

Signature page

Do nestlings increase their begging in response to enhanced sibling competition in European Starlings, *Sturnus vulgaris*?

By
Ashton Bradley

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

April 2018, Halifax, Nova Scotia

Copyright Ashton Bradley, 2018

Approved: Colleen Barber, Ph.D

Professor

Approved: Ron Russell, Ph.D

Associate Professor

Date: April 16th, 2018

Do nestlings increase their begging in response to enhanced sibling competition in European Starlings, *Sturnus vulgaris*?

By
Ashton Bradley

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

April 2018, Halifax, Nova Scotia

Copyright Ashton Bradley, 2018

Approved: Colleen Barber, Ph.D
Supervisor
Professor

Approved: Ron Russell, Ph.D
Reader
Associate Professor

Date: April 16th, 2018

Do nestlings increase their begging in response to enhanced sibling competition in European Starlings, *Sturnus vulgaris*?

Ashton Bradley

Abstract

In parent-offspring interactions, nestlings signal their hunger to parents by begging. Parents typically respond by increasing their provisioning rate. This type of communication involves specific vocalizations, postures, and gaping. Begging intensity has been found to honestly reflect hunger levels in European Starlings (*Sturnus vulgaris*), and not be a result of sibling rivalry (dishonest signal). I examined whether begging was an honest signal in a Nova Scotia population of European Starlings, or if it could be influenced by sibling rivalry. I analyzed nestling vocalizations occurring over a 30-min period in 21 nestboxes; each nestbox underwent both a control (natural conditions) and an experimental trial (3-min loop of nestling begging vocalizations from the preceding day was played back for an hour to simulate increased sibling competition for food). I predicted that if nestlings were affected by the enhanced begging of their siblings, they would have an increased number of begging bouts, and produce begging calls for longer during the experimental trial compared to that of the control. However, when looking at the total duration, there was no significant difference between control and experimental trials. Contrarily, there were significantly more begging bouts in the experimental, this did not influence the overall duration. European Starling nestlings did not beg more when presented with increased begging.

April 16th, 2018

Table of Contents

ACKNOWLEDGMENTS	5
LIST OF FIGURES	6
INTRODUCTION.....	8
<i>1.1 Signalling and Competition Theory.....</i>	<i>8</i>
<i>1.2 Sibling Rivalry</i>	<i>10</i>
<i>1.3 Experiment & Subject</i>	<i>11</i>
METHODS	13
<i>2.1 Pre-Data Collection</i>	<i>13</i>
<i>2.2 Data Collection</i>	<i>14</i>
<i>2.3 Statistical Analysis</i>	<i>15</i>
RESULTS.....	18
<i>3.1 Duration of Vocalizations</i>	<i>18</i>
<i>3.2 Abundance of Begging Calls (Begs vs Bouts).....</i>	<i>23</i>
DISCUSSION	26
<i>4.1 Duration of Vocalizations</i>	<i>26</i>
<i>4.2 Number of Beg vs Bout Calls</i>	<i>28</i>
<i>4.3 Limitations and Future Directions</i>	<i>28</i>
CONCLUSION	30
REFERENCES	31

ACKNOWLEDGMENTS

I would firstly like to thank the Saint Mary's University Faculty of Graduate Studies for providing me with summer funding of my data collection. I would also like to thank Dr. David Dansereau and Dr. Timothy Frasier for all the feedback and contributions that was given in the honours seminar class as well as all the members of this class for their support and feedback. I would also like to thank Hannah Corney for allowing me to use her data for my project. I would like to thank my lab members for their help and support. I would like to thank Dr. Jennifer Foote for being an external supervisor and for all her help with methodology and the Syrinx program. But I would most like to thank my supervisor Dr. Colleen Barber for providing me with all the help I needed as well as constantly pushing me to do my best.

LIST OF FIGURES

- Figure 1.** Design of nestboxes that were placed around the campus of Saint Mary's University, Halifax, NS. The set up for the experimental trial is shown in which additional begging was played back through an MP3 player and nestling vocalizations were collected with a recorder. **15**
- Figure 2.** Spectrogram of various European Starling nestling calls in an annotated 30-min experimental recording in Syrinx (John Burt). **16**
- Figure 3.** Quartile distribution quantifying the total duration (seconds) for all vocalizations (peep, beg, bout) that were annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests). **18**
- Figure 4.** Quartile distribution quantifying the total beg durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests). **19**
- Figure 5.** Quartile distribution quantifying the total bout durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests). **20**

- Figure 6.** Quartile distribution quantifying the total peep durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests). **21**
- Figure 7.** The percentage of beg calls compared between control (no additional begging) and experimental trials (additional begging) proportionally. The beg calls were annotated over a 30-min period for both trials. Each point represents one individual nestbox (n= 21 nests). **23**
- Figure 8.** The percentage of bout calls compared between control (no additional begging) and experimental trials (additional begging) proportionally. The bout calls were annotated over a 30-min period for both trials. Each point represents one individual nestbox (n= 21 nests). **24**

INTRODUCTION

1.1 Signalling and Competition Theory

Signalling amongst animals is a key concept in evolutionary biology and recognizing the cues of signals is vital to the understanding of communication between individuals (Ryan, 1988). Signals can be communicated through vocalizations, displays or chemicals that send information to a receiver that elicits a response that benefits either the sender or the receiver (Ryan, 1988). These benefits could include the warning of a nearby predator, territorial boundaries, mating availability, competitive potential, or food location (Ryan, 1988). Many species have evolved their own ways of communicating between each other, which can be a combination of multiple factors (both vocalizations and physical display) ranging from simple to complex (Dawkins & Guilford, 1991). Alternatively, are these signals an accurate representation of one's own fitness (reproductive ability, strength, competitive potential) or are they a manipulation to gain some sort of benefit? The debate of whether an individual will always send an honest signal or will sometimes convey dishonest signals, manipulated to benefit the sender, has been widely studied (Dawkins R. , 1989). Support has been provided for both signal types, but typically there is more in favour of individuals only sending honest signals due to the potential costs of manipulation (Smith & Harper, 1988).

