Does Reproductive Performance Improve With Age in Female European starlings,

Sturnus vulgaris?

By
Nii T. Obodai

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

April, 2018 Halifax, Nova Scotia

Approved: Dr. Colleen Barber

(Supervisor)

Approved: Dr. Michelle Patriquin

(Reviewer)

Date: 25th April 2018

Abstract

Does Reproductive Performance Improve With Age in Female European starlings, *Sturnus vulgaris?*
Nii T. Obodai

Studies have shown that the most energetically costly event in a bird's life cycle is that of breeding, particularly for females who lay nutrient-rich eggs. Studies also show that older males and females are often preferred as mates. Potential reasons include older individuals having experience with locating good feeding sites, and provisioning offspring, as well as being in better condition or possessing superior genes. European Starlings (*Sturnus vulgaris*) are cavity-nesting passerines with bi-parental care, and have hackles whose length of iridescence allows classification of adults into one of two age categories (Second year, SY, who are breeding for the first time; After Second Year, ASY, who likely bred at least once before). The objective of my study was to determine if older females had higher reproductive performance than younger females, using four years of data. I predicted that ASY females would be in better condition than SY females, and that they would have larger clutch sizes, a higher mean egg mass, and greater hatching and fledging success. In support of my predictions, ASY females were in significantly better condition than SY females, and had larger clutch sizes. ASY females also tended to have higher fledging success, although mean egg mass and hatching success did not differ between ASY and SY females. Condition and reproductive performance in this population of European Starlings were higher for older females than first-time breeding females, suggesting that these older females might be expected to be preferred as mates.

25th April, 2018

Acknowledgment

I would like to thank Dr. Colleen Barber for all the moral support through this study, her guidance and constant editing. I am also grateful to Dr. David Dansereau, Dr. Timothy Frasier, my reviewer Dr. Michelle Patriquin and my lab mates Ashton Bradley, Ceilidh McCoombs and the wonderful Honours class of 2018 for helping shape up this thesis. I would also like to thank my family for the support and last but not least I would like to thank God.

Table of Contents

List Of Figures

Page

Introduction

Survival and reproduction are the ultimate goals of life for any animal and plant species. Reproductive behaviours have been shaped by natural and sexual selection. Sexual selection targets traits concerned with increasing mating success, and it may come at a cost of lower individual fitness (Krebs & Davies, 1993). Sexual selection can be categorised into intersexual selection, where traits in one sex attract the opposite sex, or intrasexual selection, where usually males compete for the opportunity to mate (Krebs & Davies, 1993). In intersexual selection, males, who possess favoured traits such as dominance, colour of ornaments, age and breeding experience often have increased mating success (Kodric-Brown & Brown 1984, Zahavi 1975, Otter et al., 1997). In the case of birds, song complexity and size of song repertoire are also favoured traits shaped by sexual selection (Krebs & Davies, 1993).

In a field experiment, Mountjoy and Lemon (1996) studied the female choice for complex songs in the European starling (*Sturnus vulgaris*). A long, complex song by the males not only attracted females, but also influenced competitive interactions with other males. Mountjoy and Lemon (1996) tested the hypothesis that females preferred complex songs to quality of territory by comparing older males with complex songs in low quality territories to males with less complex songs in high quality territories. They observed males with more complex songs acquired mates faster than those in high quality territories. Song complexity in European starlings increases with age, as they are open-ended learners (Feare 1984; Chaiken & Böhner 2007), and males with larger repertoires also had higher mating success (Reid et al., 2004). Otter et al. (1997) analyzed honest advertisement and song output during the dawn chorus of black-capped chickadees

(*Poecile atricapillus*), more dominant males began singing earlier and on average sang longer with higher maximum rates.

