

Nestling Vocalization Development in the European Starling (*Sturnus vulgaris*)

By

Ceilidh Dorothea McCoombs

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ABSTRACT

Nestlings vocalize while begging to elicit food from parents, and although many studies examine their begging behaviour, surprisingly little is known about vocal development in nestling passerines. European Starlings (*Sturnus vulgaris*) are a cavity-nesting passerine commonly found in anthropogenic environments. Adult males are open-ended learners, increasing the complexity of their songs with age. The objective of my study was to determine the ontogeny of vocalizations in nestling European Starlings over the nestling period (0 to ~22 days old). Using spectrograms, I observed and catalogued their calls every four days during the period between hatching and fledging. I found that the largest variation in vocalizations occurred when the nestlings were 5 to 13 days of age, and not when they were older. Nestlings appear to have increased consistency in their vocalizations as they grow older and settle in to their voices. It was predicted that a larger variation in call types would occur in larger brood sizes, however it was determined that there was no correlation between brood size and number of call types.

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INTRODUCTION

Vocal behaviours of birds vary among species and are dependent on factors such as the type of habitat in which they live and the purpose of each vocalization. Male oscine birds (songbirds) use song to defend their territories and to attract females for mating (Nowicki and Searcy, 2004). In addition to the purposes of communication between adult birds, avian vocalizations also occur in parent-offspring relationships which are paramount for offspring health and development (Price, 1998). While song is practiced and learned throughout adulthood in some species, call-notes, such as those observed in nestlings, are innate (Haftorn, 1993).

Nestlings convey their hunger through honest signals of vocal begging to their parents (Kacelnik et al., 1995), but if their begging becomes too loud it could lead to increased predation risks (Leech and Leonard, 1997, Haff and Magrath, 2011). When parents arrive with food, nestlings will vocalize a begging call while standing tall with their beaks wide open and their wings flapping (Redondo and Castro, 1992, Leech and Leonard, 1997). Nestling vocalizations also occur when parents are not present, which could be classified as “false alarms” (Green and Swets, 1966, Dor et al., 2006). This occurs when nestlings incorrectly beg based on the perceived signal detection of a parent. Sibling negotiation also occurs within the nest, being when siblings communicate with each other (Johnstone and Roulin, 2003, Dor et al., 2006). Sibling competition might also occur within the nest, as shown through nestlings increasing their vocal begging intensity and jostling for position to obtain a greater share of food than their siblings (Kacelnik et al., 1995).

The European Starling, *Sturnus vulgaris*, is an invasive song bird species to North America (Feare, 1984). An estimated 100 European Starlings were released into Central Park in New York City, NY between 1890 and 1891, and now there are about 200 million Starlings populating North America (Cabe, 1993). European Starlings are thought to have arrived in Nova Scotia between 1930 and 1940 (Cabe, 1993). These birds are generally associated with disturbed anthropogenic areas, such as urban centres and neighbourhoods within North America. They are characterized by their glossy black plumage with purple and green iridescences, their pointed wings, and short square tails (Feare, 1984 and Cabe, 1993).

Their vocalizations are characterized by a range of sounds including whistles, warbling, and high-pitched trills along with other types of calls (Cabe, 1993). An interesting feature noticed in male starlings is their open-ended learning ability, meaning that they are not limited to a particular repertoire size, and can continue to learn song throughout their lives (Mountjoy and Lemon, 1995) Another interesting feature of male starling is their ability to mimic sound. They have been known to mimic the sounds of each other, humans, and even car alarms, increasing their repertoire size (Cabe, 1993). An increased repertoire size in male European Starlings is positively correlated with mating success (Eens et al., 1991). These song birds are cavity nesters and females typically produce two broods in a breeding season (Feare, 1984), laying their first clutch in April or early May (Kessel, 1957). When a brood of nestlings is produced, they are cared for by both parents and typically require 21 to 22 days after hatching before they fledge (leave the nest) (Cabe, 1993).

The study of bird song can help to gain a better understanding of the principles of behavioural development of vocalizations (Konishi, 1978). The European Starling is an interesting focus of study for this project because they are songbirds with complex repertoires that often have nesting sites in urban areas. Their mimicry abilities combined with their noisy environment add to the factors to be considered while assessing their vocal development. There is already a growing understanding of their adult song learning and song characteristics. Surprisingly, nothing has yet been published on the ontogeny of vocal development in nestlings of this species.

