Mate Fidelity in a Double-Brooded Urban Passerine

By

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Abstract

Every bird requires a mate to have a successful breeding attempt. After each brood, they are faced with the choice to stay with or separate from this mate. The choice to stay together is referred to as mate fidelity and can benefit the future reproductive success of the pairs who exhibit it. Despite these benefits, separation is still common in many populations of passerines, leading to the question of the costs of mate fidelity and under what circumstances these costs might outweigh the benefits. In this study, I examined the frequency of mate fidelity in a population of urban dwelling European Starlings (*Sturnus vulgaris*) over 15 years. Mate fidelity or subsequent separation events were then compared to average brood condition of each brood raised together to test if any correlation between them existed. Tests were run between the first and last brood raised by a faithful pair, and between the first brood from a faithful pair and the first and only brood raised by a pair that subsequently separated to determine if brood condition affected fidelity in the population. While mean brood condition followed the prediction that broods preceding fidelity would be higher in condition than those which preceded separation, the difference between the two categories was not statistically significant in either test. These findings still warrant investigation, as the difference in condition was noticeable, and sample sizes were small, so we may have lacked the statistical power to detect such influence. Brood condition could still influence the frequency of mate fidelity within this population along with other possibilities.

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Introduction

The most important thing that all avian species require for a successful breeding season, is a mate with whom to reproduce. At the end of the breeding season every individual is faced with an important choice to either stay with their previous or to find a new partner for their next attempt. The choice to remain faithful to a mate is referred to as mate fidelity (Black, 1996). Social monogamy is the predominant type of avian mating system, encompassing over 90% of avian species (Choudhury, 1995; Lv et al., 2016). Social monogamy involves the pair choosing to raise their young together, whereas genetic monogamy is when all the offspring being raised by a pair are related to both parents. Social and genetic monogamy are not mutually exclusive and occur within the same pair (Wittenberger and Tilson, 1980). Mate fidelity is most important to consider in species that are socially monogamous and that exhibit biparental care, as the pair must work together to raise their young to maturity (Wittenberger and Tilson, 1980). Fidelity is an important consideration in such species because the choice to remain faithful to an individual is closely linked to overall breeding success within an individual's life (Johns et al., 2018). If an excess of time and energy is invested into maintaining a pair-bond with a low-quality mate, there could be a detrimental effect on an individual's lifetime reproductive success (Miño and Massoni, 2017).

Mate choice can impact the lifetime fitness of the offspring produced, as both parents in a socially monogamous pair make non-genetic contributions to their offspring (Wilson, 2022). Mate fidelity is likely to increase when familiarity as a pair increases reproductive success through their improved coordination and cooperation when caring for their young. (Black, 1996; Coss et al., 2019.; Choudhury, 1995; Llambías et al., 2008; Sanchez-Macouzet et al., 2014; Williams and McKinney 1996). Pairs that remain together over multiple seasons have increased reproductive success over time; the longer the pair remains together, the more likely they are to have a successful reproductive season (Beheler et al., 2003; Sydeman et al., 1996; Wooller and Bradley, 1996). Other benefits of remaining with the same mate include earlier laying dates, improved hatching success, and raising a higher number of fledglings (nestlings that leave the nest), all of which contribute positively to the parent's lifetime reproductive success (Sanchez-Macouzet et al. 2014).

Separation can be costly both in time and energy since a new mate must be acquired and they could be of lesser quality (Coss et al., 2019). The simplest explanation for why separation occurs is the possibility of finding a higher-quality mate (Coss et al., 2019). At the beginning of a breeding season, for some species there is a limited amount of time available to assess a potential mate's quality, potentially leading to a poor choice in mates (Choudhury, 1995). Ambrosini's (2002) study of Barn Swallows (*Hirundo rustica)*, a double-brooded species (laying two broods within the same breeding season), found that pairs that were formed after a mate separation in the prior breeding season were less likely to produce a second brood, lowering their lifetime reproductive success.

