# Offspring Provisioning Rates in an Urban Passerine: Do they Change with Parental Age?

by
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# Abstract

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Studies have shown that offspring provisioning is one of the most demanding of parental activities in terms of both time and energy. European starlings (*Sturnus vulgaris*) are a socially monogamous yet facultatively polygynous passerine species. They exhibit biparental care in which both parents incubate the eggs and provision the offspring. Adult European starlings return to the study site to breed every year, making them an ideal species to examine the relationship between parental age and offspring provisioning rates. They have hackle (throat) feathers whose iridescent length allows classification of adults into one of two age categories 1) second year (SY, first-time breeders), or 2) after second year (ASY). The objective of my study was to examine offspring provisioning rates by both male and female parents who have been observed over at least two years. I predicted that adult males and females would provision their offspring at a higher rate than they did when they were younger (in the prior year). In support of my predictions, ASY males tended to provision the brood at a higher rate on days 7 or 8 of the nestling period. However, ASY males on day 13 or 14 of the nestling period tended to have a lower provisioning rate (provisions/hr/nestling) than when they were a year younger. I found no significant differences between the provisioning rates of ASY females on days 7 or 8 and 13 or 14 of the nestling period, which did not support my predictions. There were no significant differences in the number of provisions/nestling/hr made by SY or ASY males or females on day 7 or 8 of the nestling period. Understanding whether parental investment changes with parental age and how this might affect the reproductive success of European starlings is important in aiding the global population decline in avian species.

# Table of Contents

# List of Figures

# Introduction:

## I. Theory of Parental Investment

Survival and reproduction are the ultimate goals for any animal and plant species. Parental care is an important attribute of many organisms worldwide and is widely defined as any activity that parents put toward their offspring that has the potential to enhance the fitness of offspring (Smith et al. 1996). In avian species, this care can occur in an array of complex behaviours, such as building and defending of the nest, incubating eggs, and provisioning offspring (Smith et al. 1995). Parental care is therefore intrinsically linked with reproductive success in many avian species. Since Fisher (1930) first proposed the concept of reproductive effort, theories of reproductive strategies have been developed and revised. All reproductive strategies imply compromise, and individuals must balance their energy demands by resolving trade-offs between reproducing now and surviving to reproduce again. Therefore, reproductive effort is measured by reproductive cost in the form of energy investment and risk of reproductive mortality incurred by reproducing (Pugesek 1983).

An essential aspect of parental care is Trivers's (1972) concept of parental investment which he defined as the amount of effort a parent dedicates to their young for survival and reproductive success. Biparental care is widespread in birds, where it occurs in over 80% of species (Chutter et al. 2016). In European starlings (*Sturnus vulgaris*), a large portion of males breed monogamously and exhibit biparental care. However, sex-biased parental care has been shown to occur in several avian species where both parents provision offspring. In some species, females provision nestlings more frequently than males (Nordlund & Barber, 2005), while in others, males provision at higher rates (Lien et al., 2015). The two main forms of avian parental care after the eggs hatch are that of provisioning offspring and defending the nest from predators. Provisioning offspring is one of the most demanding of parental activities in terms of both time and energy (Nordlund & Barber, 2005). Studies have shown that parental energy expenditure is positively correlated with both the age and number of nestlings (Emms and Verbeek 1991).

II. Parental Age

A study by Bruce Pugesek (1983) examined how the age of breeding pairs affected their reproductive effort in the California gull (*Larus californicus*). He monitored and observed 196 California gulls in Wyoming island on Bamforth Lake. He discovered that older California gulls had a higher reproductive success than younger gulls due to foraging effort increasing with parental age. Older gulls provisioned more and rested less. Therefore, older parents invested more time in foraging effort. Pugesek (1983) also found that older parents defended their nest more frequently than younger parents did. He suggested that parental experience may influence reproductive success by improving efficiency in such a way that more offspring can be raised without extra reproductive effort. Specifically, he suggested that older gulls may have better foraging skills and knowledge of their environment, which can help them provide more food to their offspring, resulting in a higher survival rate. This could lead to a higher overall reproductive success without requiring additional reproductive effort.

Galbraith et al. (1999) identified 276 known-aged male Common terns (*Sterna hirundo*) with known laying dates and found that the number of offspring provisioning trips made by males varied significantly with age. This number increased approximately three-fold between the ages of 6 and 12 years of age. Their data also suggested that the increase in reproductive performance with age resulted primarily from this increase in provisioning efficiency (Galbraith et al. 1999).

In a study that examined the relationship between parental age and reproduction in Marsh tits (*Parus palustris*), Smith (2008) hypothesized that parental age would have a positive effect on reproductive success due to the Poor Breeder hypothesis which states that individuals will be more successful with reproduction when older because younger breeders lack experience in breeding and foraging. Smith (2008) discovered that there was a positive correlation between parental age and (1) hatching success, and (2) fledging success. Older females had significantly higher reproductive success, measured in terms of these two factors, than did younger females. However, no significant effect of male age on reproductive success was observed. These results suggest that maternal age is important in determining reproductive success, which Smith concluded could be due to the experience and knowledge of older individuals.

Limmer and Becker (2009) found that first-time breeding Common terns (*Sterna hirundo*) were less proficient at provisioning chicks than older breeders. They attributed it to better foraging skills and thus enhanced efficiency. Experienced parents were better at locating and catching prey, therefore more efficient at delivering food to their chicks (Limmer and Becker 2009).

A study by McGraw et al. (2001) found that nestling provisioning rates on female House finches (*Carpodacus mexicanus*) increased between second and third-year females. However, there was a decrease in offspring provisioning rates among females in the oldest age group which suggests that the relationship between age and condition is not linear (McGraw et al. 2001). This suggests that much older birds invest less in reproduction. McGraw et al. (2001) also found that older males fed their offspring more frequently and for longer durations than younger males. McGraw et al. (2001) found male House finches provided more parental care during the second breeding season, while females provided more parental care in the third breeding season. This suggests that males invest more in reproduction early in life, whereas females tend to invest more later in life.

## III. European Starling

The European starling (*Sturnus vulgaris*) is a songbird of the family Sturnidae, widely distributed throughout North America. They are known to be an urban-thriving species and were first introduced to North America in 1890. They are a secondary cavity-nester, typically breeding in enclosed areas such as holes in trees (Feare 1984). The European starling is a socially monogamous species, and adults usually remain together throughout one breeding attempt. Females lay an average of 3-6 eggs per clutch (Dunnet 2008). This species exhibits biparental care in which both parents incubate the eggs for about 12 days before the nestlings hatch (Sandell et al., 1996). The nestlings remain in the nest for approximately 20 days; both parents provision them and remove their faecal sacs (Dunnet 2008). Starlings are generally capable of first breeding when in their second year (SY; they hatched the year before), but not all can find a nesting site (Kessel, 1951). Starlings produce up to two broods a year with an early brood in April-May and a late brood in June-July.

## IV. Objective and Question for This Study

The purpose of this study is to examine offspring provisioning rates of male and female adult European starlings over subsequent breeding periods. The different factors involved in this study include sex of the provisioning parent (male, female), and the age of the parent (SY, ASY, ASY+1).