The earliest vocalizations in nestlings are short in duration due to physical constraints and motor control that is underdeveloped, as observed in wild Green-rumped parrotlets (*Forpus passerinus*) (Berg et al., 2013). While these initial begging calls are innate, it was found in male chipping sparrows (*Spizella passerina*) that their early begging calls include several song learning characteristics (Liu et al. 2009). Their begging calls were incorporated into their subsong development, which is when vocal learning starts to emerge (Liu et al., 2009). While research of song development and learning exists for different stages of a starling's life (eg. Bertin et al., 2007), there is little known about their vocalization growth while they are still nestlings. The study that I am conducting will be the first to examine the general vocalization development of European Starlings before they leave the nest.

As there is still little known about their vocal development as nestlings, the objective of my study was to describe the pattern of early vocal development in nestling European Starlings from the day after hatch (day 1) until the day before fledge (day 18-21). By examining every type of vocalization observed during the nestling period, I can

determine the number of call types produced over time and track when new calls emerge and when they stop occurring altogether. I will also determine if brood size is correlated with the number of call types produced, as I predict there will be a positive correlation since call rates tend to increase in larger broods, as seen in Indigo Buntings (*Passerina cyanea*) (Dearborn, 1999).

METHODS

To conduct this study, pre-recorded sound files from the 2011 breeding season were analyzed from eight European Starling nest boxes located on the campus of Saint Mary's University in Halifax, Nova Scotia, Canada (44.6316° N, 63.5822° W). Three nest boxes contained brood sizes of three nestlings, while the others had brood sizes of one, two, four, and six nestlings. Microphones were placed in the nest boxes one day after nestlings started hatching (hatch day is day 0). These recorders captured nestling vocalizations in nest boxes from 07:30 to 13:30 each day until the young fledged. The audio files were examined visually using the audio software, *Syrinx* (John Burt).

Starting on day 1, vocalizations were described every fourth day after the brood of nestlings hatched. Thus, nestling vocalizations were examined on days 1, 5, 9, 13, 17, and on the final day before fledging, which varied between days 18 to 21. For each of these days, the nestling calls were closely examined for a one-hour period, starting at four hours past sunrise that day. This time was adjusted every day according to Environment Canada's sunrise data (<https://www.nrc-cnrc.gc.ca/eng/services/sunrise/>). Every type of vocalization observed was annotated in the sound file and was tagged and catalogued into

a database of call types. These call types were organized by myself based on their visual shape (length, height, pattern, complexity) and sound. The remainder of each sound file was then scanned for any calls that were unique from those seen over the one-hour period analyzed.

As the study progressed, a table was made that consisted of every type of call identified and the stage of nestling development for which they were observed. Calls that were unique to each brood were noted and organized separately. The stage at which each type of vocalization was observed was compared across nest boxes and formatted into tables consisting of call types observed on each day, and the number of nest boxes in which they were observed. The data were analyzed using the software GraphPad Prism 6. To determine whether the data concerning the number of call types observed at each stage of development in each nest box were normal, a D'Agostino & Pearson omnibus normality test was used. The data were found to not differ significantly from normal so a repeated measures ANOVA test was conducted to test for differences among ages as well as among nest boxes, along with a Tukey's multiple comparison post-hoc test to see where differences lay between days. A Chi-squared goodness of fit test was conducted to compare the number of call types that were observed in all nest boxes with those that were not observed in all nest boxes. The total number of different types of calls over all six sampling days were also compared among the nest boxes containing different brood sizes using a Pearson correlation test to determine whether brood size had an impact on the number of call types observed. Differences were considered to be significant when $P \leq 0.05$.

RESULTS

A total of 65 call types were observed across the eight nest boxes during the three-week long nestling period. An additional 40 call types were observed, however these were unique to individual nest boxes and were therefore not considered to be included in the 65 main call types.

Across nest boxes, there was a total of 9 different call types vocalized on day 1 (Table 1), 24 vocalized on day 5 (Table 2), 49 vocalized on day 9 (Table 3), 51 vocalized on day 13 (Table 4), 45 vocalized on day 17 (Table 5), and 39 vocalized on the final day before fledging (Table 6).