In the field of ornithology (study of birds), there has been a rising interest to determine whether successful reproductive performance variables increase with parental age of small passerine birds. Passerines are perching birds characterized by having four toes with three directed forward and the other backward (Ehrlich et al., 1988). Breeding in birds is one of the most energetically costly events in their life cycle, especially for females as eggs are large and need to be food-rich, requiring more energy to produce and can result in a reduced survival or fecundity (Krebs & Davies, 1993). Because of this high cost, the more experienced mates, who show their physical signal of fitness through songs and colours, are therefore usually selected as mates (Krebs & Davies, 1993). A positive correlation has been observed between age and reproductive variables, at least until ten years of age in both males and females when reproductive success can decrease (Reid, 1988; Martin, 1995; Forslund and Pärt, 1995 reviewed by Angelier et al. 2006). Many species can determine age and previous breeding experiences of mates by observing features such as size, plumage pattern and colouration, mating calls, song length and complexity as well as size of song repertoire (Krebs & Davies, 1993). Goutte et al. (2010) found that older birds reproduced earlier in the breeding season, and had higher breeding success due to the increased availability. Older birds are believed to have the best knowledge of feeding sites, which is directly correlated to better nutrition and higher quality of nestlings (Goutte et al. 2010).

The European Starling, the focus of this study, is an invasive passerine bird that was first introduced to North America in the 1890s, and has since become one of the most

successful invasive birds in North America (Linz et al. 2007). Starlings were used in this study due to the ease of finding nest boxes, their adaptability, the ability to discriminate between Second Year (SY), individuals who hatched the year before and After-Second Year (ASY) individuals, and the knowledge that their hackle length increases with age (Barber & Wright, 2017) as does their song complexity (Mountjoy & Lemon, 1996). Kessel (1951) used iridescent length of hackles (adult throat feathers) to classify starlings into Second Year (SY) and After Second Year (ASY) categories. Iridescence is a type of structural colouration that is dependent on reflection and refraction of light (Ehrlich et al. 1988; Barber & Wright, 2017). The SY and ASY males have longer iridescent hackle than females of the same category. Starlings are typically socially monogamous and exhibit bi-parental care (Linz et al. 2007; Kessel 1957). They may sometimes be polygynous when males can defend another nesting cavity. Female starlings are generally capable of first breeding when they are in their second year (SY) (Kessel 1957, Feare 1984, Komdeur et al. 2005, Barber & Wright 2017). Starlings typically have two breeding periods, from late spring to mid-summer, producing clutches of three to six pale greenish-blue eggs, which they begin incubating once the last egg is laid for an average period of 12 days (Linz et al. 2007, Feare, 1984). After hatching, parents alternate between feeding the nestlings for 21 to 23 days until they fledge (Feare, 1984).

Reproductive variables in birds, the focus of this study, include clutch size, mean egg mass, as well as hatching and fledging success. Reproductive success of younger birds is usually lower in comparison to older experienced breeders. Older females have greater clutch sizes and heavier eggs and nestlings (Curio, 1983; Blem et al., 1999; Geslin et al. 2004). In an attempt to verify these studies, a study by Smith (1993) on Marsh Tits, *Parus*

paludtris, showed there was a positive correlation between age and several reproductive factors including (1) clutch size, (2) mass of eggs per clutch, (3) hatching success, (4) nestling mass and (5) fledging success. Smith (1993) however found no correlation between increased age and the mass of eggs, though he concluded that reproductive performance was overall lower in first-time breeders. The purpose of this study is to therefore determine if reproductive performances: clutch size, mean mass of eggs per clutch, hatching success as well as nestling mass and fledging success, increased with the age and condition of female European starlings. It is predicted that ASY females will be in better condition than SY females, will lay larger clutch sizes, and have higher mean egg and nestling masses and greater fledging success than SY females.