V. Predictions

I predict that adult males and females caught in the subsequent year will provision their offspring at a higher rate than they did when they were younger (in the prior breeding season) on days 7-8 and 13-14 of the nestling period. Number of provisioning trips/h and number of provisioning trips/nestling/h will both be examined. I also predict that ASY individuals will provision their offspring at a higher rate than would the SY adults.

This research will aid in the understanding of parental investment with respect to parental age in European starlings. It will further increase our knowledge about their provisioning behaviour over time. Knowing whether parental investment changes with parental age and how this affects the reproductive success of European starlings is important to understand as there is a global decline in bird populations (Rosenburg et al. 2019). We can then apply this information to potentially help passerine species achieve better reproductive success.

## Methods:

I. Study Site and Species

This study was conducted on the campus of Saint Mary's University located in Halifax, Nova Scotia, Canada (448 $37^{0}54.07^{00}$N, 638 $34^{0}47.09^{00}$W) demonstrated in Figure 1. The study of this population of European starlings has been ongoing since 2007. European starlings are a non-native species, which were likely brought over from Europe to North America in 1890 (Linz et al. 2007). Their large population size, relatively large clutch size and high fledging success make them a common passerine species for research (Feenders et al. 2011). European starlings are a socially monogamous species and typically exhibit biparental care, in which both parents provision their offspring.

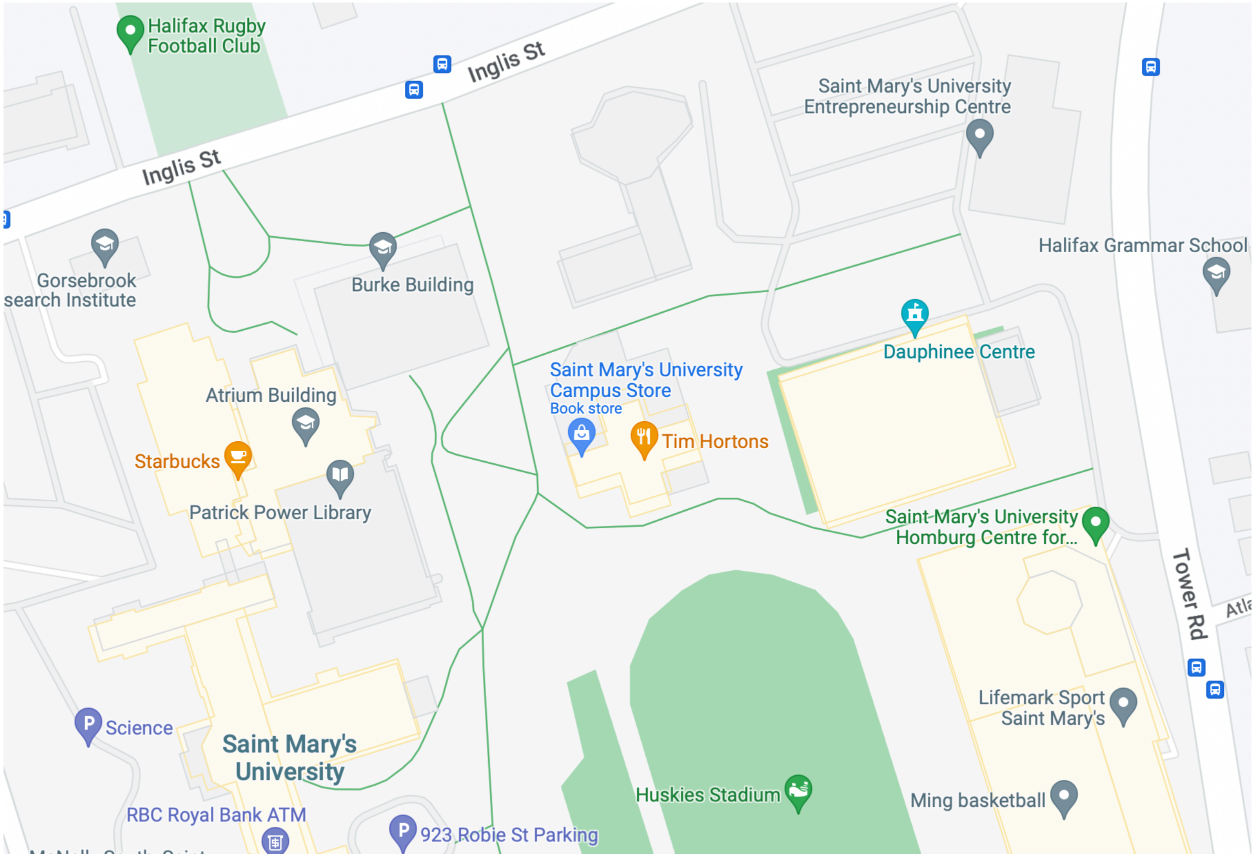


*Figure 1:* A map of Saint Mary's University campus located in Halifax, NS, Canada. This is the location where nest boxes were examined.

## II. Field Techniques

There were 45 nest boxes on the Saint Mary's University campus (Figure 1), and all were located approximately two to three meters off the ground, secured to the trunk of a tree. Nest checks began in late April to monitor the status of each nest and determine first egg dates. Each nest was checked on the day prior to the expected hatching day, with day 0 being assigned to the first day that nestlings hatched. All collection methods followed those approved by the Saint Mary's University Animal Care Committee protocols.

Adults were caught and sexed by the colour at the base of their bill (blue for males, pink for females) and the iris ring which is only present in females (Kessel, 195; Feare, 1984). Adults were banded with a Canadian Wildlife Service band and a unique colour combination of plastic bands was given for individual identification (Barber & Wright, 2017). The weight of adult and nestling European starlings was taken with a Pesola spring scale to the nearest 0.5 grams. Tarsus length was measured using digital calipers to the nearest 0.01 mm. Seven hackle feathers were plucked from the throat area for aging purposes (Kessel, 1951).

To determine the frequency of parental provisionings (number of provisioning trips/ brood and per nestling/h), nests were observed with binoculars for one-hour periods between 6:00 and 11:00am (ADT) on days 7 or 8 and 13 or 14 of the nestling period. Two days were allocated in the event of stormy weather on one of the days. Provisioning observations began when one member of the pair made the first provisioning trip into the nest. The observations that we looked for included which adult (male or female) brought food to the nestlings and how many times they did so (Nordlund & Barber, 2005).

III. Iridescent Length

The sample size consists of a total of 75 females and 47 males who were captured at least twice between 2007 and 2022. Adults were placed into one of two age groups the first time they were captured: 1) second year (SY), or 2) after second year (ASY) by measuring the iridescent length of their hackle feathers. The seven hackles per individual were measured using an Olympus dissecting microscope and illuminator. A ruler was used to measure the iridescent length from the top of the feather to the end of the iridescence portion of the feather as demonstrated in Figure 2. After the feathers were measured for each adult, an average iridescent length $\pm$ SE was calculated for each individual. Females were considered to be SY when their mean hackle iridescence length was less than 6.5 mm. They were ASY females when the iridescence length was 6.5mm or more. Males were considered to be SY when their mean hackle iridescent length was less than 11.0 mm and ASY when that length was 11.0 mm or greater (Kessel, 1951; Barber and Wright, 2017).