Using the repeated measures ANOVA test with Tukey's post-hoc test, significant differences in the mean number of call types in each nest box were detected at different ages ($F_{2.7,19.1}=27.32$, $P<0.0001$) (Figure 1). With Tukey's multiple comparison test, it was then determined that there were significant differences in the mean number of call types between days 1 and 5 ($q=9.947$, $P<0.01$), days 1 and 9 ($q=23.01$, $P<0.0001$), days 1 and 13 ($q=6.573$, $P<0.05$), days 1 and 17 ($q=8.986$, $P<0.01$), day 1 and the final day ($q=12.16$, $P<0.001$), as well as day 5 and day 9 ($q=12.38$, $P<0.001$).

A total of 13 call types were observed across all nest boxes while 52 call types were not (unique calls were not included). Significantly more call types were not shared among nest boxes than were shared ($\chi^2=23.400$, $P<0.0001$).

No significant relationship existed between the number of nestlings contained in the nest box and the number of call types vocalized ($r=-0.4914$, $n=8$, $P=0.22$) (Figure 2).

There was a trend observed in the earlier days of calls, where they were shorter in duration and softer in sound, and a trend in the later days of calls, where they were of increased volume and longer in duration (Figures 3, 4, and 5), however duration and amplitude were not quantified in this study.

DISCUSSION

The mean number of call types observed on the day after nestlings hatched was significantly lower than those observed every other day before fledging. Therefore, the number of different types of calls vocalized by European Starling nestlings increased after their first full day in the nest. With significant differences between calls observed on days 1 versus 5 and days 5 versus 9, it is evident that there is a rapid growth pattern in vocal development over the first nine days. This rapid increase in call types was not linear (Figure 1). This early peak in call type numbers at day 9 could be related to nestling developmental morphology, such that vocalizations were less stereotypical when first learning to vocalize. It was at this age where the nestling calls really started to show change and I liken to consider this the ‘voice-crack’ stage. It was found in Green-rumped parrotlet nestlings that the first 13 days after hatch consisted of short-duration calls and more broadband noise (high entropy), which was classified as the “early noisy stage” (Berg et al., 2013). These characteristics are considered to be a result of smaller air cavities and respiratory structures in younger nestlings (Vleck and Bucher, 1998) and rapid growth, leading to difficulties in call precision (Berg et al., 2013).

The number of call types began to level off around day 17 and the final day of the nestling period, exhibiting 8 to 24 call types. This age range is when the nestlings are thought to 'settle into' their voices before fledging. It was found in Green-rumped parrotlets that at 14 to 22 days old, calls became more precise and could be consistently repeated by the same individual (Berg et al., 2013). It is also known that as nestlings get older they may exhibit call redundancy, which can lead to a decrease in call repetition (Leonard and Horn, 2006). Since nestling calls typically become louder and longer as the nestlings grow older, they may exhibit call redundancy to overcome acoustic interference with others in the nest (Leonard and Horn, 2006). This could explain why the greatest number of variable call types are observed around day 9. Consistent repetition of calls was not as evident on day 9, however they could have occurred. If the nestlings were to exhibit a greater frequency of call repetition attempts at this age, there would likely be more room for variability to occur, since they are out of practice. Therefore, the large number of call types on day 9 could have resulted from an increase in variability potential due to increased repetition.

Since there was a significant difference between the number of call types observed in all nest boxes and those that were not, it can be interpreted that variation in calls occurs among nest boxes where they do not all exhibit the same calls. That being said, there were 13 call types observed in all nest boxes, which explains that environmental variables, such as the nest location on site, likely do not have an impact on the performance of these 13 call types. These shared call types were observed mostly during days 1, 13, 17 and the final day before fledging. This could imply that the first and final innate calls vocalized by nestlings are similar across all broods, and the days in between are when the

inconsistent call types occur. Therefore, nestling calls are highly stereotyped during the early and late days of the nestling period.