Methods

This study was conducted on the campus of Saint Mary's University, Halifax, Nova Scotia, Canada (448 37^0 54.07^{00} N, 638 34^0 47.09^{00} W). The studies on this population of European starlings have been ongoing since 2007 when 40 nest boxes were attached onto trees, and another five nest boxes were installed in 2009. The data for this study were collected by previous Honours students from April-July 2013 (n = 30 female adults), 2014 (n = 20), 2015 (n = 22) and 2016 (n = 25). Adult female European starlings were caught using nest traps (Stutchbury & Robertson, 1986; Barber & Wright, 2017) when nestlings were 5-12 days of age, and were identifiable by their light pink lower mandibular base (Kessel 1951, Feare 1984). The adults were banded with a Canadian Wildlife Service band, and a unique combination of colour bands for individual identification, weighed with a Pesola spring scale to the nearest 0.05 grams, measured for tarsus lengths with a digital calipers to the nearest 0.01mm and seven hackles were

plucked from the throat region for ageing purposes.

The adult females were aged into SY or ASY categories by measuring the iridescent length of each of the seven feathers (based on Kessel's 1951 criteria). Length of iridescence increases with age, making iridescence a good determinant of age (Barber & Wright, 2017). Hackles were measured to the nearest 0.05mm under a VanGuard dissecting microscope and a Schott-Fostec illuminator. A ruler was used to ascertain the length of the iridescent section, from the tip of the feather to the midpoint of the barbules where iridescence ends, excluding the white tip observed on some hackles. Average iridescent length $\pm$ SE was calculated from the seven feathers for each female. Mean hackle iridescence less than 6.5mm indicated the female was SY while females having measurements greater than or equal to 6.5mm were classified as ASY. The ASY category comprises a broader range of ages, hence female may be anywhere from three to eight years (Kessel, 1951; Barber and Wright, 2017).

Female condition, much like how humans derive a Body Mass Index (BMI) value using weight and height, often uses mass and tarsus length. A simple linear regression was run on female mass vs. tarsus length and the residuals used as an index of condition (Green, 2001). For each female the following data was collected: (1) clutch size, (2) hatching success, (3) mean egg mass (total egg mass/number of eggs in nest), (4) nestling mass and (5) fledging success – when the nestling leaves the nest. Nest boxes were checked daily for eggs over the laying period to determine clutch size. Eggs were weighed to the nearest 0.1g using a AWS-250 Digital weight scale. Nestlings were weighed on days 5 and 11 (day 0 is a hatch day) with a Pesola spring scale to the nearest 0.05 grams. Hatching success was determined as a proportion of eggs hatched compared

to the number of eggs laid. To determine fledging success, nest boxes were inspected at about day 24 of the nestling period, after nestlings should have fledged (Feare, 1984). Fledging success was calculated as the proportion of nestlings that successfully left the nest compared to the number of eggs in the nest.

All statistical analyses were performed with the GraphPad Prism 6 software (Graph-Pad Software Inc., La Jolla, CA, USA), and variables were tested for normality using the d'Agostino and Pearson omnibus normality test. Normally distributed data were analysed using parametric statistics, and non-parametric statistics were used for non-normally distributed data. Results were considered statistically significant when $P \leq 0.05$.

Results

ASY females were in significantly better condition than SY females (Mean $\pm$ SE: 0.49 $\pm$ 0.48 vs. -1.37 $\pm$ 0.58 for ASY and SY females respectively; unpaired t= 2.1, d.f. = 91, P = 0.039; Fig. 1), laying significantly more eggs per nesting attempts than did SY females (Mean$\pm$SE: 4.7 $\pm$ 0.084 vs. 4.0 $\pm$ 0.19; unpaired t = 3.76, d.f. = 93, P = 0.0003 Fig. 2).