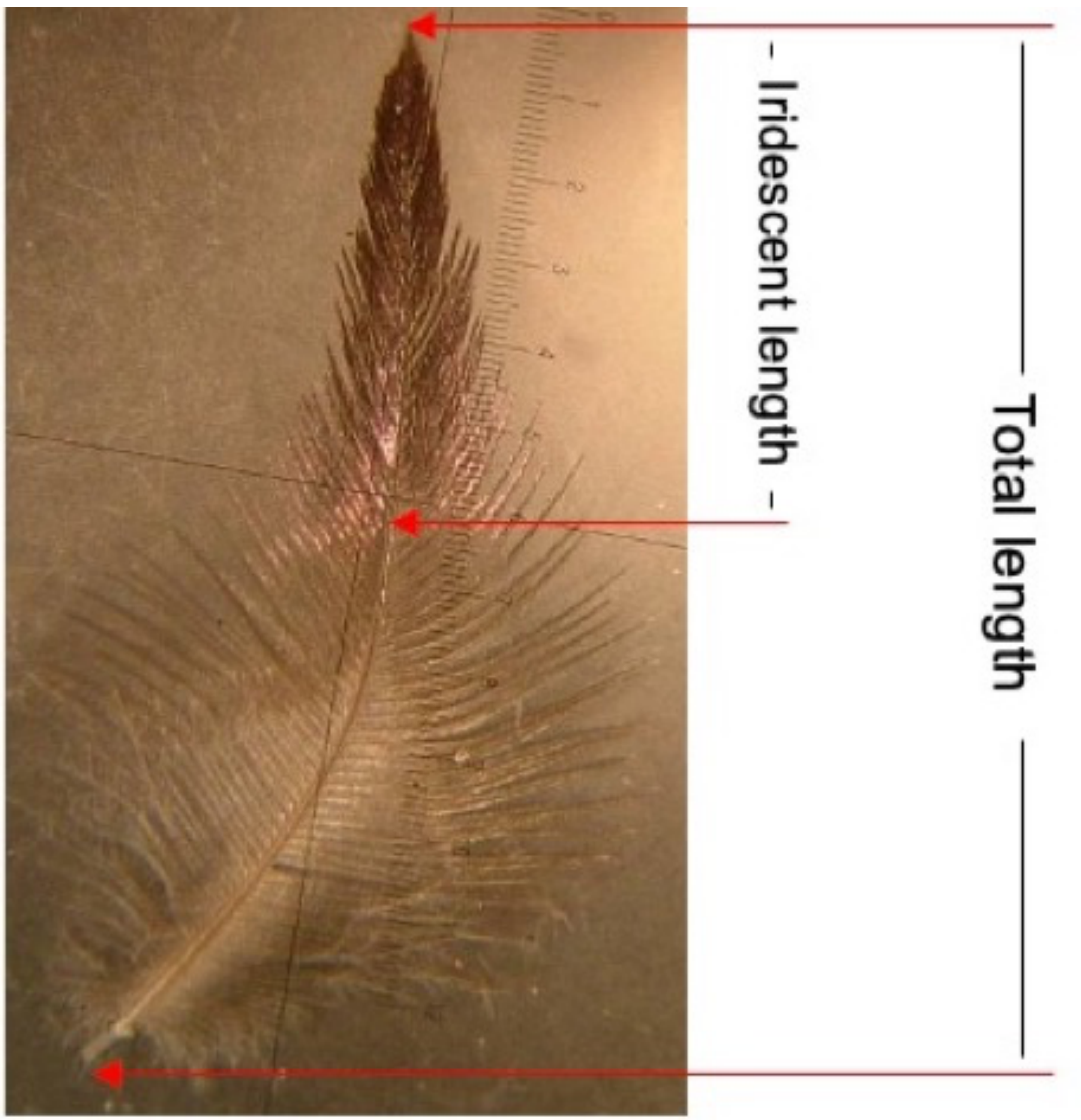


Figure 2: A hackle feather under an Olympus dissecting microscope and illuminator. The image iridescent length from the top of the feather to end of the iridescent portion.

IV. Statistical Analysis

All statistical analyses were performed using GraphPad Prism software (GraphPad Software Inc., La Jolla, CA, USA). The data were tested for normality using a d'Agostino-Pearson normality test. The number of provisioning visits/nestling/h and the number of provisioning trips/h made by a) male and b) female European starlings in the year they were first captured (and aged as SY or ASY) were compared to the following year (ASY or ASY+1, respectively). Normally distributed data were analysed using paired *t*-test statistics, and a Wilcoxon signed rank test was used to statistically analyse the paired non-parametric data. Also, the number of provisioning visits/nestling/h and the number of provisioning trips/h made by SY vs. ASY adults was compared using an unpaired non-parametric analysis (Mann-Whitney U test) with no individual being counted in both categories. Wilcoxon signed rank tests were used when possible to compare provisioning rates of individuals when they were SY to the following year when they became ASY. All tests were two-tailed. Mean $\pm$ SE or Median and range are given. Results were considered to be statistically significant when $P \leq 0.05$.

## Results:

I. Analysis of the number of provisions/nestling/h by male and female European starlings

The number of provisioning visits/nestling/h made by males on days 7-8 of the nestling period tended to be higher when males were a year older (Median, range: 2.30, 1.4 - 4.25) than in the previous year (1.99, 0.86 - 5.5; W = 35.00, n = 10, P = 0.08; Figure 3). However, there was also a statistical tendency for males provisioning day 13-14 nestlings to have a lower number of provisions/nestling/h when they were a year older (Median, range: 2.38, 1.0 – 4.6) than the year before (2.67, 2.0 - 5.5; W = -19.0, n = 6 males, P = 0.06; Figure 4)

No significant difference existed in the number of provisions/nestling/h made by females to 7-8 day old nestlings when they were first captured (2.50, 0.0 – 7.00) in relation to the following year (ASY+1) (2.33, 0.75 – 8.50; W = -10.0, n = 21, P = 0.86). The number of provisioning visits/nestling/h made by females on day 13 or 14 of the nestling period also showed no significant difference between females when they were first captured (3.29 $\pm$ 0.44) in relation to the following year (4.12 $\pm$ 0.54; paired $t$ = 1.187, n = 16, P = 0.25).