Competition within an ecosystem is defined as the behaviour in which individuals react towards interactions among or within a species over limited resources, that is essential to both, potentially resulting in harm (Keddy, 2001). The potential resources may include; availability of food, number of females available to reproduce, territory, parental attention and any other factor that is deemed beneficial to an individual (Tilman,

1982). Consequently, these interactions form what is known as competition theory and can be more specifically defined through the separation into two branches; intraspecific (within species) and interspecific (amongst species) (Saito & Takeshi, 2010).

When one species is competing against another species for a limited resource, it is defined as interspecific competition (Tilman, 1982). This form of competition typically occurs through the exploitation of resources that are available in a particular environment (Schoener, 1983). These resource availabilities and competitive capacities between species both contribute to the evolution of competition, that has allowed many individuals the opportunity to fight for the best resources (Tilman, 1982). Additionally, there may be situations where different predators are competing for the same prey, different prey competing for a food source, or everyone fighting for the same home in a habitat (Leisnham, et al., 2014). For example, in the Netherlands, artificial oyster reefs were set up with two species of crab; the European green crab (*Carcinus maenas* Linnaeus) and the brush clawed crab (*Hemigrapsus takanoi* Asakura & Watanabe) (van den Brink & Hutting, 2017). There was one native juvenile species (green crab), and one exotic species (brush clawed crab) in each reef that were initially the same size. The authors found that interspecific competition was present among them for both space and food on the reef, due to significantly greater aggressive behaviours from the European green crab (van den Brink & Hutting, 2017).

The other branch of competition theory is when individuals of the same species compete against one another for the access to a limited resource, defined as intraspecific competition (Bolnick & Smith, 2004). In nature, most adult intraspecific competition occurs amongst the males of a species, but male-female and female-female competition sometimes does occur as well (Bolnick & Smith, 2004). For the most part, the ultimate

goals of male individuals are to increase their overall reproductive success (Davies, et al., 2012). Consequently, male-male competition is shown most often as battle for a single female or a harem of females within a territory (Davies, et al., 2012). This 'battle' may be vocal, visual, physically aggressive or include all the above, but most of the time there is some form of ritualistic pattern being performed (Davies, et al., 2012). This pattern typically starts by assessing their opponent's capabilities before escalating to a physical fight to see whether the benefits of competing outweigh the costs of losing (Bolnick & Smith, 2004).

1.2 Sibling Rivalry

The adult individuals are not the only ones who can participate in competition; many juveniles do as well. More specifically, a form of intraspecific competition amongst juveniles of the same species for food and parental attention is defined as sibling rivalry (Krebs & Davies, 1993). This type of competition may have detrimental effects on the animal's health. For example, one or more individuals may be underdeveloped if some siblings are better competitors (Krebs & Davies, 1993). Additionally, when extreme consequences, such as death occur due to sibling competition, it is defined as siblicide. For example, when there is a shortage of food, senior chicks in a nest of blue-footed boobies (*Sula nebouxii* Milne-Edwards) have typically been seen to kill their siblings (Anderson, 1990). This consequence could have been due to a lack of food, causing an increase in aggressive behaviours (Anderson, 1990). Once the chicks got the necessary food supply their behaviour changed and they became less aggressive. Thus, when selective pressures, such as food and predation, are applied to nestlings it might be

advantageous for one to try and outcompete/eliminate other siblings to increase their own chance for survival (Anderson, 1990).

1.3 Experiment & Subject

The European Starling (*Sturnus vulgaris* Linnaeus) was introduced into North America from 100 individuals that were released in Central Park, New York, in the 1890s (Long, 1981). Since then, the number of individuals has grown exponentially into one of the most abundant species of song birds on the continent (Linz, et al., 2007). These medium-sized, perching birds, display a dark, iridescent plumage coloration that is consistent between males and females (Linz, et al., 2007). However, the only way to distinguish between the two is during the breeding season, when males develop a blue tinge at the base of their beak, and females develop a pink tinge (Smith, et al., 2005). European Starlings are cavity nesters that live in various habitats all over the world but are mostly frequently found in large communal roosts in cities or highly anthropogenic areas (Linz, et al., 2007). A unique feature about this species of song bird is that they possess an endless capacity for vocal learning and can mimic various sounds (Smith, et al., 2005). Correspondingly, the complexity and capacity of their vocal repertoire has been found to benefit male reproductive success, due to female choice (Smith, et al., 2005).

Females typically lay 3-6 eggs, and both parents incubate the eggs over a period of approximately 10-18 days (Kessel, 1957). Once hatched, nestlings lack most feathers and the ability to care for themselves. Both parents feed and care for their offspring over a 20-22 day nestling period (Kessel, 1957). These nestlings start off with a naked body and

a disproportionately large, yellow beak (Linz, et al., 2007). Nestlings are only able to produce innate calls for the first few months of their lives that contribute towards hunger or interpersonal communication (Konishi, 2010). Once males can produce songs, they start learning through the social interactions and song tutors (Chaiken, et al., 1993).

The European Starling is an ideal study species for examining whether begging signals are honest or dishonest as nests are easy to access and the adults adapt well to human presence (Chaiken, et al., 1993). This model organism has been the focus for many studies that have looked at learning behaviour as well as nesting behaviour, but for my study I wanted to focus specifically on nestling-nestling communication. Furthermore, I wanted to examine whether increasing the begging vocalizations in the nest would elicit competition behaviour amongst the sibling's present.

There have been previous studies that support the idea of increased nestling begging as an honest and reliable signal of hunger (Cotton et al., 1996), as well as studies that support increased begging as dishonest signals for sibling rivalry (Kacelnik et al., 1995). My study looked at previously recorded data from the summer of 2016 that contained two types of trials differing in the manipulation of additional vocalizations; control had no added vocalizations, while experimental had additional pre-recorded vocalizations. There was a total of 21 nestboxes used for each control and experimental trial. The objective of this study was to examine whether nestlings increased their begging calls in response to enhanced sibling rivalry. I predict that the experimental trials, having enhanced begging vocalizations, will have a greater total duration of begging than the control trials due to the nestlings competing among each other. I also predict that bout calls will be longer in total duration.