There were no significant differences in the mass of eggs per nest box (Mean $\pm$ SE: 7.14 $\pm$ 0.069 vs. 7.36 $\pm$ 0.12; Mann-Whitney $U_{70, 25}$ = 707, n_1 = 70, n_2 = 25, P = 0.16; Fig. 3) and the hatching success of ASY females vs. SY females (Mean $\pm$ SE: 0.86 $\pm$ 0.022 vs. 0.91 $\pm$ 0.03; Mann-Whitney $U_{70, 24}$ = 734.5, n_1 = 70, n_2 = 24, P = 0.32). Similarly, no significant differences were detected in the mass of nestlings (Mean $\pm$ SE: 67.22 $\pm$ 1.17 vs. 65.69 $\pm$ 1.81; Mann-Whitney $U_{67, 21}$ = 602, n_1 = 67, n_2 = 21, P = 0.32). However, ASY females did tend to fledge more nestlings than the SY females (Mean $\pm$

SE: 3.58 ± 0.15 vs. 2.91 ± 0.35; Mann-Whitney $U_{66, 21}$ = 512.5, n_1 = 66, n_2 = 21, P = 0.066 Fig. 4).

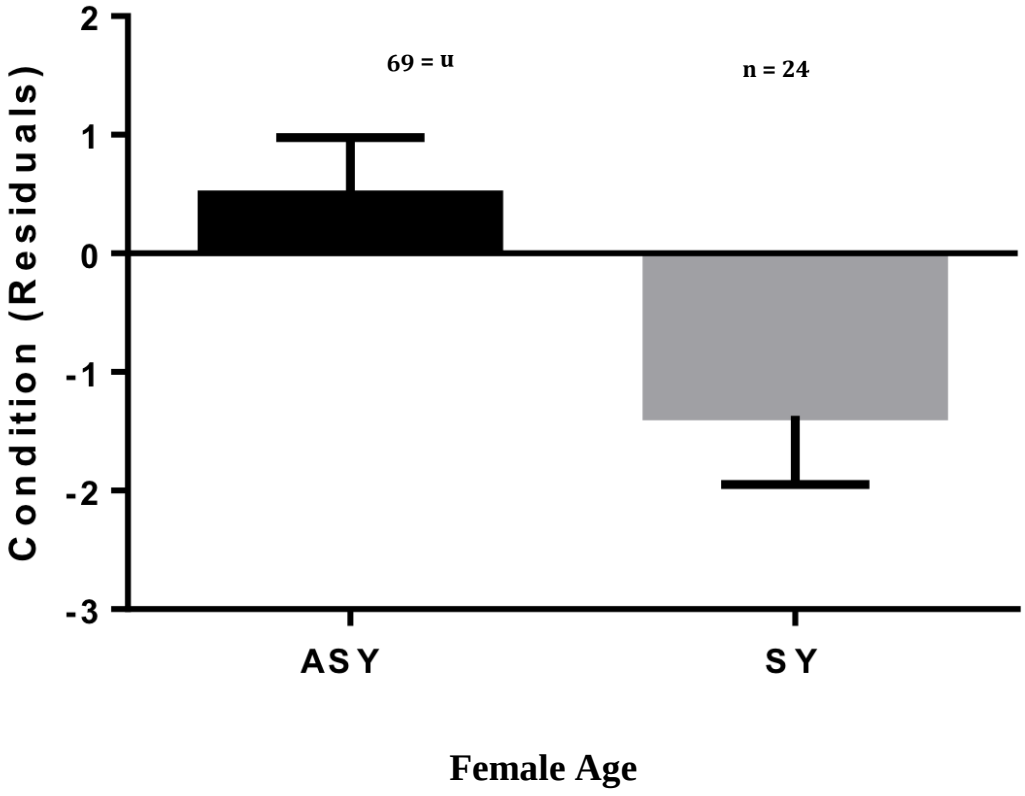
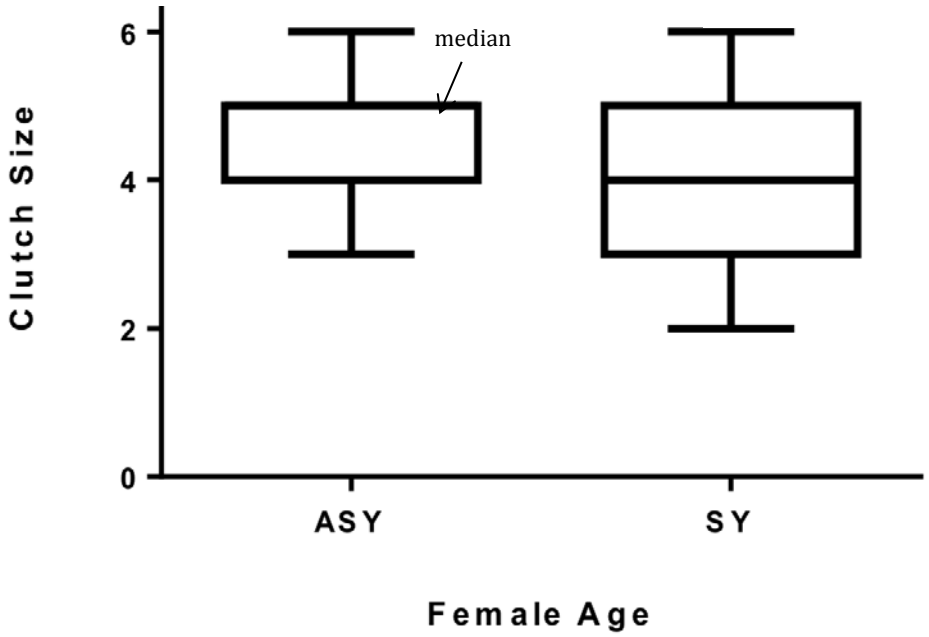