If the breeding attempt results in failure and the offspring do not fledge from the nest, then separation is a likely outcome (Dubois and Cezilly, 2002; Jeschke and Kokko, 2008). Jeschke and Kokko (2008) reviewed the determinants of bird separation rates and found that breeding success was negatively correlated with separation rates across many studies. A similar conclusion was drawn after Coulson's (1972) study of Kittiwakes (*Rissa tridactyla)* showed that pairs experiencing an unsuccessful breeding attempt separated more often than did successful pairs. Wilson et al. (2022) showed that separation rate in Zebra Finches (*Taeniopygia guttata)* decreased as the number of fledglings increased, indicating that nestling mortality had an influence on the decision to remain paired with each other.

Two hypotheses have been proposed to explain why pairs separate to increase their reproductive success. The Incompatibility Hypothesis (Coulson, 1972; Rowley 1983), states that when both individuals are fit but do not work well together, their partnership leads to a decrease in reproductive success. The 'Better Option' Hypothesis proposes that when one individual is less fit than the other, the fitter individual can increase their reproductive success by deserting their mate in favour of a better one (Ens et al. 1993).

Certain aspects of each population's life history can also influence how often separation occurs. The lifespan of a bird limits how many reproductive events an individual has during their lifetime, allowing longer-lived species the ability to be choosy with their partners, as they stand to gain more in terms of their overall lifetime reproductive success than do shorter-lived species with a fewer reproductive opportunities (Choudhury, 1995). The migration habits of a species can also influence their degree of fidelity. Resident species tend to show higher rates of mate fidelity because they have less difficulty relocating a previous mate than would a migratory species (Choudhury, 1995). However, the most important aspect of whether a pair remains together appears to be the success of their previous breeding attempt. A study of separation in European Blackbirds (*Turdus merula*) showed a that a pair's prior breeding success had a significantly positive influence on fidelity, with unsuccessful breeding attempts often leading to a pair's separation in the subsequent breeding season (Desrochers and Magrath, 1996). Therefore, overall brood condition (the average body condition of all nestlings within a nest) can be a predictor of mate separation in birds (Coss et al., 2019; Ens et al., 1996).

Studies that examine the relationship between offspring success and parental fidelity have been limited in the past by their definition of success. A review by Dubois and Cézilly (2002) looked at past studies that analyzed fledging success and brood condition in different avian species and found that breeding success was defined as having fledged at least one young rather than the number of young successfully fledged. This definition can affect the conclusions of studies as fledging one young may not be considered a great success for a pair who produces many offspring during a single reproductive attempt.

Double-brooded socially monogamous passerine species with biparental care are ideal for examining mate fidelity and mate separation. European Starlings (*Sturnus vulgaris*) are double-brooded, giving twice the amount of data to be collected in each breeding season, and allowing fidelity to be tracked both within a breeding season and over multiple seasons (Feare, 1984). European Starlings have shown in the past a high rate of mate switching between the two attempts within a single season (Bart, 1990). Nevertheless, starlings exhibit bi-parental care with their nestlings, which predisposes them to have lower rates of separation as they gain more benefits from long-term partnership because they are actively coordinating with their partner to care for their young (Feare, 1984; Williams and McKinney, 1996). Their approximate eight-year lifespan gives them up to 14 breeding attempts in their whole life, allowing them to be choosier with their mates than other passerines who have shorter lifespans (Choudhury, 1995; Kessel; 1957). European Starlings are also nonmigratory, which should enhance their likelihood to remain monogamous since they are likely to have less difficulty relocating their previous mate and nest box (Choudhury, 1995). Their residency to the breeding site also gives them ample time to assess the quality of their potential partner before the breeding season (Choudhury, 1995).

Relocation of individuals within the population is not a problem as adult Starlings are shown to have a high philopatry to the breeding grounds (Feare, 1984).

The objectives of my study are to 1) measure the frequency of mate fidelity among the European Starling population of Saint Mary's campus over a 15-year study period and 2) test the impacts of brood condition on mate fidelity. I predict a positive correlation will exist between mate fidelity and brood condition. Therefore, broods in poor condition will likely result in the pair separating immediately following that reproductive attempt.