METHODS

2.1 Pre-Data Collection

Audio recordings of nestlings from 21 nestboxes were obtained from a previous experimental study that investigated parental provisioning with artificially increased begging amongst European starlings (Corney & Barber, In Press). These nest boxes were scattered across the campus of Saint Mary's University in Halifax, Nova Scotia, Canada (44° 37' 54.07" N, 63° 34' 47.09" W). Observations were made by watching a nest box for one hour and recording the number of times each parent provisioned the nestlings. Each of the 21 nestboxes had both a control and an experimental trial. The experimental trial differed from that of the control by the addition of playing a 3-min audio loop of these same nestlings begging from the previous day. In this way, there was enhanced begging in the experimental trials (Figure 1).

My study was determining whether sibling rivalry existed more so in the experimental versus the control due to each nestling hearing more begging. Further, I also looked at the presence or absence of sibling rivalry by quantifying various call time lengths. There were two categories of calls that were examined: begging vs. non-begging calls (Leonard & Horn, 2001). From these groups three vocalizations begging calls were classified as; begs (0.1-0.3 seconds long) and begging bouts (+0.3 seconds long). The non-begging calls were classified as peeps (0.01-0.1 seconds long).

To control for consistency and accurate repetition, each audio file was opened in Audacity and spliced at the 30-minute mark, after the first parental provision, while everything after in the recording was removed. These new 30-minute audio files were

then exported and saved as MP3s. All audio files were stored in the same computer folder, establishing a location thread for further analysis.

2.2 Data Collection

The new audio files were opened and analyzed one at a time in the Syrinx software program (John Burt, Seattle, Washington). Once opened, an annotation link was added to the audio file and from this an audio metafile was created for that specific audio file. These files were then saved at the same location as the original audio file. As soon as everything was established, the annotation process began. The audio metafile linked to each audio file was then annotated (marked) for each defined call. This was done by starting at time 0.0 seconds, where the first feeding occurred and going through the entire 30 minutes marking every call as a peep, beg or begging bout depending on the criteria previously mentioned. Annotations were created by using the mouse on the computer to draw a box from the beginning of a call's spectrogram (visible wave on program) to its end (Figure 2).

The contrast of these visible representations of sound was decreased to allow more accurate annotation of the calls. The experimental recording had the 3-min loop of nestling begging in the background, but these vocalizations were easily distinguished from the actual nestling calls due to the decreased contrast and frequency difference between the two. Once all calls on the entire metafile were annotated, the next audio file was opened, and the process was repeated. Each audio metafile automatically created an annotated metafile with a list of all the marked calls throughout the analysis, with start

and end time differences for all. This procedure was done until all 42 recordings (n=21 broods) were completed

After the data were collected, an Microsoft Excel (V1802) spreadsheet was made for each nest box. The information contained in the annotated metafiles was then copied and pasted into their corresponding spreadsheet.

2.3 Statistical Analysis

The data were analyzed in the computer program Graphpad Prism 7 for all tests. Since the data collected were in the form of count information, a two-way comparison test was performed to look at variability.

A normality test was performed on all data sets being observed to determine normality of the distribution. After the normality tests were completed, either a two-way paired t-test or a Wilcoxon rank sum test were performed. Results were considered significant when $p \leq 0.05$.

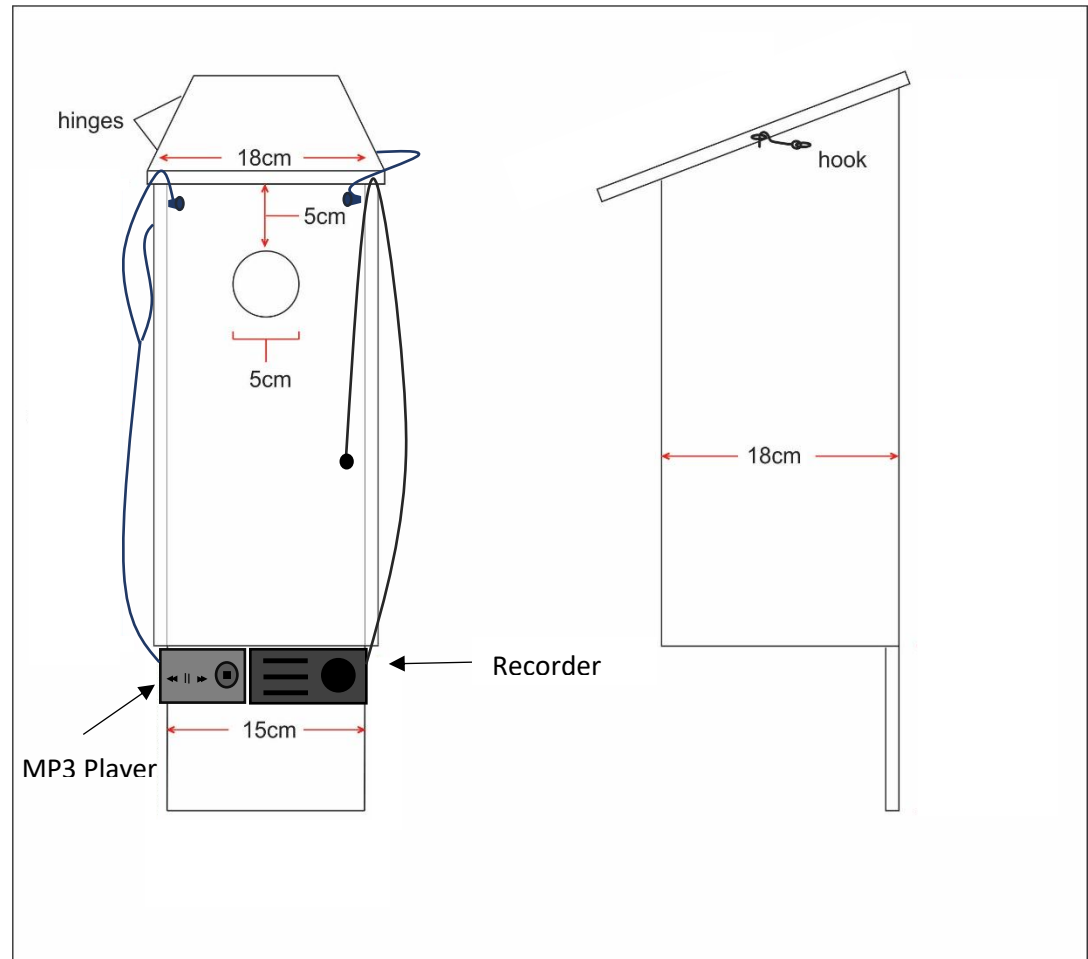


Figure 1. Design of nestboxes that were placed around the campus of Saint Mary's University, Halifax, NS (Corney & Barber, In Press). The set up for the experimental trial is shown in which additional begging was played back through an MP3 player and nestling vocalizations were collected with a recorder.