Figure 1. Condition ± **S.E** of 69 ASY and 21 SY females as determined from the residuals of body mass vs. tarsus length

Figure 2. Boxplot displaying the median number of eggs and ranges of clutch sizes of 70 ASY and 25 SY females



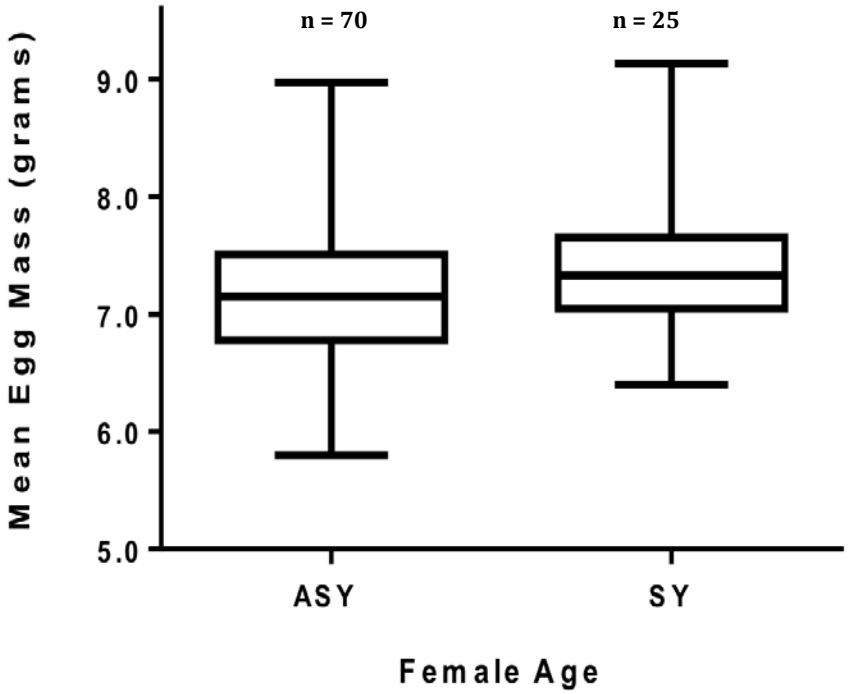
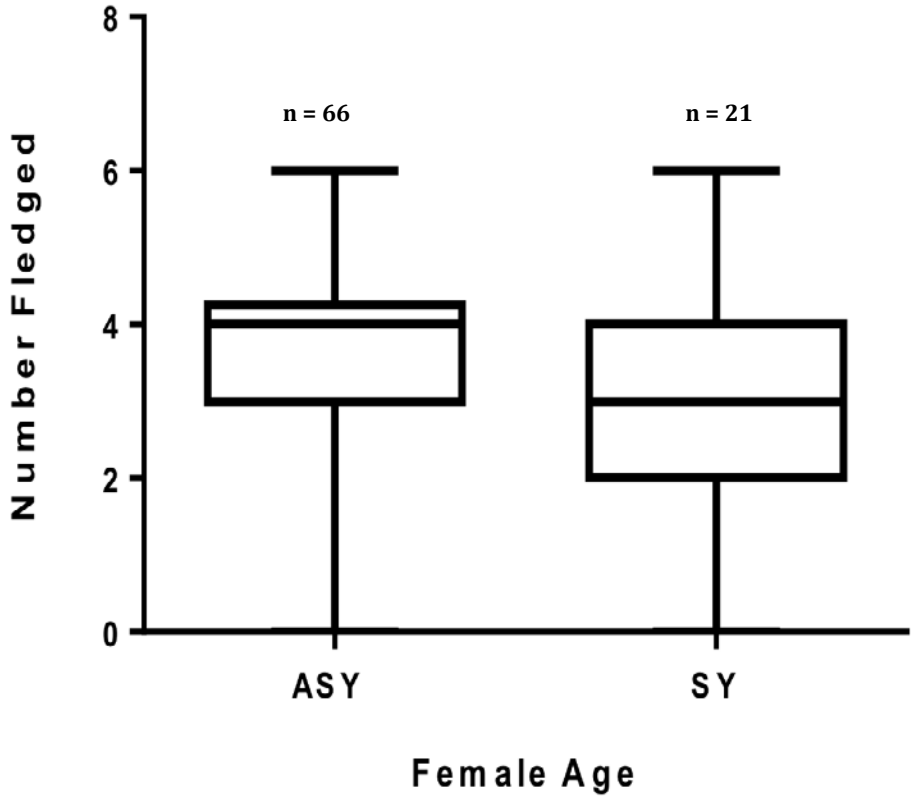