Methods

Field Work

Data for this project were collected on the campus of Saint Mary's University in the South end of Halifax, Nova Scotia, Canada (44.6313° N, 63.5815° W). The urban study site is approximately 32 hectares in size and contains a wide diversity of trees, shrubs, and open areas of grass, creating a typical urban park habitat. While positioned in the core of the city, there are many other urban parks and larger green spaces nearby, as well as an abundance of other trees throughout the city. There are approximately 42 nest boxes attached to various deciduous trees around the study site, and each is a minimum of 2.5m off the ground. Boxes were hung on campus in 2007 and have remained there with minor movements due to maintenance and upkeep. These nest boxes provide a nesting site to a breeding population of European Starlings (*Sturnus vulgaris*) who lay up to two broods each summer. Early clutches are laid between late April and early May whereas late clutches are laid in early to mid June.

Data on mate fidelity and brood condition were collected over a total of 13 years ranging from 2007-2022 (excluding 2010 and 2017, when no field data were collected). Mate fidelity is defined as two individuals choosing to raise a brood together for two or more breeding attempts (Black, 1996). Brood condition is a measurement of the body condition of all the nestlings within a nest, calculated by taking the average of the individual condition of every nestling within a nest.

Quantifying the frequency of fidelity begins with identifying all breeding adults who have raised more than one brood throughout the study period. Individuals are tracked based off a unique Canadian Wildlife Service (CWS) number printed on a metal band, which is placed onto the right tarsus of each individual when they are first caught. Adults were predominantly caught with a Swiffer® Sweeper covering the entrance to the nest box when the adult was inside, once the nestlings were at least five days old (day 0 is day of first hatch). A Mo-trap (Stutchbury and Robertson, 1986) was sometimes used, but not as successfully. Once contained within the nest box, the lid is covered with a dark piece of fabric and the adult is retrieved from within the box. Adults that were caught for the first time were given a CWS band on their right tarsus, as well as a sex-identifying band above the CWS band (males yellow, females pink). Adults also received a unique two band colour scheme allowing for individual identification from a distance. Adults who were already banded were also caught to record their CWS number, allowing for individuals to be tracked over multiple breeding seasons. Pairs who raised at least two broods and who had recorded CWS numbers were considered faithful breeding pairs for the purpose of this study.

All animal handling was conducted in adherence to standard animal handling and ethics approval from the Canadian Council on Animal Care through the SMU Animal Care Committee. Nestling condition is estimated from mass and tarsus length measurements. Nestlings were measured for mass and tarsus length on day 11 of their life (day of first hatch is considered day 0). Nestlings were placed in a sock and then weighed using a Pesola spring scale to the nearest 0.5 gram. The right tarsus was measured to the nearest 0.01mm using Fowler digital calipers. The average tarsus length per nestling was calculated from 3-5 measurements. Every nestling was also banded with a CWS band at this time, allowing us and other researchers to identify them if they are caught as adults.

Body condition measurements of these nestlings were split into two categories: early brood and late brood, depending on when in the season they hatched. This is because later broods tend to be in poorer condition and condition would be skewed negatively should they be compared against early brood nestlings. Separating these two categories allows for a fairer analysis. Mass and tarsus data were tested for normality using the D'Agostino and Pearson normality test (D'Agostino and Pearson, 1973). Linear regressions of mass against tarsus length were used to integrate the two measurements into a single indicator of brood condition, one for early brood nestlings and one for late brood nestlings. These linear regressions gave each nestling a condition residual, with positive numbers indicating good quality nestlings, and negative numbers indicating poor quality nestlings. The average of the condition residuals for every nestling within a nest was taken to determine brood condition (See Supplementary Figures 1&2 for the linear regressions, and Supplementary Figures 3&4 for nestling condition plots).