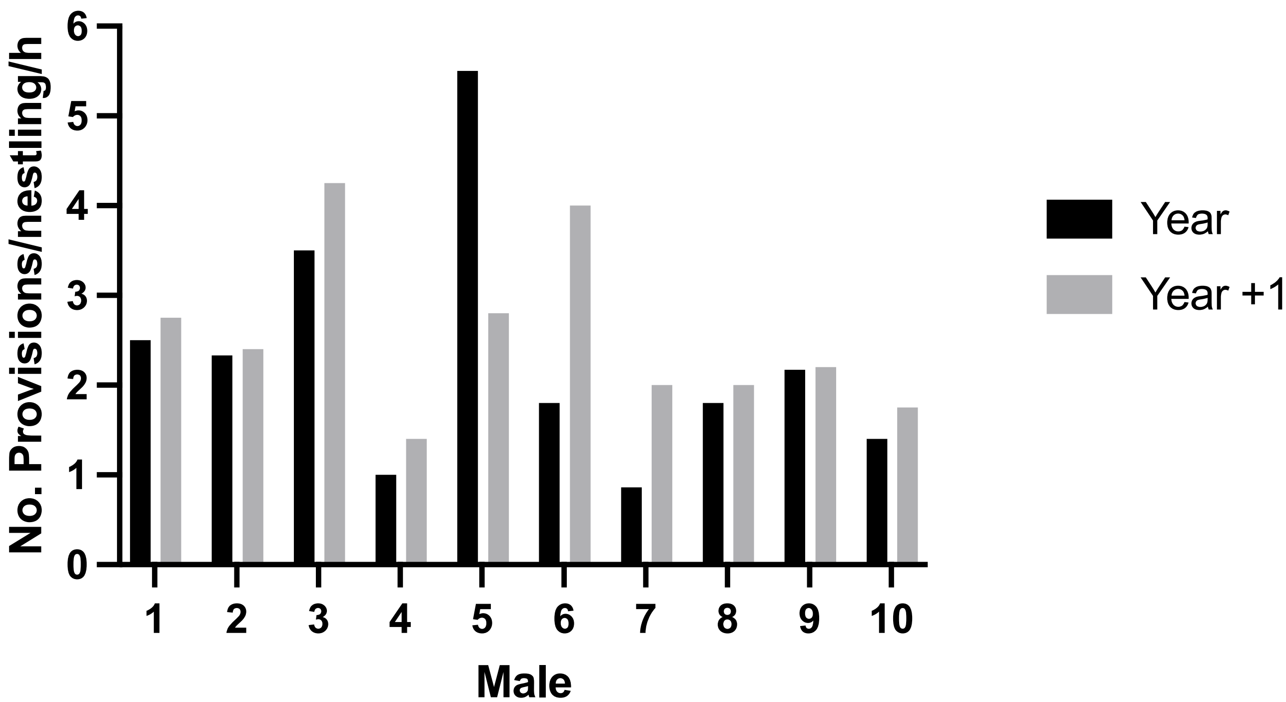


Figure 3: A bar graph demonstrating the number of provisioning visits/nestling/h made by 10 male European starlings when they were first captured (ASY) in relation to the following year (ASY+1) on day 7 or 8 of the nestling period.

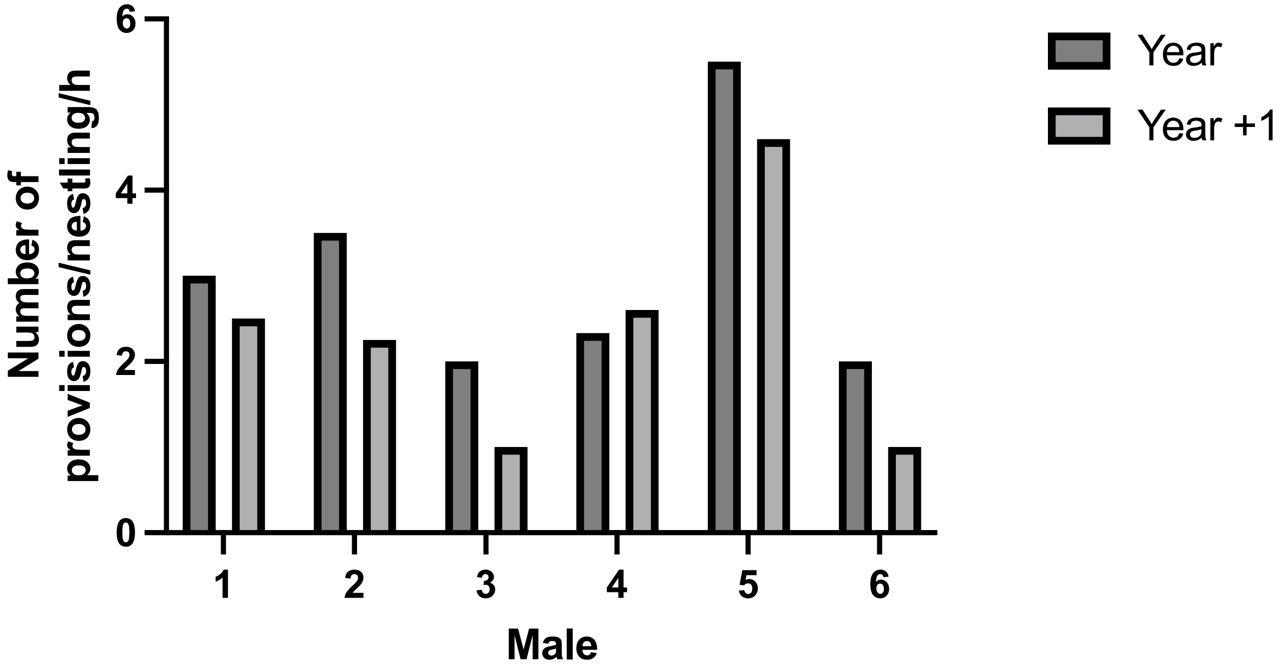


Figure 4: A bar graph demonstrating the number of provisioning visits/nestling/h made by six male European starlings when they were first captured (ASY) in relation to the following year (ASY+1) on day 13 or 14 of the nestling period.

II. Analysis of the number of provisions/h made by male and female European starlings

No significant differences were detected in the number of provisioning visits/h made by males to day 7-8 nestlings when males were one year older (Median, range: 10.00, 4 – 17) compared to the previous year (9.5, 4 – 14; W = 14.0, n = 10, P = 0.52). There were also no significant differences detected in the number of provisioning visits/h that males made to 13-14 day old nestlings when males were one year older (11.50, 8 – 22) compared to the previous year (14, 2 – 25; W = -5.0, n = 6, P = 0.69).

Similarly, no significant differences were detected in the number of provisioning visits/h that females made to nestlings at 7-8 days of age when females were a year older (9.00, 0 - 20) compared to the previous year (11.00, 0 – 32; W = -19.00, P = 0.74). However, the number of provisioning visits/h made by females to day 13 or 14 nestlings was significantly higher when females were a year older (16.0, 4 - 36) than the previous year (10, 2 – 24; W = 92.0, df = 16, P = 0.03; Figure 5).

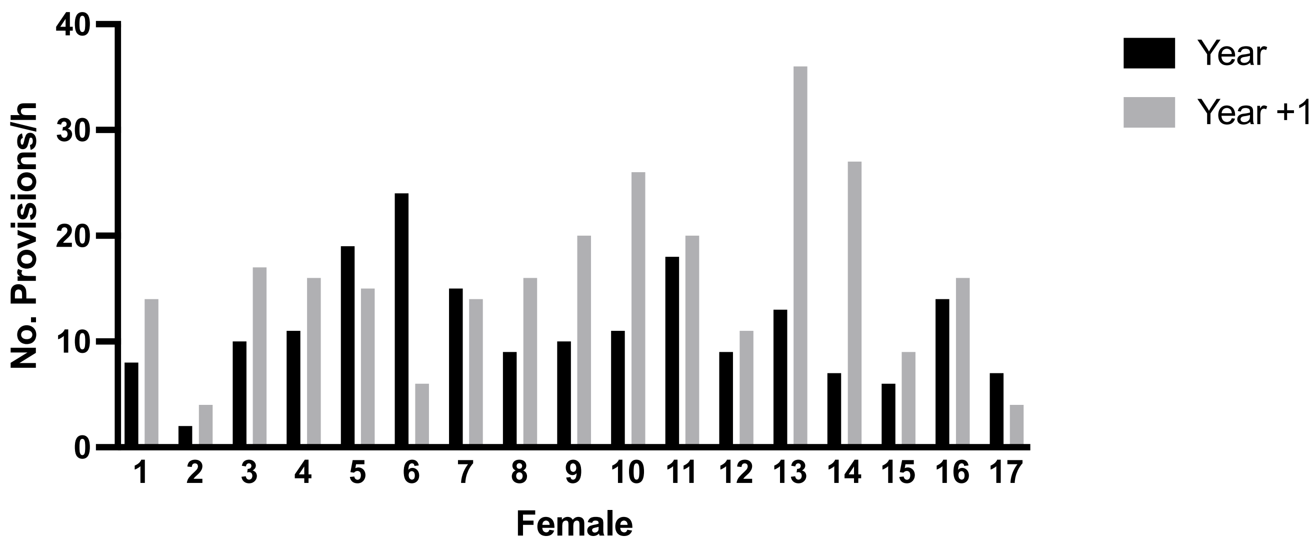


Figure 5: A bar graph demonstrating provisioning rates (provisions/h) of 17 female European starlings when they were first captured (ASY) in relation to the next year they were captured (ASY+1) on day 13 or 14 of the nestling period.