Figure 3. Boxplot illustrating median mass of eggs per clutch laid by 70 ASY and 25 SY females



÷ **Figure 4.** The number of successful nestlings that left the nest box parented by 66 ASY and 21 SY females.

Discussion

As found in similar studies on reproductive variables in small passerine bird species, the reproductive performance of European starlings was higher overall in older females (Collins, 1966; Gromadzki, 1980 & Smith, 1993). Though not all the variables were statistically higher in other studies, clutch size and fledging success were constantly decreased in SY females (Collins, 1966; Gromadzki, 1980; Stutchbury & Robertson, 1988 & Smith, 1993). From my results, a statistically significant difference was observed in condition and clutch size, though no effect was seen in the mean mass of eggs and nestlings, fledging success and hatching success although the results tended to be higher for ASY females. However, hatching and fledging successes were observed to be significantly higher in older female Tree swallows (Stutchbury & Robertson, 1988).

ASY females were found to be in considerably better condition, which is a factor in determining their reproductive performance. Females in better conditions are fitter and more likely to produce a greater reproductive output.

ASY females produced significantly larger clutches than SY females. This could be attributed to older females being in better condition and having the experience in raising more nestlings (Pyle et al., 1991 reviewed by Forslund & Pärt, 1995 & Chastel et al., 1995). In a study by Smith (1993), he observed that clutch size in Marsh Tits was higher for pairs with former breeding experience i.e. older females. Perrins and McCleery (1985) also observed larger clutches and higher fledgling survival in experienced breeders of the Great Tit, *Parus major*.

Clutch size however did not affect the average mass of eggs, as there was no significant difference between the ASY and SY females. Interestingly, despite no significant difference in egg mass, the eggs of SY females weighed 7.33g on average compared to 7.15g in ASY females, which may be because SY females could invest more in their eggs due to fewer a number of eggs. In Great Tits, Perrins (1965) observed that larger clutch sizes produced lighter eggs compared to those with smaller clutches.