Data Analysis

A linear mixed effects analysis was run to account for the random effects of year, and number of nestlings within each nest. The fixed effects of this test were brood condition as the dependent variable and fidelity occurrence as the independent variable. This test was used to find out whether the two random impacted the overall relationship between brood condition and fidelity occurrence and explain any errors that could be related to these variables. This analysis was done using R Studio (R Core Team, 2022) and the *lme4* package (Bates et al., 2015). An ANOVA was used to determine if the effects of the random variables had any statistical significance, using the *car* package (Fox and Weisberg, 2019).

Mate fidelity was then compared between two groups of data for this study, and GraphPad Prism Software (version 9.5.0) was used to conduct all the following data analysis. The first group compared fidelity rates between 23 breeding pairs during the study period. Five pairs were excluded as their last recorded brood occurred in the last possible breeding attempt of the data period, so no conclusion could be made on their status following this brood. Brood condition data were tested for normality using a D'Agostino and Pearson normality test, and then a paired t-test was used to compare mean brood condition of the first brood raised by these pairs (stayed category) against the mean brood condition of the last brood raised by these pairs (separated category). The dependent variable of this test was fidelity occurrence, while the independent variable was brood condition, and a critical alpha error threshold of 0.05 was chosen to indicate significance. This test was used to determine if a decrease in mean brood condition would lead to the separation of the pair.

The second group of data analysis compared the mean brood condition against the first brood raised by the same 23 breeding pairs against the mean brood condition of any nest where no fidelity occurred making the categories fidelity and no fidelity respectively. The no fidelity category had a sample size of 81. All brood condition data were once again tested for normality using the D'Agostino and Pearson normality test, and then compared using an unpaired t-test ($\alpha_{crit} = 0.05$), and the same dependent and independent variables. This test was done to determine if there was a significant decrease in mean brood condition in the no fidelity category, potentially leading to the conclusion that fidelity rates were dependent on a high mean brood condition.

Results

Fidelity Occurrence

A total of 121 breeding adults were caught in at least two years throughout the study period. Of these, 46 were males and 75 were females. Within these 121 individuals there were 28 breeding pairs who raised more than two broods together. The highest number of broods raised by one pairs was six broods between 2009 and 2013 before separation. These 28 breeding pairs raised a total of 68 broods, comprising 19% of the 348 broods raised on the Saint Mary's University campus over the study period.

Brood Condition

Analysis of Random Effects on the Model

The analysis of the random effects of year and number of nestlings resulted in year accounting for 4.26% of the variability of brood condition in response to fidelity, while number of nestlings accounts for 4.40×10^{-17}% of the variability. There remains a residual variability of 22% that cannot be explained by these two effects (Table 1). There were no significant effects of year or number of nestlings within the categories, showing that the random effects had no significant influence on the overall model ($F_{1,121}$= 2.4479, P=0.12).

First and Last Brood of Breeding Pairs Before Separation

Although mean brood condition apeared to decrease between the first brood raised by the confirmed breeding pairs who stayed together for a subsequent brood (stayed; mean + SE: 1.801±1.039) and their last brood (after which they separated; 0.447±1.102), the difference was not statistically significant (paired *t*=1.266, df=22, P=0.22; Figs 1&2).

Fidelity vs No Fidelity

Mean brood condition appeared to be greater for pairs displaying mate fidelity (1.801±1.039) than for pairs that did not (0.177±0.574) but again this difference was not statistically significant (unpaired *t*=1.341, df=102, P=0.18, Fig 3&4).

Table 1: Linear Mixed Model analysis of the variability (+SD) within brood condition based on fidelity occurrence explained by the random intercept effects. Residual shows the variability in the relationship that is not accounted for.