It was important to test for correlation between the number of nestlings in a nest box and the amount of times that different call types were observed to understand whether brood size has an impact on nestling vocalization development. I had predicted there would be a positive correlation between the number of nestlings and the number of call types vocalized, but none was detected. No correlation existed between the quantity of call types exhibited and brood size (Figure 2). When considering ideas of peer-influence and individual nestling vocal uniqueness, the nest box containing only one nestling exhibited similar call types and numbers of call types as those that contained more than one nestling. This result implies that nestlings do not learn these calls from each other, so they truly are innate, and perhaps their vocalization development patterns are relatively predetermined.

This result is also supported by the nature of begging behaviour in response to the effort of siblings. Begging effort in European Starling nestlings is thought to not be influenced by a competitive nest environment, indicating that begging is an honest signal of hunger in this species (Cotton et al., 1996). With honest signals of begging occurring irrespectively of nest environment, it is likely that the rate of begging would be similar among nest boxes containing different brood sizes, resulting in similar frequencies of call types throughout the nesting period. However, offspring condition can be attributed to brood size, where nestlings in smaller brood sizes are typically in better condition than those in larger brood sizes (Neuenschwander et al., 2003). In larger brood sizes, nestlings may beg for longer periods due to hunger (Cotton et al., 1996) and these brood sizes

would also have more individuals to vocalize throughout the nestling period. These factors corresponding to brood size would likely not result in changes to call type variance and vocalization rate, given that no correlation existed between the quantity of call types and brood size. However, information regarding individual nestling condition, for example, would be required to further examine how these factors could influence the performance of different call types.

The shapes of calls vocalized by nestlings changed greatly throughout the duration of the nestling period (Figures 3, 4, and 5). The calls observed during the earlier days were shorter and more pulse-like and tended to increase in duration with age, similar to Spanish sparrow (*Passer hispaniolensis*) nestlings (Marques et al., 2010). These pulse-like calls could be a result of structural stress that occurs when nestlings begin vocalizing at an early age (Marques et al., 2010). The increase in call duration that was observed but not quantified during the later days of the nestling period could be attributed to the progression of calls towards more adult-like vocalizations, as observed in Black-capped chickadees *Poecile atricapilla* (Baker et al., 2003). This vocalization change could be a result of an increased body size that can exhale a more continuous flow of air while vocalizing (Brackenbury, 1982). Future research should determine if changes in nestling call duration are significant in European starlings.

CONCLUSION

A wide range of call types was observed in all eight nest boxes containing different brood sizes of European starling nestlings. Significantly more calls were not shared in all nest boxes than calls that were, suggesting that variance of call types occurs among nest boxes. The number of call types vocalized increased significantly after day 1, as their

respiratory structures and vocal capacities grew. The majority of mean call types were vocalized on day 9, which would be part of the early noisy stage as seen in other passerines. The number of call types vocalized began to level-off during the final days of the nestling period, which could be attributed to more precise repetition of calls. While no correlation existed between call types and brood size, further research is required to assess whether nestling condition influences development of call types and call type repetition. This study is one of the few to examine call type development in passerine nestlings, and the first to do so for European Starlings.

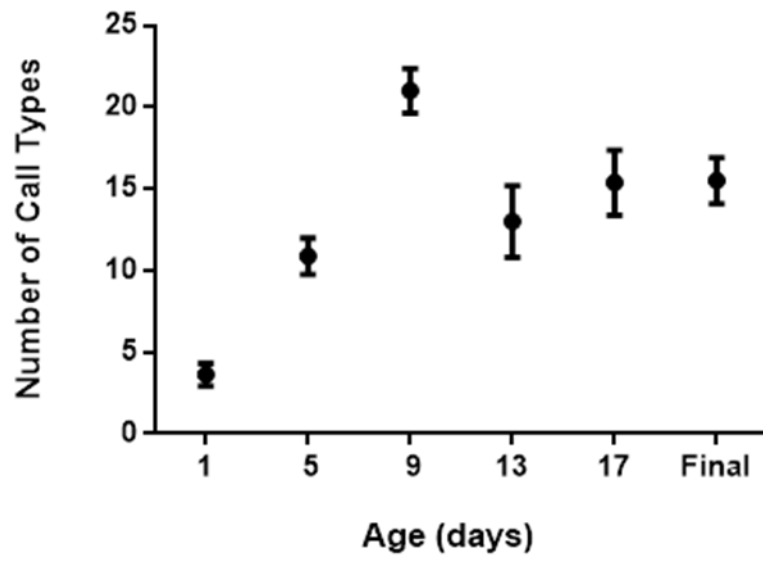


Figure 1. The mean number of different types of calls \pm SE observed from nestlings in eight different nest boxes over time.