Clutch size can also be used to explain why there was no significant difference in the hatching success. ASY and SY females both had a median of 1. As ASY females laid more eggs, it would be expected they would have a greater mean hatching success, however, this was not so (0.86 eggs for ASY vs. 0.91 eggs for SY). This occurrence can be due to the difficulty in incubating more eggs, unlike SY females that have fewer eggs to incubate and invest in (Jetz et al., 2008 reviewed by McDonald, 2008).

There was no significant difference in the mass of nestlings between ASY and SY females, though nestlings of ASY females had a median of 68.6g compared to 65.83g for SY females. It can be assumed that ASY females know the best foraging sites from previous breeding experience and spend more time foraging, but as they had more nestlings to feed, they had to provision more, requiring more trips to foraging sites (Robertson & Rendell, 2002). There was no significant difference however as SY females did not have to find as much food, as they had fewer nestlings to feed.

Fledging success, which is the number of young that leave the nest, is a good indicator of the number of young that become part of the population of breeding adults. ASY females tended to fledge more nestlings than SY females with a median of four nestlings compared to three fledglings of SY females

ASY females were superior in both of these variables, raising larger clutches and fledging more nestlings. Studies have assumed SY females typically have smaller clutches and therefore fledge fewer young due to their decreased foraging efficiency (Stutchbury & Robertson 1988, Perrins 1965, Perrins & McCleery 1985). ASY females and SY females had no significant differences in variables such as the average egg and nestling masses and hatching success, however, significant differences were observed in the main factors contributing to the genetic flow of individuals, the clutch size and the number of successful fledglings.

REFERENCES

Angelier, F., Shaffer, S. A., Weimerskirch, H. and Chastel, O. (2006). Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: The wandering albatross. *Science Direct, 149*(1), 1-9.

Barber, C., & Wright, M. M., (2017). Length of hackle iridescence increases with age in European Starling (*Sturnus vulgaris). The Wilson Journal of Ornithology, 129*(1), 165-171.

Blem, R. C., Blem, B. L. & Barrientos, I. C. (1999). Relationships of clutch size and hatching success to age of Female Prothonotary Warblers. *The Wilson Bulletin, 111*(4), 577-581

Chaiken, M., & Böhner, J. (2007). Song learning after isolation in the Open-Ended Learner the European Starling: Dissociation of Imitation and Syntactic Development. *The Condor, 109*(4), 968-976.

Chastel, O., Weimerskirch, H. & Jouventin, P. (1995). Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *The Auk, 112*(4), 964-972.

Collins, B. V. 7 De Vos, A. (1966). A nesting study of the starling near Guelph, Ontario. *The Auk, 83*(4), 623-636.

Curio, E. (1983). Why de young birds reproduce less well? *IBIS 125*(3), 400-404.

Ehrlich, R. P., Dobkin, D. S. & Wheye, D. (1988). Passerines and songbirds. Stanford

Birds, Stanford University. Stanford, CA.

Feare, C. (1984). The Starling. Oxford University Press

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds – hypotheses and tests. *Trends in Ecology and Evolution*. *10*(9). 374-378.

Geslin, T., Questiau, S. & Eybert, M. C. (2004). Age-related improvement of reproductive success in Bluethoats, *Luscinia svecica. Bird Study*, *51*(2). 178-184.

Goutte, A., Antoine, É., Weimerskirch, H. and Chastel, O. (2010), Age and the timing of breeding in a long-lived bird: a role for stress hormones? *Functional Ecology, 24*, 1007–1016.

Green, A. J. (2001). Mass/length Residuals: measures of Body Condition or Generators of Spurious Results? *Ecology, 82*(5). 1473-1483.

Gromadzki, M. (1980). Reproduction of the starling, *Sturnus vulgaris*, in {uBawy Wi[lane, North Poland. *Acta Ornithologica*, *17.* 195-226.