III. Analysis of the number of provisioning visits /nestling/h made by first-time breeders (SY)

There was no significant difference in the number of provisions/nestling/h made by SY males (2.12, 0.83 – 4.00) as compared to ASY males (2.17, 0.5 – 5.5; Mann-Whitney U = 50, $n_1$ = 6, $n_2$

= 17, P = 0.96) on day 7 or 8 of the nestling period. There was also no significant difference in the number of provisions/nestling/h made by SY males (3.00, 1.80 – 3.50) as compared to ASY males (2.75, 0.75 – 5.50; Mann-Whitney U = 44.5; $n_1$ = 5, $n_2$ = 18, P = 0.99) on day 13 or 14 of the nestling period.

Similarly, on day 7-8 of the nestling period, the number of provisioning visits/nestling/h made by SY females (2.75, 1.6 – 3.5) did not differ significantly from those made by ASY females (2.80, 0 – 7; Mann-Whitney U = 66.5, $n_1$ = 6, $n_2$ = 24, P = 0.79). There were also no significant differences on day 13-14 in the number of provisions/nestling/h made by SY females (3.50, 0.5 – 6) as compared to ASY females (2.38, 1.5 – 7; Mann-Whitney U = 38; $n_1$ = 6, $n_2$ = 16, P = 0.48).

I had data for only two SY males who became ASY the following year for day 7-8 of the nestling period. Figure 6 suggests that these males increased their number of provisions/nestling/h over that one year. The sample size was too small to do statistical analysis. However, on day 13 - 14 of the nestling period the bar graph demonstrated in Figure 7 tends towards a decrease in the number of provisions/nestling/h as the male European starling ages, but again, this could not be tested statistically.

There was no significant difference detected between the same female in their SY (2.50, 1.60 – 3.00) compared to ASY year (2.33, 1.20 – 8.50; W = -1, n = 5, P > 0.99) on day 7 or 8 of the nestling period. Similarly, no significant difference existed between females who were in their SY (3.50, 0.96 – 6.00) compared to when they were a year older (ASY) (3.96, 1.05 – 8.00; W = 2, n = 4, P = 0.88).

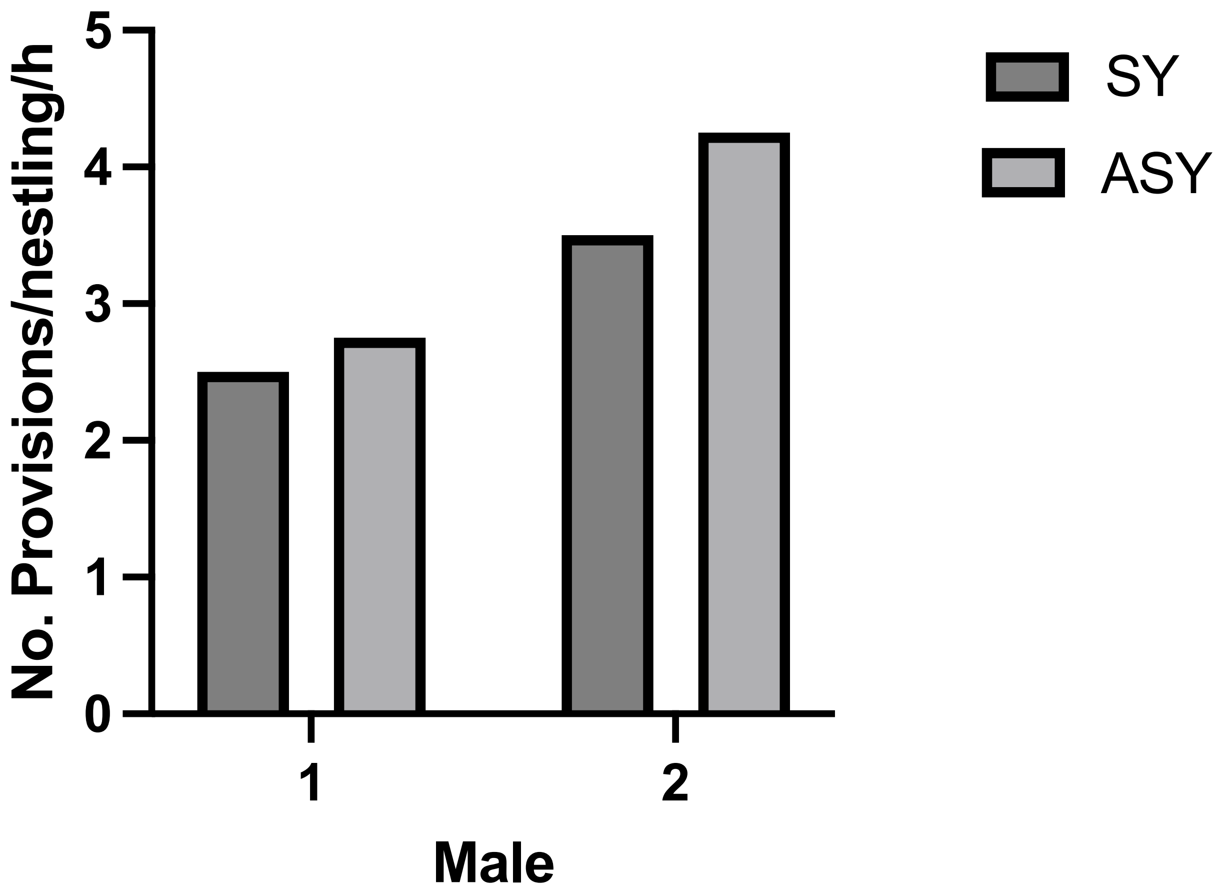


Figure 6: A bar graph demonstrating the number of provisioning visits/nestling/h made by two male European starlings when they were first captured (SY) in relation to the following year (ASY) on day 7 or 8 of the nestling period.