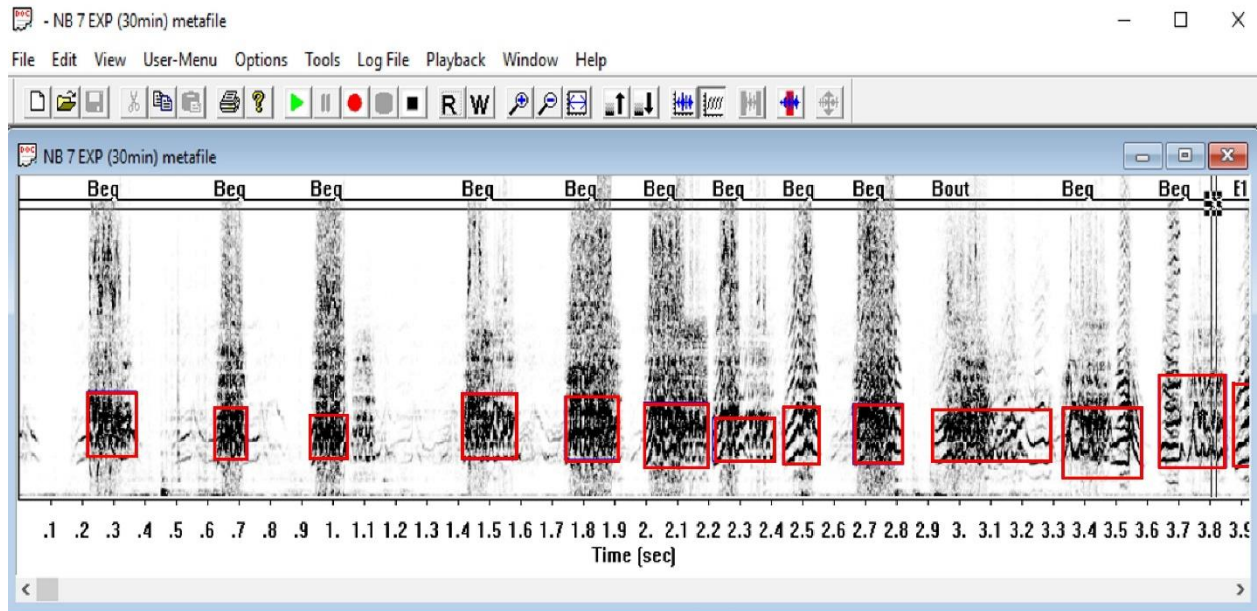


Figure 2. Spectrogram of various European Starling nestling calls in an annotated (see boxes) 30-min experimental recording in the Syrinx software program (John Burt).

RESULTS

3.1 Duration of Vocalizations

The total duration of all vocalizations (peeps, begs and bouts), did not differ significantly between the control trials (no additional begging) and experimental trials (additional begging), (Wilcoxon $W= 9.00$, $n= 21$ nestboxes, $p= 0.89$, Figure 3). Nestlings produced similar durations of overall vocalizations amongst the control and experimental trials (Figure 3).

The total duration of individual begs (0.1 - 0.3 seconds) was significantly longer in control trials than in experimental trials (Wilcoxon $W= -221$, $n= 21$ nestboxes, $p < 0.0001$, Figure 4). These nestlings produced more of this type of call in the control trials (no additional begging) than they did in the experimental trials (Figure 4).

The total duration of bouts (0.3+ seconds) was significantly shorter in controls than experimental trials (Wilcoxon $W= 193$, $n= 21$ nestbox, $p= 0.0003$, Figure 5). Therefore, the nestlings produced more bouts in the experimental trials (additional begging) than in the control trials, overall (Figure 5).

Lastly, total duration of peeps (0.01 - 0.1 seconds) did not differ significantly between the control and experimental trials (Wilcoxon $W= -74$, $n= 21$ nestbox, $p= 0.18$, Figure 6). Nestlings vocalized similar amounts of peep calls between both trials (Figure 6).