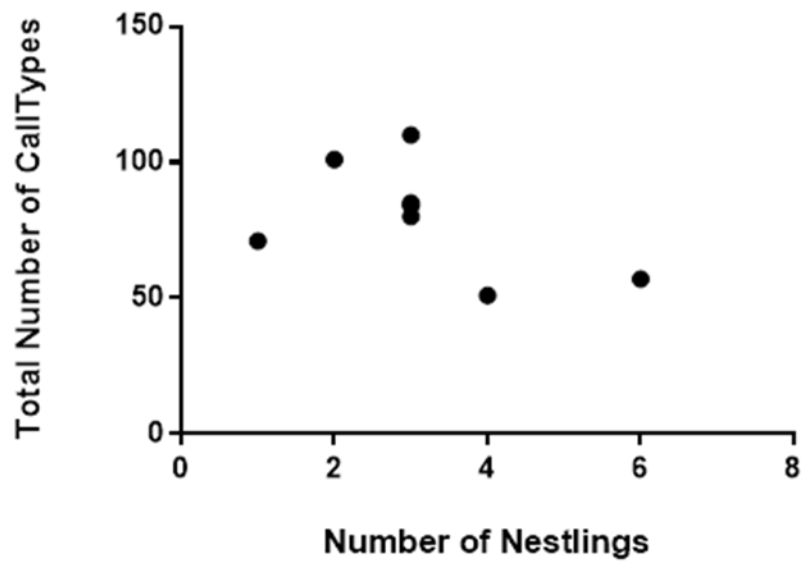


Figure 2. The total number of call types observed (collectively from each day) in nest boxes containing different brood sizes (number of nestlings).

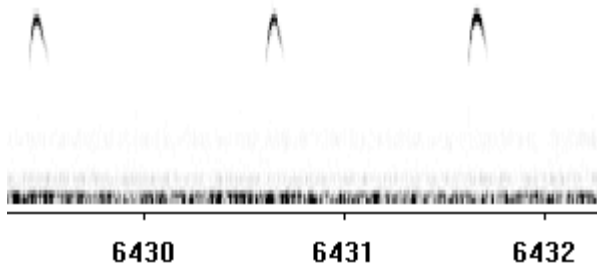


Figure 3. Calls observed on day 1, where time is measured in seconds.

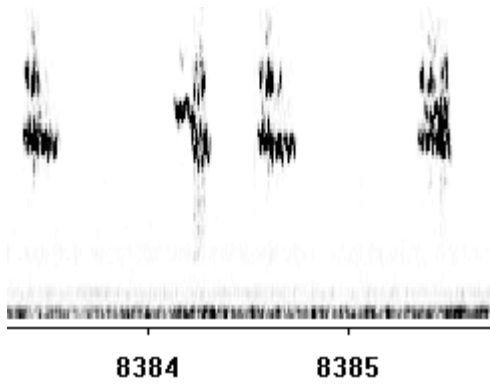


Figure 4. Calls observed on day 9, where time is measured in seconds.