Groups	Variance	SD
Year	4.26	2.06
Nestlings	4.40E-17	6.63E-09
Residual	22.04	4.7

Number of Observations: 126, Groups: Year, 12; Nestlings, 6

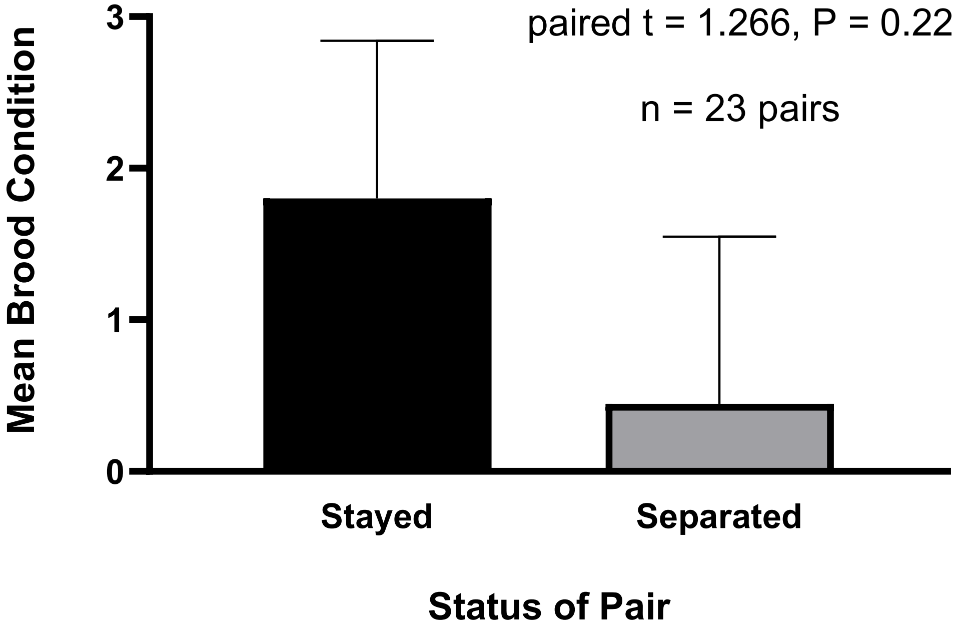

Figure 1. Mean brood condition (+SE) of the first brood raised by 23 breeding pairs (stayed category) and their last brood raised before separating (separated category).