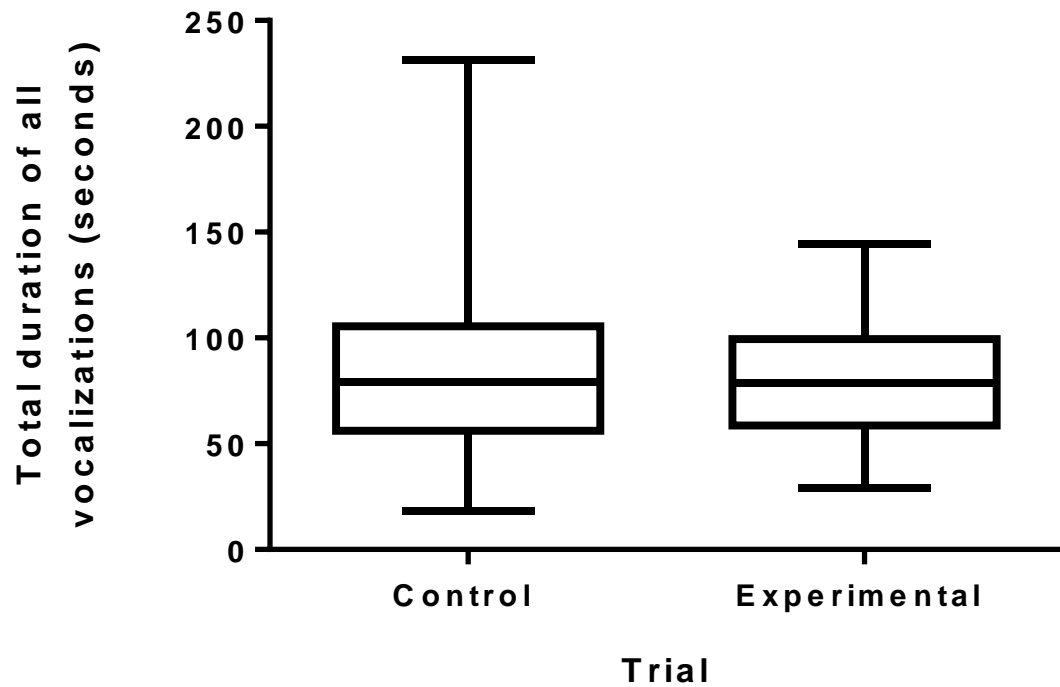


Figure 3. Quartile distribution quantifying the total duration (seconds) for all vocalizations (peep, beg, bout) that were annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests).

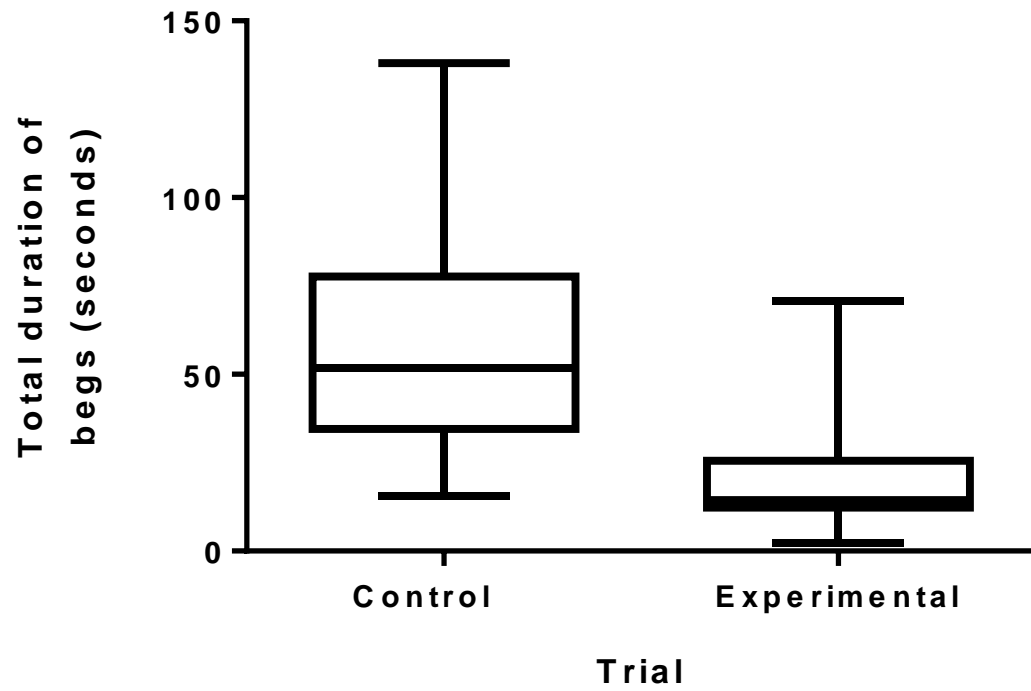


Figure 4. Quartile distribution quantifying the total beg durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests).

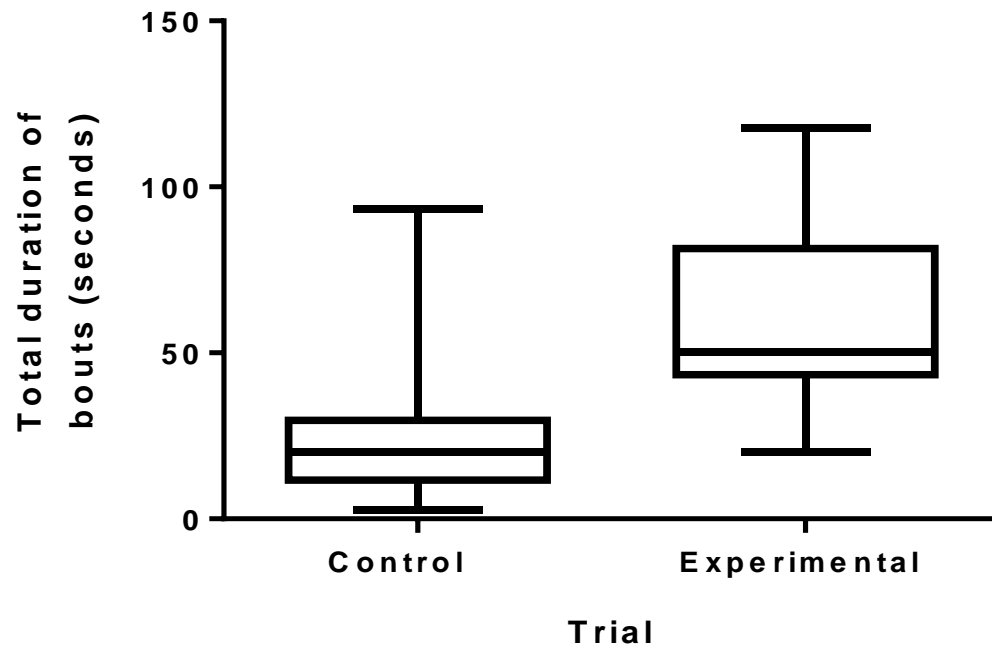


Figure 5. Quartile distribution quantifying the total bout durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests).