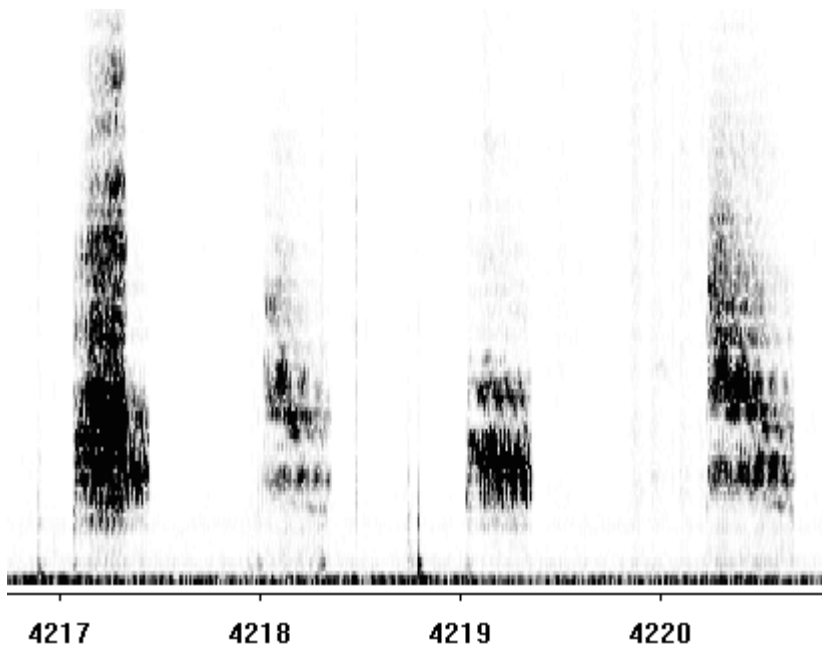


Figure 5. Calls observed on the day before fledge, where time is measured in seconds.

Table 1. Total call types observed in nest boxes when nestlings are one day old.

Call Type	Number of Nest Boxes Observed
1	7
2	7
3	2
4	3
5	4
8	1
11	2
17	1
20	1

Table 2. Total call types observed in nest boxes when nestlings are 5 days old.

Call Type	Number of Nest Boxes Observed
1	7
2	6
3	5
4	5
5	7
6	4
7	3
8	6
9	6
10	6
11	4
12	7
13	3
14	1
16	1
20	3
21	1
22	1
23	1
26	2
32	2
33	1
45	1
52	1

Table 3. Total call types observed in nest boxes when nestlings are 9 days old.

Call Type	Number of Nest Boxes Observed
2	2
4	3
6	2
7	2
9	1
10	1
11	1
12	2
13	4
14	4
15	5
16	4
17	5
18	6
19	3
20	5
21	6
22	2
23	7
24	3
25	6
26	3
27	3
28	4
29	3
30	5
31	1
32	5
33	3
34	3
35	2
36	2
37	2
38	1
39	3
40	1
41	3
42	1
43	4
44	5
45	3
46	1
47	5
48	1
49	2
50	2
51	3
52	5
55	1

Table 4. Total call types observed in nest boxes when nestlings are 13 days old.

Call Type	Number of Nest Boxes Observed
4	1
5	1
6	1
7	1
13	1
14	2
15	2
16	1
17	3
18	3
19	1
20	3
21	3
22	1
23	1
24	1
25	1
26	1
27	1
28	1
31	1
34	3
35	1
36	1
37	4
38	2
39	2
40	2
41	2
42	2
43	4
44	4
45	4
46	2
47	1
48	1
49	2
50	3
51	3
52	3
53	2
54	2
55	2
56	1
57	1
59	3
60	3
61	4
62	3
63	3
64	1

Table 5. Total call types observed in nest boxes when nestlings are 17 days old.

Call Types	Number of Nest Boxes Observed
3	1
4	2
6	1
7	1
8	1
13	1
14	1
15	2
16	2
17	1
18	2
19	1
21	2
23	1
24	1
26	2
28	1
30	2
33	1
34	2
35	3
36	1
37	2
39	1
41	1
42	3
43	1
44	3
45	1
49	7
51	1
52	3
53	1
54	7
55	5
56	3
57	3
58	4
59	5
60	6
61	6
62	5
63	5
64	6
65	5

Table 6. Total call types observed in nest boxes on the last day before nestlings fledge.

Call Types	Number of Nest Boxes Observed
7	1
14	3
16	2
17	3
18	1
19	1
20	1
21	3
23	3
31	1
32	1
34	1
36	1
37	5
38	1
39	3
40	1
42	2
43	1
44	4
45	3
47	3
48	1
49	3
51	3
52	4
53	1
54	5
55	2
56	1
57	1
58	4
59	6
60	4
61	7
62	7
63	7
64	6
65	6

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LITERATURE CITED

- Baker, M.C., Baker, M.S.A., and Gammon, D.E. 2003. Vocal ontogeny of nestling and fledging black-capped chickadees *Poecile atricapilla* in natural populations. *Bioacoustics* 13: 265-296.
- Berg, K.S., Beissinger, S.R., and Bradbury, J.W. 2013. Factors shaping the ontogeny of vocal signals in a wild parrot. *The Journal of Experimental Biology* 216: 338-345.
- Bertin, A., M. Hausberger, L. Henry, M. Richard-Yris. 2007. Adult and peer influences on starling song development. *Wiley Periodicals, Inc. Dev Psychobiology* 49:362-374.
- Brackenbury, J.H. 1982. The structural basis of voice production and its relationship to sound characteristics. In *Acoustic communication in birds: production, perception, and design features of sound* (Ed. D.E. Kroodsma and E.H. Miller), pp 537-573. New York: Academic Press.