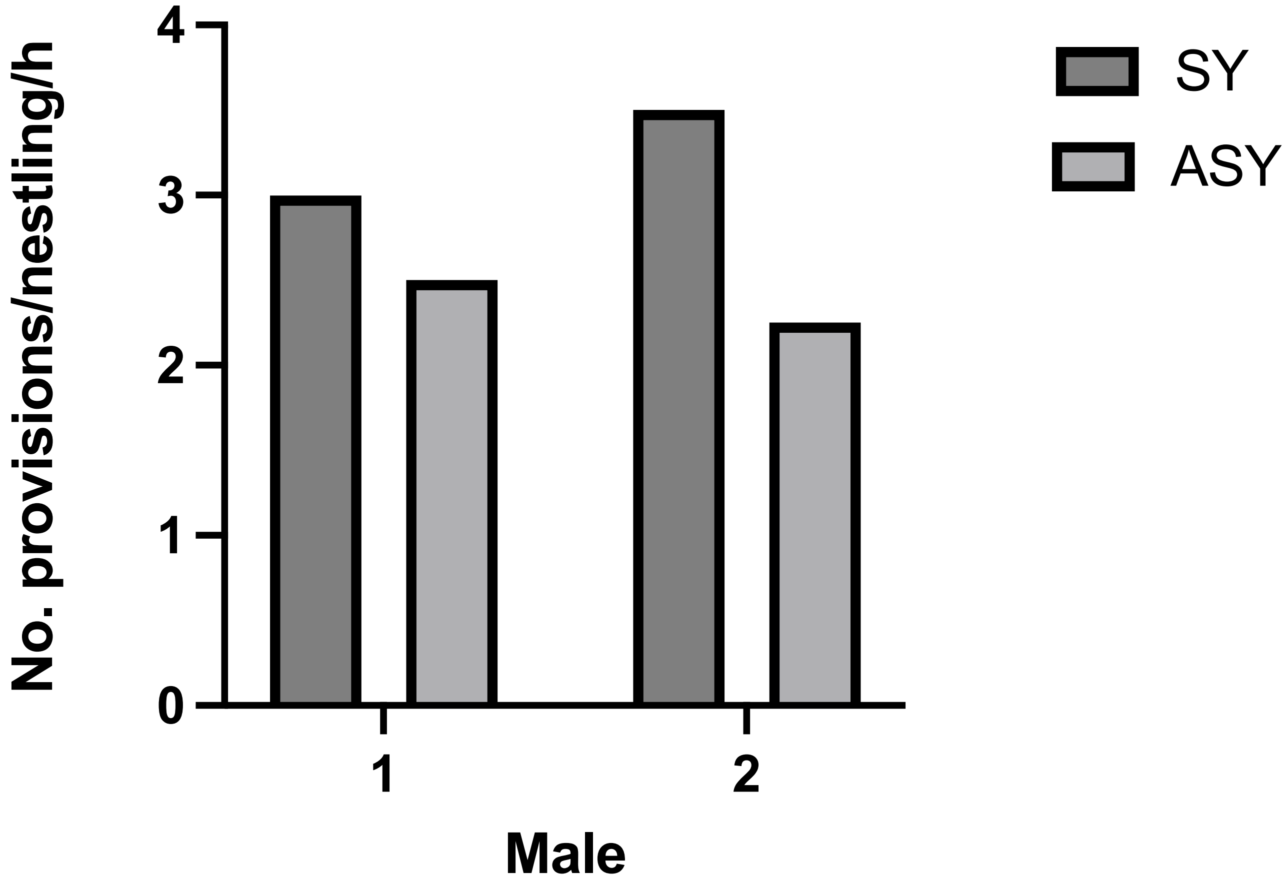


Figure 7: A bar graph demonstrating the number of provisioning visits/nestling/h made by two male European starlings when they were first captured (SY) in relation to the following year (ASY) on day 13-14 of the nestling period.

IV. Analysis of the number of provisioning visits/h made by first time breeders (SY)

There was also no significant difference made by SY males (7.50, 3.00 – 14.0) as compared to ASY males (9, 2.00 – 14.00; Mann-Whitney U = 45; $n_1$ = 6, $n_2$ = 17, P = 0.69) on day 7 - 8 of the nestling period. Similarly, no significant difference was found in the number of provisions/ h made by SY males (12.00, 9.00 – 18.00) as compared to ASY males (8.00, 3.00 – 22.0; Mann-Whitney U = 15, $n_1$ = 5, $n_2$ = 10, P = 0.242) on day 13 - 14 of the nestling period.

No significant difference in the number of provisions made per hour between SY females (9.00, 7.00 – 12.0) and ASY females (11.0, 0 – 32.0; Mann U = 67.5, $n_1$ = 6, $n_2$ = 25, P = 0.72) was detected on day 7 - 8 of the nestling period. There was also no significant difference detected in the number of provisions made between SY females (9.50, 2.00 – 24.00) and ASY females (10.00, 4.00 – 19.00; Mann U = 44, $n_1$ = 6, $n_2$ = 16, P = 0.78) on day 13 - 14 of the nestling period.

There were only two males during observed in both their SY and the following year when they became ASY. Figure 8 suggests that they provisioned the day 7-8 brood more often when they become ASY, but the sample is too small to analyze these data statistically. However, on day 13-14 of the nestling period, they reduced their number of provisions/h as they become ASY, but the sample size was too small to make any conclusions.

No significant differences were detected between the same female in their SY (10.0, 7.00 – 12.0) and their ASY year (7.00, 4.00 – 17.0; W = -5.0, n = 5, P = 0.56) on day 7-8 of the nestling period. Similarly, no significant differences were found between females who were in their SY (10.5, 2.00 – 24.0) compared to when they were a year older (ASY; 11.0, 4.00 – 27.0; W = 4.0, n = 4, P = 0.63) on day 13 or 14 of the nestling period, however, the sample size is small.