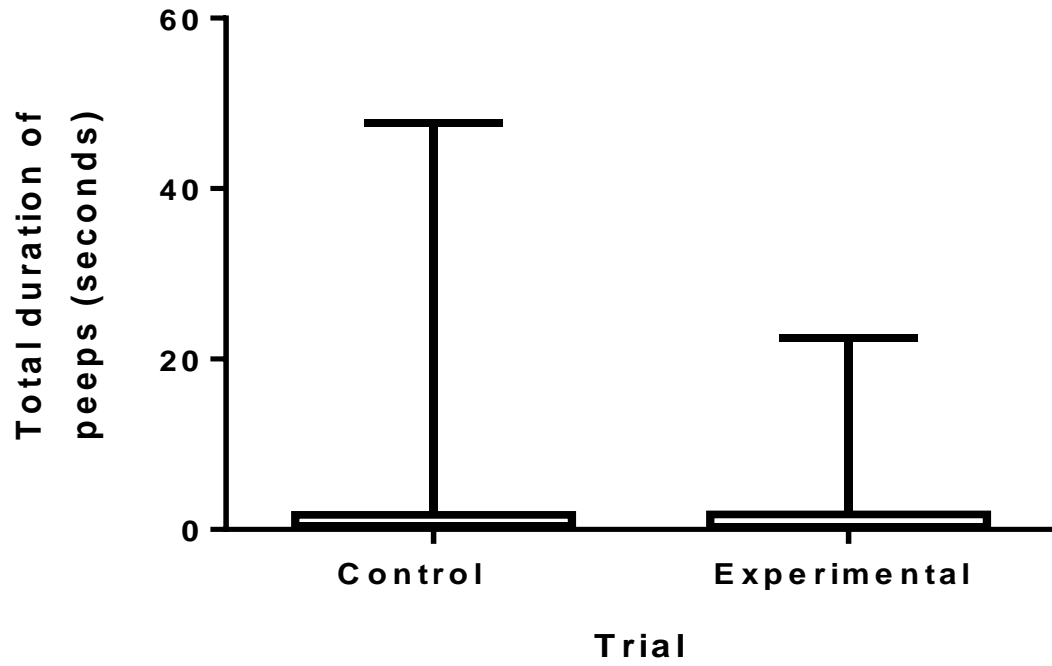


Figure 6. Quartile distribution quantifying the total peep durations (seconds) annotated over a 30-min period for both control (no additional begging) and experimental (additional begging) trials over 21 nestboxes (n=21 nests).

3.2 Abundance of Begging Calls (Begs vs Bouts)

The percentage of begs (%) and the percentage of bouts (%) within the 30 min periods were compared between the control and experimental trial for each of the 21 nestboxes. Firstly, beg calls were found to be more numerous in the control compared to the experimental trials (Paired t-test $t = 10.429$, $n = 21$ nestbox, $p < 0.0001$, Figure 7).

A significantly greater percentage of bouts occurred in the experimental trials as compared to the controls (Paired t-test $t = -11.067$, $n = 21$ nestbox, $p < 0.0001$, Figure 8).

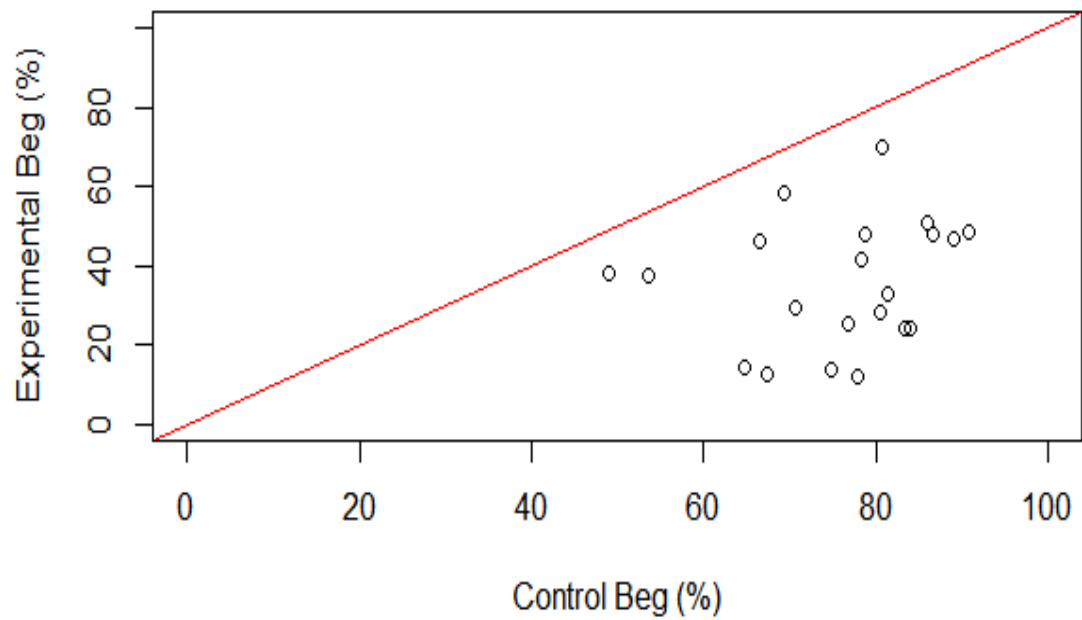


Figure 7. The percentage of beg calls compared between control (no additional begging) and experimental trials (additional begging) proportionally. The beg calls were annotated over a 30-min period for both trials. Each point represents one individual nestbox (n= 21 nests).