- Cabe, Paul R. 1993. European Starling (*Sturnus vulgaris*), version 2.0. In *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Cotton, P.A., Kacelnik, A., and Wright, J. 1996. Chick begging as a signal: Are nestlings honest? *Behavioural Ecology* 7(2): 178-182.
- Dearborn, D.C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *The Auk* 116(2): 448-457.
- Dor, R., H. Kedar, D.W. Winkler, and A. Lotem. 2006. Begging in the absence of parents: a “quick on the trigger” strategy to minimize costly misses. *Behavioural Ecology* 18:97-102.
- Eens, M., R. Pinxten, and R.F. Verheyen. 1991. Male song as a cue for mate choice in the European Starling. *Behaviour* 116: 210-238.
- Feare, C.J. 1984. *The Starling*. Oxford University Press, Oxford, UK.
- Green, D.M., and Swets, J.A. 1966. *Signal detection theory and psychophysics*. Wiley, New York.
- Haff, T.M., and R.D. Magrath. 2011. Calling at a Cost: elevated nestling calling attracts predators to active nests. *Biology Letters* 7,4: 493-495. DOI: 10.1098/rsbl.2010.1125.
- Haftorn, S. 1993. Ontogeny of the Vocal Repertoire in the Willow Tit *Parus montanus*. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 24(4): 267-289.
- Johnstone, R.A. and Roulin, A. 2003. Sibling negotiation. *Behavioural Ecology* 14(6): 780-786.

- Kacelnik, A., P. Cotton, L. Stirling, and J. Wright. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proceedings of the Royal Society B: Biological Sciences* 259:259-263.
- Kessel, B. 1957. A study of the breeding biology of the European Starling (*Sturnus vulgaris* L.) in North America. *Am. Midland Nat.* 58: 257-331.
- Konishi, M. 1978. Auditory environment and vocal development in birds. *Perception and Experience* 1:105-117.
- Leech, S.M., and Leonard, M.L. 1997. Begging and the risk of predation in nestling birds. *Behavioural Ecology* 8: 644-646.
- Leonard, M.L. and Horn, A.G. 2006. Age-Related Changes in Signalling of Need by Nestling Tree Swallows (*Tachycineta bicolor*). *Ethology* 112: 1020-1026.
- Liu, W-c., Wada, K., and Nottebohm, F. 2009. Variable food begging calls are harbingers of vocal learning. *PLoS One* 4(6): e5929.
- Marques, P.A., De Araújo, C.B., and Vicente, L. 2010. Nestling call modification during early development in a colonial passerine. *Bioacoustics* 20: 45-58.
- Mountjoy, D.J. and Lemon, R.E. 1995. Extended song learning in wild European Starlings. *Animal Behaviour* 49: 357-366.
- Neuenschwander, S., Brinkhof, M., Kolliker, M., and Richner, H. 2003. Brood size, sibling competition, and the cost of begging in Great Tits (*Parus major*). *Behavioural Ecology* 14: 457-462.

- Nowicki, S. and W.A. Searcy. 2004. Song Function and the Evolution of Female Preferences. *Behavioural Neurobiology of Birdsong* 1016:704-723. DOI: 10.1196/annals.1298.012
- Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. Price, K. *Animal Behaviour* 56:571-577.
- Redondo, T., and Castro, F. 1992. The increase in risk of predation with begging activity in broods of Magpies *Pica pica*. *Ibis* 134: 180-187.
- Vleck, C.M., Bucher, T.L. 1998. Energy metabolism, gas exchange and ventilation. In *Avian Growth and Development* (ed. J.M. Starck and R.E. Ricklefs) pp. 89-1111. New York: Oxford University Press.