory perspective. *Annual Review of Ecology and Systematics*. Vol.18:453–487
- Maurer G., Magrath R.D., Leonard M.L., Horn A.G. & Donnelly C. (2003) Begging to differ: scrubwren nestlings beg to alarm calls and vocalize when parents are absent. *Animal Behaviour*. Vol.65:1045-1055
- Maynard Smith J. & Harper D. (2003) Animal Signals. Oxford University Press, New York.
- McCarty J.P. & Winkler D.W. (1999) Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. *Ibis*. Vol.141:286–296
- McIntyre E., Leonard M.L. & Horn A.G. (2014) Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. *Animal Behaviour*. Vol.87:85-89
- Mennill D.J. & Ratcliffe L.M. (2000) A Field Test of Syrinx Sound Analysis Software in Interactive Playback. *Animal Sound and its Recording*. Vol.11:77-86
- Merino S. & Potti J. (1995) Mites And Blowflies Decrease Growth And Survival In Nestling Pied Fly- Catchers. *Oikos*. Vol.73:95–103
- Møller A.P. (2011) Behavioural and life history responses to extreme climatic conditions: studies on a migratory songbird. *Current Zoology*, Vol.57:351-362
- Møller A.P. (1997) Parasitism and the evolution of host life history. In: Host–Parasite Evolution: General Principles and Avian Models. Oxford Univesity Press, Oxford
- Møller A.P. & Saino N. (2004) Immune response and survival. *Oikos*. Vol.104:299–304

- Mondloch C.J. (1995) Chick hunger and begging affect parental allocation of feedings in pigeons. *Animal Behaviour*. Vol.49:601–613
- O'Brien E.L. & Dawson D. (2000) Parasite mediated growth patterns and nutritional constraints in cavity - nesting bird. *Animal Ecology*. Vol.77:127-134
- Parker G.A., Royle N.J. & Hartley I.R. (2002) Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology*. Vol.5:206–215
- Pinxten R., Eens M. & Verheyen R.F. (1990) Intermediate clutches in the Starling (*Sturnus vulgaris*): replacement clutches, additional clutches of polygynous males or late first clutches. *Journal of Ornithology*. Vol. 131:141-150
- Redondo T. & Castro F. (1992) The increase in risk of predation with begging activity in broods of magpies *Pica pica*. *Ibis*. Vol.134:180–187
- Richner H., Oppliger A. & Christe P. (1993) Effect of an ectoparasite on reproduction in great tits. *Animal Ecology*. Vol.62:703–710
- Roulin A. (1999) Fécondité de la mouche *Carnus hemapterus*, ectoparasite des jeunes chouettes effraies *Tyto alba*. *Alauda*. Vol.67:205–212
- Roulin A., Kolliker M. & Richner H. (2000) Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society of London B*. Vol.267:459-463
- Schwagmeyer P.L. & Mock D.W. (2008) Parental provisioning and offspring fitness: size matters. *Animal Behaviour*. Vol.75:291–298
- Serra L., Pirrello S., Caprioli M., Griggio M., Andreotti A., Romano A., Pilastro A., Saino N., Sacchi R., Galeotti P., Fasola M., Spina F. & Rubolini D. (2012) Seasonal decline of offspring quality in the European starling *Sturnus vulgaris*: an immune challenge experiment. *Behavioural Ecology Sociobiology*. Vol.66:697-709
- Simon A., Thomas D., Blondel J., Perret P. & Lambrechts M.M. (2004) Physiological ecology of Mediterranean blue tits (*Parus caeruleus* L.): effects of ectoparasites (*Protocalliphora* spp.) and food abundance on metabolic capacity of nestlings. *Physiological and Biochemical Zoology*. Vol.77:492–501
- Slabbekoorn H. & Peet M. (2003) Birds sing at a higher pitch in urban noise. *Nature*. Vol.424:267
- Soler J.J. & Avilés J.M. (2010) Sibling Competition and Conspicuousness of Nestling Gapes in Altricial Birds: A Comparative Study. *Plos ONE*. Vol.5:1-8

- Stephens P.A., Buskirk S.W. & Martinez del Rio C. (2007) Inference in ecology and evolution. *Trends in Ecology and Evolution*. Vol.22:192–197
- Tarwater C.E., Kelley J.P. & Brawn J.D. (2009) Parental response to elevated begging in a high predation, tropical environment. *Animal Behaviour*. Vol.78:1239-1245
- Thompson M.L.P. (1992) Reproductive success and survival of swallows *Hirundo rustica*: effects of age and breeding condition. Ph.D. thesis, University of Stirling
- Thompson A.M., Ridley A.R., Hockey P.A.R., Finch F.M., Britton A. & Raihani N.J. (2013) The influence of siblings on begging behaviour. *Animal Behaviour*. Vol.86:811-819
- Thorogood R., Kilner R.M., Karadas, F. & Ewen, J.G. (2008) Spectral mouth colour of nestlings changes with carotenoid availability. *Functional Ecology*. Vol.22:1044–1051.
- Tinbergen J.M & Verhulst S. (2000) A fixed energetic ceiling to parental effort in the great tit? *Ecology*. Vol.69:323-334
- Verhulst S. & Wiersma P. (1997) Is begging cheap? *Auk*. Vol.114:134
- Webb J.N., Székely T., Houston A. I. & McNamara, J.M. (2002) A theoretical analysis of the energetic costs and consequences of parental care decisions. *Philosophical Transactions of the Royal Society of London, Series B*. Vol.357: 331-340
- Wiens J.A. (1989) The ecology of bird communities. *Processes and variations*. Cambridge University. Press, Cambridge. Volume 1
- Wilk T., Dubiec A. & Cichoń M. (2006) Seasonal decline in cell-mediated immunity of collared flycatcher *Ficedula albicollis* nestlings: does the sex of offspring matter? *Ornithology*. Vol.148:199–205
- Wright J. & Leonard M.L. editors. (2002) The evolution of begging: competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer Academic Publishers.