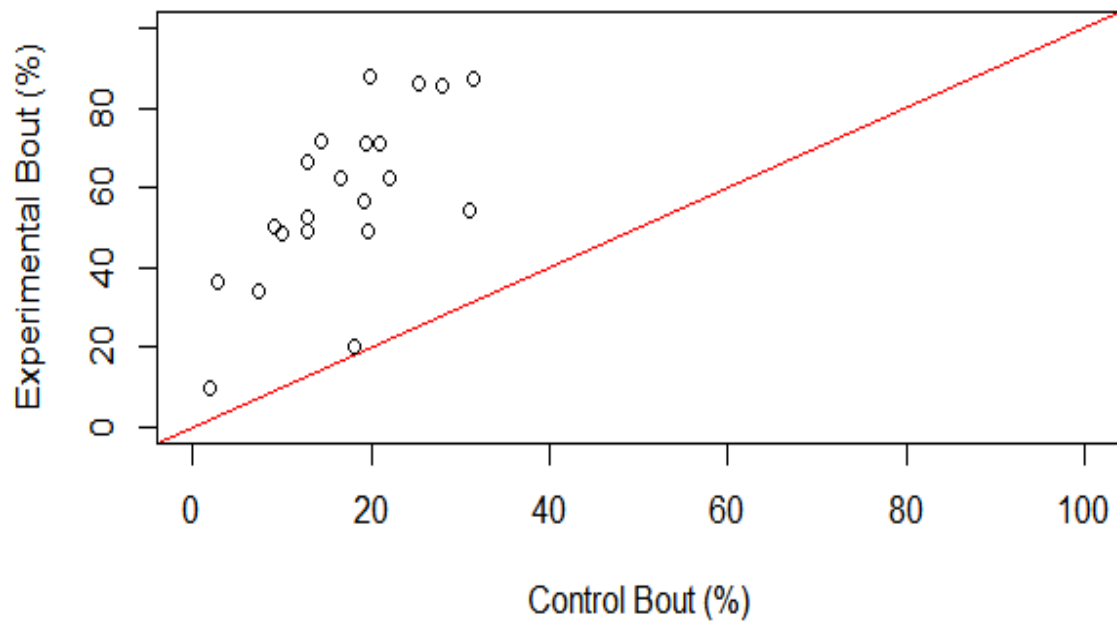


Figure 8. The percentage of bout calls compared between control (no additional begging) and experimental trials (additional begging) proportionally. The bout calls were annotated over a 30-min period for both trials. Each point represents one individual nestbox (n= 21 nests).

DISCUSSION

4.1 Duration of Vocalizations

The main finding from this study was that the total duration of begs and begging bouts combined, did not vary significantly between the control and experimental trials. Therefore, the prediction that total duration of nestling vocalizations would be greater in the experimental trial than in the control trial was not supported. According to Wright & Leonard (2002), nestlings should produce begging calls for a longer duration when there is increased begging due to the number of nestling's present (e.g. larger clutch size). The nestboxes used in my study had different numbers of nestling's present (3-5). Therefore, begging calls in the nestboxes with fewer individuals (lower nestling density) would possibly be less intense and of less duration since there are smaller numbers of vocalizations being produced.

When examining begs and bouts separately, a difference in duration was detected between control and experimental trials. The total duration of bout calls was greater in the experimental trials than in the control trials. A study done on nestling tree swallows (*Tachycineta bicolor*) found that larger numbers of nestlings and therefore more vocalizations being made, begging intensity and duration was greater (Leonard et al., 2000). The results from their study only correlate with my findings on the level of individual calls and not the overall duration of all vocalizations (Leonard et al., 2000). Perhaps the explanation for the difference between these two analyses of duration lies not with what is being exhibited but by how and how much it costs to display with the development of learning among the nestlings.

If total duration between the control and experimental trials is the main indicator of increased vocalizations, then why is it that the longer bout calls are produced more in the experimental manipulation? A possible reason for this could be due to the cost-benefit conflict of the nestling's energy expenditure (Parker & Macnair, 1979). The more intense and longer the call is, the more energy that is needed from the nestling to produce it (Parker & Macnair, 1979). Therefore, when a nestling is in a situation where there are a greater number of perceived competitive individuals (physical, audio), costs versus benefits are assessed (Parker & Macnair, 1979). For example, a nestling that is present in the experimental trial, with the greater number of perceived competitors, would have to beg more intensely to get the same amount of resources (food, parental attention) as compared to when they would be alone or have fewer siblings, due to that individual receiving all the resources. Correspondingly, there would be an important trade-off for this individual between the intensity of begging and likelihood of predation because the more time spent on begging and the louder it is, the greater is the risk of being heard by a predator (Lima, 1987). On the other hand, a nestling in the control trial would have fewer perceived competitors and therefore would not need to beg as loud or as long to get the same amount of resources (Parker & Macnair, 1979). Therefore, the apparent contradiction between no significant difference in total duration of combined begs and bouts and percentage of begs and the significant difference found examining duration of each call type separately, might possibly be explained by a balancing effect between energy intake and output that is exhibited differently but has similar overall values in the end. This would be related to Optimal Foraging Theory.

4.2 Number of Beg vs Bout Calls

The total number of begging calls (begs and begging bouts) was compared between the control and experimental trials. The findings from this analysis resulted in significant variation in both call types, showing that bout calls were more abundant in the experimental trials. Bout calls were longer (+0.3 seconds) and more intense than beg calls and are associated with intense hunger as well as competition (Wright & Leonard, 2002). Therefore, since there is a larger number of bout calls in the experimentally manipulated trials, begging intensity could be perceived as being greater. On the other hand, abundance is not as good an indicator as is total duration when examining intraspecific competition because it does not compare everything together. A possible reason as to why these two variables differ in results could be explained by cooperative begging. Johnstone (2004) hypothesized that sibling begging is cooperative and therefore benefits the brood, such that an individual who increases their begging intensity to attract parental attention, ultimately provides more resources for all the nestlings (Johnstone, 2004), by increasing provisioning rates (Corney & Barber, In Press). This theory supports honest signaling of current individual capacities and possibly explains why one type of call is more abundant than another in a particular situation (Johnstone, 2004).

4.3 Limitations and Future Directions

The main limitation found in this study was the loudness difference between the added vocalizations and the actual nestlings during the experimental trials. The nestlings may not have perceived the audio recording as other individuals present in the nestbox due to their being less loud, even though they were loud enough to be heard. Furthermore,

this may have influenced why total duration did not vary between trial types. Therefore, quantifying the recordings as competitors would be difficult to do unless loudness was equal. The variation in the number of nestlings between the observed nestboxes may have also influenced the outcome of this study. The nestboxes with fewer nestlings may have produced fewer vocalizations, therefore, limiting the total duration and abundance of calls that could have been analyzed. Another important limiting factor from this study could be the location of the nestboxes and their surrounding environments. One nestbox might encounter more anthropogenic noise than another (noise pollution) (Rabin et al., 2003). These could include: traffic (foot and vehicles), construction, and human contact and abundance, as well as, natural variables such as weather, predators and other animals (Rabin et al., 2003). Therefore, all these factors could possibly affect the number of vocalizations, type of call and the amount of parent provisioning.