Hogstedt, G. (1981). Effect of Additional Food on Reproductive Success in the Magpie (Pica pica). *Journal of Animal Ecology, 50*(1), 219-229.

Jetz, W., Sekercioglu, C. H. & Böhning-Gaese, K. (2008). The worldwide variation in Avian clutch size across species and space. *PLoS Biol 6*(12).

Kessel, B. (1951). Criteria for sexing and aging European Starlings (*Sturnus vulgaris*). *Bird-banding, 22*(1), 16-23.

Kessel, B. (1957). A Study of the Breeding Biology of the European Starling (*Sturnus vulgaris L.)* in North America. *The American Midland Naturalist, 58*(2), 257-331.

Kodric-Brown, A., & Brown, J. H. (1984). Truth in Advertising: The kinds of Traits favoured by Sexual Selection. *The American Naturalist, 124* (3). 309-323

Komdeur, J., Oorebeek, M., Van Overveld, T. & Cuthill, I.C. (2005). Mutual ornamentation, age, and reproductive performance in the European starling. *Behavioral Ecology 16*(4), 805-817

Krebs, J. R. & Davies, N. B. (1993). An Introduction to Behavioural Ecology (3rd ed.) Oxford, United Kingdom.

Krist, M. (2011). Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews, 86.* 692-716.

Linz, G. M., Homan, H. J., Gaukler, S. M., Penry, L. B. & Bleier, W. J. (2007). European Starlings: A Review Of An Invasive Species With Far-Reaching Impacts. *National Wildlife Research Centre.* Fort Collins, CO.

Martin, K. (1995). Patterns and mechanisms for age-dependent Reproduction and Survival in Birds. *American zoologists, 35,* 340-348.

McDonald, K. (2008). Why do some bird species lay only one egg? UC San Diego study offers some answers. *UC San Diego News Center.*

Mountjoy, D. & Lemon, R. (1996). Female choice for complex song in the European

starling: a field experiment *Behavioral Ecology Sociobiology, 38*(65).

Otter, K., Chruszcz, B., Ratcliffe, L. (1997). Honest advertisement and song output during the dawn chorus of black-capped chickadees, *Behavioural Ecology, 8* (2), Pages 167–173.

Perrins, C. M. (1965). Population Fluctuations and Clutch-Size in the Great Tit, *Parus major L. Journal of Animal Ecology, 34*(3). 601-647.

Perrins, C. M. & McCleery, R. H. (1985). The effect of age and pair bond on the breeding success of Great Tits *Parus major*. *IBIS, 127*(3). 306-315

Pyle, P., Spear, L. B., Sydeman, W. J. & Ainley, D. G. (1991). The effects of experience and age on the breeding performance of Western Gulls. *The Auk 108,* 25-33.

Reid, V. W. (1988). Age correlation within pairs of breeding birds. *Department of Zoology,* University of Washington, Seattle, Washington USA.

Reid, M. J., Arcese, P., Cassidy, V. E. L. A., Hiebert, M.S., Smith, M. N. J., Stoddard, K. P., …. Keller, F. L. (2004). Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia. The Association for the Study of Animal Behaviour, 68.* 1055-1063.

Robertson, R. J. & Rendell, W. B. (2002). A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. *Journal of Animal Ecology, 70*(6), 1014-1031.

Smith, G. H. 1993. Parental age and reproduction in the Marsh Tit (*Parus palustris*). Department of Ecology, Lund University, *S-223* 62 Lund, Sweden

Stutchbury, B. J. & Robertson, R. J. (1988). Within-season and age-related patterns of reproductive performance in female tree swallows (*Tachycineta bicolor). Canadian Journal of Zoology, 66*(4). 827-834.

Weatherhead, P. J. 7 Dufuor, K.W. (2000). Fledging success as an index of recruitment in Red-winged Blackbirds. *The Auk, 117*(3). 627-633.

Zahavi, A. (1975). Mate Selection- A Selection for a Handicap. *Journal of Theoretical Biology 53.* 205-214.