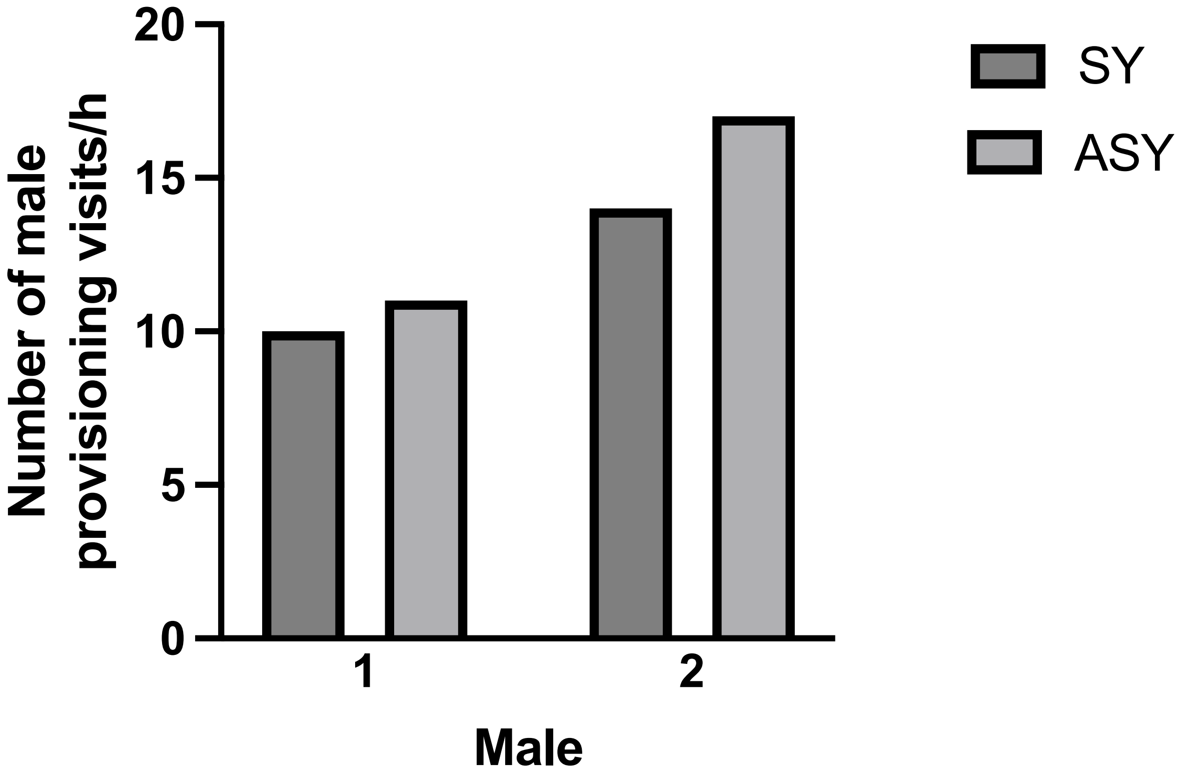


Figure 8: A bar graph demonstrating the number of provisioning visits /h made by two male European starlings when they were first captured (SY) in relation to the following year (ASY) on day 7 - 8 of the nestling period.

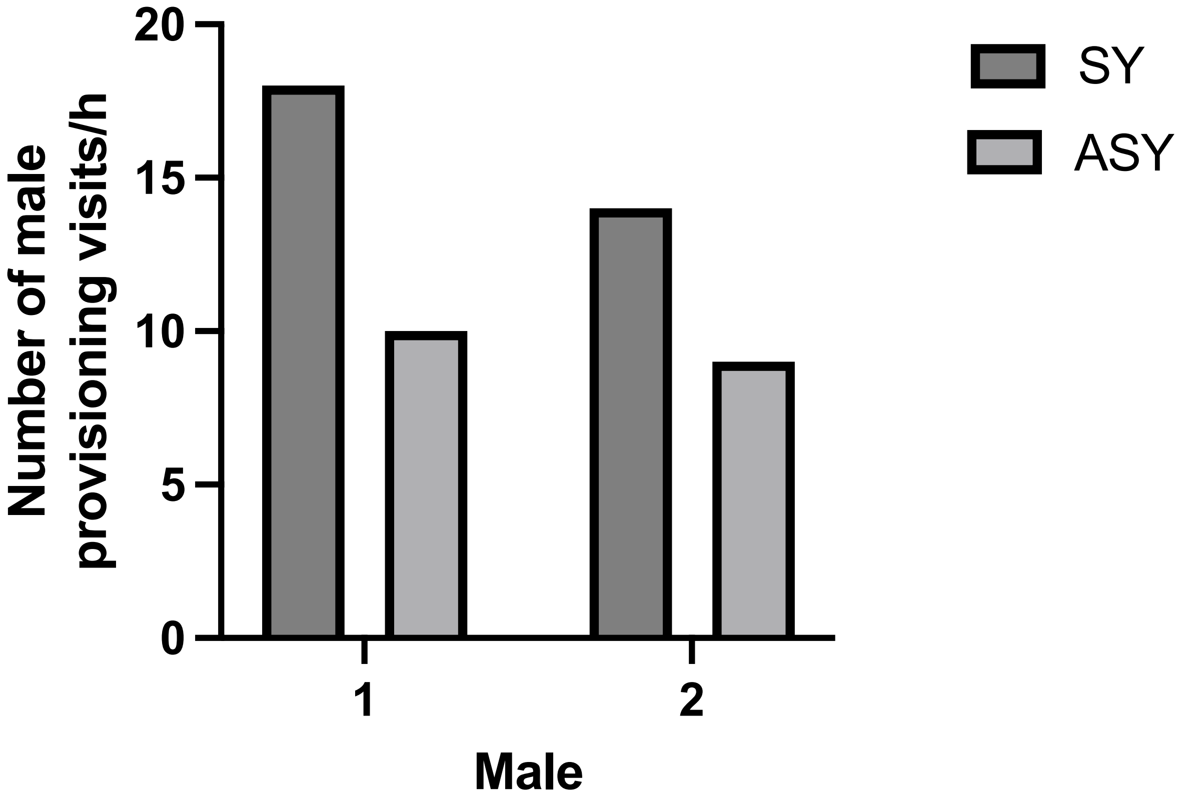


Figure 9: A bar graph demonstrating the number of provisioning visits/ h made by two male European starlings when they were first captured (SY) in relation to the following year (ASY) on day 13 - 14 of the nestling period.

## Discussion:

When accounting for the number of nestlings present, male European starlings tended to provision each of their day 7-8 nestlings at a higher rate when they were a year older than they did the previous year, supporting my prediction. Surprisingly, contrary to my prediction, these same males tended to provision each of their day 13-14 nestlings at a lower rate when they were a year older than they did the previous year. Older males who are more experienced with breeding likely know the best foraging sites and are therefore more efficient foragers (Lien et al., 2015). Kessel (1957) found that in European starlings, offspring provisioning rates initially increase until day 17 of the nestling period, and then decline until fledging (between days 20-24 of the nestling period). In a study on European shags, Daunt et al (2007) discovered that foraging efficiency was significantly higher among experienced than naïve (first-time breeding) males in the early season. However, experienced males later in the breeding season had a lower foraging efficiency than their same-experience counterparts earlier in the season. He suggested that this may be due to a trade-off between experience and other factors that affect foraging success, such as decline in food availability or increased competition (Daunt et al., 2007). Another study on Carolina wrens (*Thryothorus ludovicianus*) found that males tended to provision nestlings more than females earlier in the nestling stage (Neudorf et al. 2012). They suggested that males initially made more provisioning trips to demonstrate their quality to females.

There was no significant difference found in female provisioning rates/nestling from one year to the next on either day 7-8 or 13-14 of the nestling period. Kluijver (1933) found a difference between the clutch size of SY and ASY European starlings with the older starlings tending to have a larger clutch size than the younger females. In a study on Northern flickers (*Colaptes auratus*), another cavity nester, Musgrove and Wiebe (2014) discovered that provisioning rates and brood size were positively correlated. They found an increase in provisioning rates within enlarged broods and that feeding rates generally increased with brood size. They also found that there was a general decline in the per-nestling provisionings, indicating that the parents were not able to fully compensate for additional nestlings in their larger broods.

No significant differences were detected in the number of provisioning visits/h that male European starlings made to their brood when they were one year older compared to the previous year when nestlings were either 7-8 or 13-14 days old. Similarly, the number of provisioning visits/h made by females to day 7-8 nestlings did not differ significantly from one year to the next. However, females fed their day 13-14 broods at a significantly higher rate when females were a year older than in the prior year. This suggests that female offspring provisioning increases with nestling age, especially when the growth rate is at its peak (Riechert et al., 2012).

When comparing SY males with ASY adults, no significant differences were detected in the number of provisions/h made on days 7-8 and 13–14 of the nestling period for either males or females. Unfortunately, sample size was too small for males, but for females, the number of provisioning visits/brood and per nestling made by SY females on days 7-8 and 13-14 of the nestling period also displayed no significant differences than when they were a year older (became ASY). These findings did not support my prediction of higher provisioning rates with parental age. Perhaps older females are bringing bigger load sizes (more food at any one time) to their offspring, resulting in fewer provisioning visits, but more food.