In future studies, there are a few things that should be changed and added to the experiment to allow a more comprehensive understanding of sibling rivalry. Firstly, when looking at vocalizations, the added begging would need to match a particular range that resembles that of the actual nestlings present in the nestbox to allow competition to be quantified. Secondly, alternative variables such as; video recording, nestling tagging (fluorescent dot to keep track of everyone), and metabolic analysis of hunger (blood glucose sampling before and after trials), should be conducted to give a more accurate conclusion supporting or refuting sibling competition.

CONCLUSION

Overall, the main findings from this study did not support my prediction of there being an increase in the total duration of all vocalizations in the experimental trials. The energy expenditure value of the costs and benefits for each call type (beg vs. bout), could have possibly produced a balancing effect on the overall duration, similar to the Optimal Foraging Theory. Therefore, this may show that time and energy were accurately and honestly represented by no statistical difference in total duration and number of vocalizations present when compared between the control and the experimental trials.

REFERENCES

- Anderson, D. J. (1990). Evolution of Obligate Siblicide in Boobies: A Test of the Insurance-Egg Hypothesis. *The American Naturalist*, 135, 334-350.
- Bolnick, D., & Smith, T. (2004). Can Intraspecific competition Drive Disruptive Selection? An Experimental Test in Natural Populations of Sticklebacks. *Evolution*, 58, 608-618.
- Chaiken, M., Bohner, J., & Marler, P. (1993). Song acquisition in European starlings, *Sturnus vulgaris*: a comparison of the songs of live-tutored, tape-tutored, and wild-caught males. *Animal Behaviour*, 46, 1079-1090.
- Corney, H. (2017). Do parents listen to their children?: Begging does not go unanswered in European Starlings (*Sturnus Vulgaris*). Halifax, Nova Scotia, Canada.
- Cotton, P., Kacelnik, A., & Wright, J. (1996). Chick begging as a signal: are nestlings honest? *Behavioural Ecology*, 7, 178-182.
- Davies, N., Krebs, J., & West, S. (2012). Competing for Resources. In N. B. Davies, J. R. Krebs, & S. A. West, *An Introduction to Behavioural Ecology* (4 ed., pp. 131-162). Chichester: Wiley-Blackwell.
- Dawkins, M., & Guilford, T. (1991). The corruption of honest signalling. *Animal Behaviour*, 41, 865-873.
- Dawkins, R. (1989). *The Selfish Gene* (2 ed.). Oxford: Oxford University Press.
- Greene, E., Lyon, B., Muehler, V., Ratcliffe, L., Oliver, S., & Boag, P. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Letters to Nature*, 407, 1000-1003.
- Johnstone, R. (2004). Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist*, 163, 388-406.

- Kacelnik, A., Cotton, P., Stirling, L., & Wright, J. (1995). Food allocation among nestling starlings; sibling competition and the scope of parental choice. *Proceedings of the Royal Society B*, 259, 259-263.
- Keddy, P. (2001). The Importance of Competition. In P. A. Keddey, *Competition* (Vol. 2, pp. 1-58). Louisiana: Kluwer Academic Publishers.
- Kessel, B. (1957). A Study of the Breeding Biology of the European Starling (*Sturnus vulgaris* L.) in North. *The American Midland Naturalist*, 58, 257-331.
- Konishi, M. (2010). From central pattern generator to sensory template in the evolution of birdsong. *Brain & Language*, 115, 18-20.
- Krebs, J., & Davies, N. (1993). *An Introduction to Behavioural Ecology*. Oxford: Blackwell Scientific Publications.
- Leisnham, P., LaDeau, S., & Juliano, S. (2014). Spatial and Temporal Habitat Segregation of Mosquitoes in Urban Florida. *PLoS One*, 9, 1-10.
- Leonard, M., & Horn, A. (2001). Begging in the absence of parents by nestling tree swallows. *Behavioral Ecology*, 12, 501-505.
- Lima, S. (1987). Clutch Size in Birds: A Predation Perspective. *Ecology*, 68, 1062-1070.
- Linz, G., Homan, J., Gaulker, S., Penry, L., & Bleier, W. (2007). European starlings: a review of an invasive species with far-reaching impacts. *Managing Vertebrate Invasive Species*, 24, 378-386.
- Long, J. (1981). Introduced Birds of the World. *Agricultural Protection Board of Western Australia*, 21-493.

- Parker, G., & Macnair, M. (1979). Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Animal Behaviour*, 27, 1210-1235.
- Rabin, L., McCowan, B., Hooper, S., & Owings, D. (2003). Anthropogenic Noise and its Effect on Animal Communication: An Interface Between Comparative Psychology and Conservation Biology. *International Journal of Comparative Psychology*, 16, 172-192.
- Ryan, M. J. (1988). Energy, calling and selection. *American Zoology*, 28, 885-898.
- Saito, Y., & Takeshi, M. (2010). Species coexistence under resource competition with intraspecific and interspecific direct competition in a chemostat. *Theoretical Population Biology*, 78, 173-182.
- Schoener, T. (1983). Field Experiments on Interspecific Competition. *The American Naturalist*, 122, 240-285.
- Smith, E., Cuthill, I., Griffiths, R., Greenwood, V., Goldsmith, A., & Evans, J. (2005). Sexing starlings *Sturnus vulgaris* using iris colour. *Ringing & Migration*, 22, 193-197.
- Smith, M., & Harper, D. (1988). The evolution of aggression: can selection generate variability? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 319, 557-570.
- Tilman, D. (1982). Resource competition and community structure. *Limnology and Oceanography*, 28, 1043-1045.
- van den Brink, A., & Hutting, S. (2017). Clash of the crabs: Interspecific, inter-cohort competition between the native European green crab, *Carcinus maenas* and the exotic brush clawed crab *Hemigrapsus takanoi* on artificial oyster reefs. *Journal of Sea Research*, 128, 41-51.

Wright, J., & Leonard, M. (2002). In *The evolution of begging: competition, cooperation and communication*. Dordrecht (Netherlands): Kluwer Academic Publishers.