Unlike my study, McGraw et al. (2001) found that nestling provisioning rates by female House finches (*Carpodacus mexicanus*) increased between second and third-year females. However, there was a decrease in offspring provisioning rates among females in the oldest age group which suggests that the relationship between age and condition is not linear (McGraw et al., 2001). This suggests that older birds may be more efficient at foraging and provisioning due to accumulated experience over their lifetime, but only up to a point.

To conclude, male but not female European starlings tended to provision each of day 7-8 nestlings at a higher rate when males were a year older than they did the previous year. This may be due to males trying to demonstrate their quality to females. These same males tended to provision each of their day 13-14 nestlings at a lower rate when they were a year older than they did the previous year. One-year older females fed day 13-14 nestlings at a significantly higher rate than they did the prior year. Perhaps males are reducing their visits as females are increasing theirs, or males may be bringing more food at any one time, and thereby tending to make fewer provisioning trips.

Finally, there was no significant difference in the number of provisions/ h made by SY and ASY males on days 7-8 and 13–14 of the nestling period, contrary to my prediction. The number of provisioning visits made by SY females on days 7-8 and 13-14 of the nestling period also displayed no significant difference between females who were at least a year older than when they were in there SY.

This European starling population in both North America and their native range are declining (Rosenberg et al., 2019). Future studies in determining how parental investment behaviours change over time and whether it causes negative effects such as a decrease in fledging success, can allow us to better understand the contributions of parental investment. This study allows for a more in-depth understanding of European starlings and the parental provisioning efforts they exhibit as they age.

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# References:

Amininasab, S. M., Kingma, S. A., Birker, M., Hildenbrandt, H., & Komdeur, J. (2016). The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. Behavioral Ecology and Sociobiology, 70(9), 1591–1600.

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

Bodt, L. H., Rollins, L. A., & Zichello, J. M. (2020). Contrasting mitochondrial diversity of European starlings (*Sturnus vulgaris*) across three invasive continental distributions. Ecology and Evolution, 10(18), 10186–10195. https://doi.org/10.1002/ece3.6679

Burnham, H., & Cruz, L. (2020). Parental investment does not directly affect reproductive success in the Saffron Finch. Journal of Avian Biology, 51(11).

Chutter, Christopher M., Redmond, L., Cooper, N., Dolan, A., Duffield, D., & Murphy, M. (2016). Paternal behaviour in a socially monogamous but sexually promiscuous passerine bird. Behaviour, 153(4), 443–466.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B: Biological Sciences, 273(1592), 1375–1383.

Daunt, F., Wanless, S., Harris, M., Money, L., & Monaghan, P. (2007). Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. Functional Ecology, 21(3), 561–567.

Dunnet, G. (2008). The breeding of the starling Sturnus Vulgaris in relation to its food supply. Ibis, 97(4), 619–662.

Emms, S. K., & Verbeek, N. A. M. (1991). Brood Size, Food Provisioning and Chick Growth in the Pigeon Guillemot Cepphus columba. The Condor, 93(4), 943.

Feenders, G., Klaus, K., & Bateson, M. (2011). Fear and exploration in European Starlings (*Sturnus vulgaris*): A comparison of hand-reared and wild-caught birds. PLoS ONE, 6(4), e19074.

Jamieson, I. (1988). Provisioning Behaviour in a Communal Breeder: an Epigenetic Approach To the Study of Individual Variation in Behaviour. Behaviour, 104(3-4), 262–280.

Kessel, B. (1951). Criteria for Sexing and Aging European Starlings (*Sturnus vulgaris*). Bird-Banding, 22(1), 16.

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

Komdeur, J., Wiersma, P., & Magrath, M. (2002). Paternal care and male mate–attraction effort in the European starling is adjusted to clutch size. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1497), 1253–1261.

Lien, L., Millsap, B., Madden, K., & Roemer, G. (2015). Male brood provisioning rates provide evidence for inter-age competition for mates in female Cooper's Hawks. Ibis, 157(4), 860–870.

Limmer, B., & Becker, P. (2009). Improvement in chick provisioning with parental experience in a seabird. Animal Behaviour, 77(5), 1095–1101.

McGraw, K., Nolan, P., Stoehr, A., & Hill, G. (2001). Intersexual differences in age-specific parental effort in the house finch (*Carpodacus mexicanus*). Etologia.

Musgrove, A., & Wiebe, K. (2014). Northern Flickers increase provisioning rates to raise more but poorer quality offspring when given experimentally enlarged broods.

Neudorf, D., Brodrick, M., & Cureton, J. (2013). Parental Provisioning by Carolina Wrens. The Wilson Journal of Ornithology, 125(1), 179–184.

Nordlund, C., & Barber, C. (2005). Parental Provisioning in *Melospiza melodia* (Song Sparrows). Northeastern Naturalist, 12(4), 425–432.

Ortega, S., Sánchez-Macouzet, O., Urrutia, A., Rodríguez, C., & Drummond, H. (2017). Age-related parental care in a long-lived bird: implications for offspring development. Behavioral Ecology and Sociobiology, 71(9).

Patrick, S., Corbeau, A., Réale, D., & Weimerskirch, H. (2020). Coordination in parental effort decreases with age in a long lived seabird. Oikos, 129(12), 1763–1772.

Pittet, F., Coignard, M., Houdelier, C., Richard-Yris, M.-A., & Lumineau, S. (2012). Age Affects the Expression of Maternal Care and Subsequent Behavioural Development of Offspring in a Precocial Bird. PLoS ONE, 7(5), e36835.

Pugesek, B. (1983). The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). Behavioral Ecology and Sociobiology, 13(3), 161–171.

Riechert, J., Chastel, O., & Becker, P. (2012). Why do experienced birds reproduce better? Possible endocrine mechanisms in a long-lived seabird, the common tern. General and Comparative Endocrinology, 178(2), 391–399.

Ritchison, G., Lewis, L., & Heist, C. A. (2022). Provisioning behavior of male and female Loggerhead Shrikes. Avian Biology Research, 15(2), 93–99.

Rosenberg, K., Dokter, A., Blancher, P., Sauer, J., Smith, A., Smith, P., Stanton, J., Panjabi, A., Helft, L., Parr, M., & Marra, P. (2019). Decline of the North American avifauna. Science, 366(6461), 120–124.

Sandell, M., Smith, H., & Bruun, M. (1996). Paternal care in the European starling, *Sturnus vulgaris*: nestling provisioning. Behavioral Ecology and Sociobiology, 39(5), 301–309.

Smith, H. (2008). Parental age and reproduction in the Marsh Tit Paras palustris. Ibis, 135(2), 196–201.

Steen, R., Sonerud, G. A., & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). Journal of Ornithology, 153(4), 1087–1099.

Wetzel, D., & Westneat, D. (2013). Parental Care Syndromes in House Sparrows: Positive Covariance Between Provisioning and Defense Linked to Parent Identity. Ethology, 120(3), 249–257.

Wilcoxen, T., Boughton, R., & Schoech, S. (2010). Older can be better: physiological costs of paternal investment in the Florida scrub-jay. Behavioral Ecology and Sociobiology, *64*(10), 1527–1535.