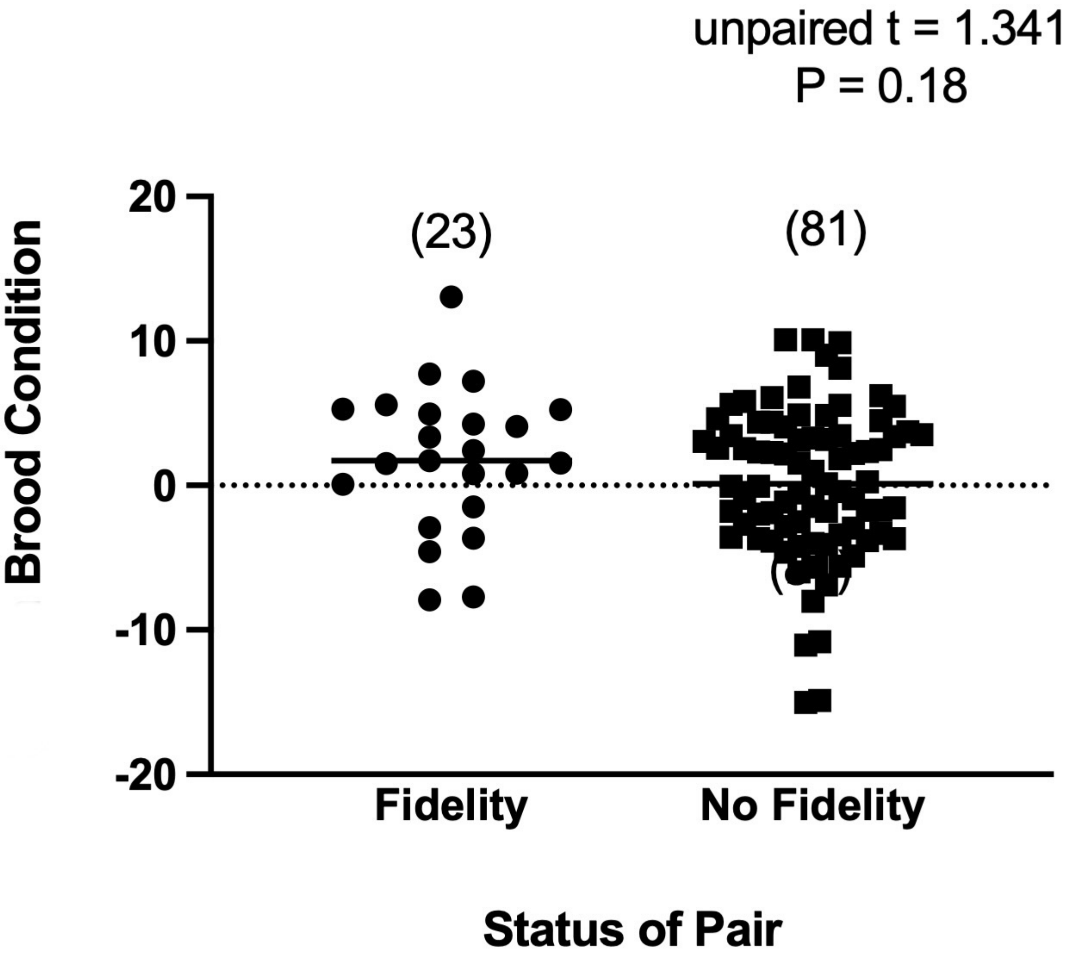

Figure 2. Brood condition of the first brood raised by 23 breeding pairs (stayed category) and their last brood raised before separating (separated category).

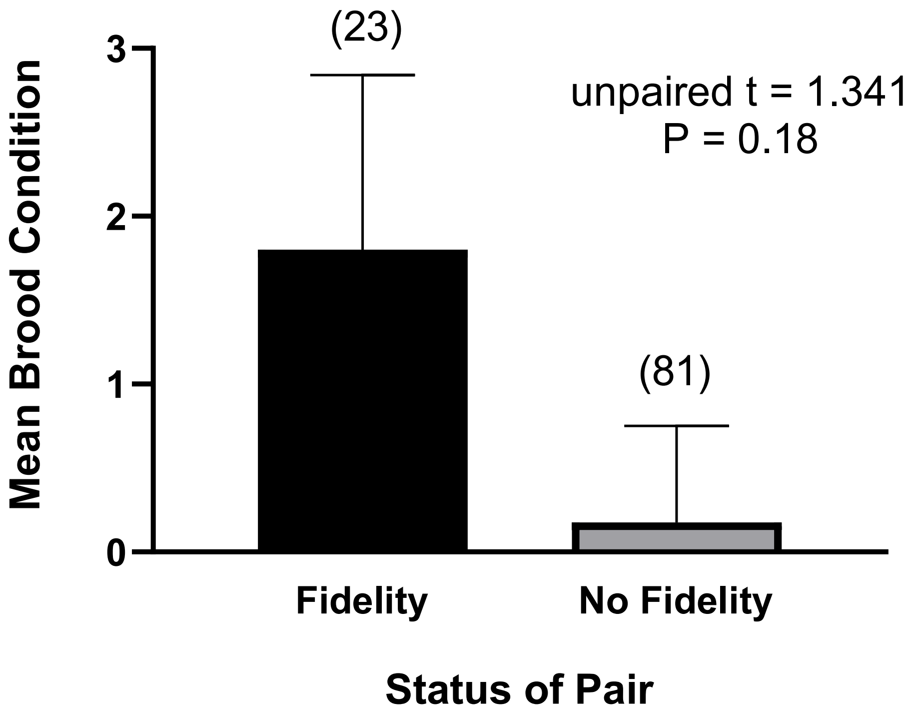

Figure 3. Mean brood condition (+SE) of pairs showing subsequent mate fidelity and those not showing subsequent mate fidelity. Sample size of each category shown in the brackets.

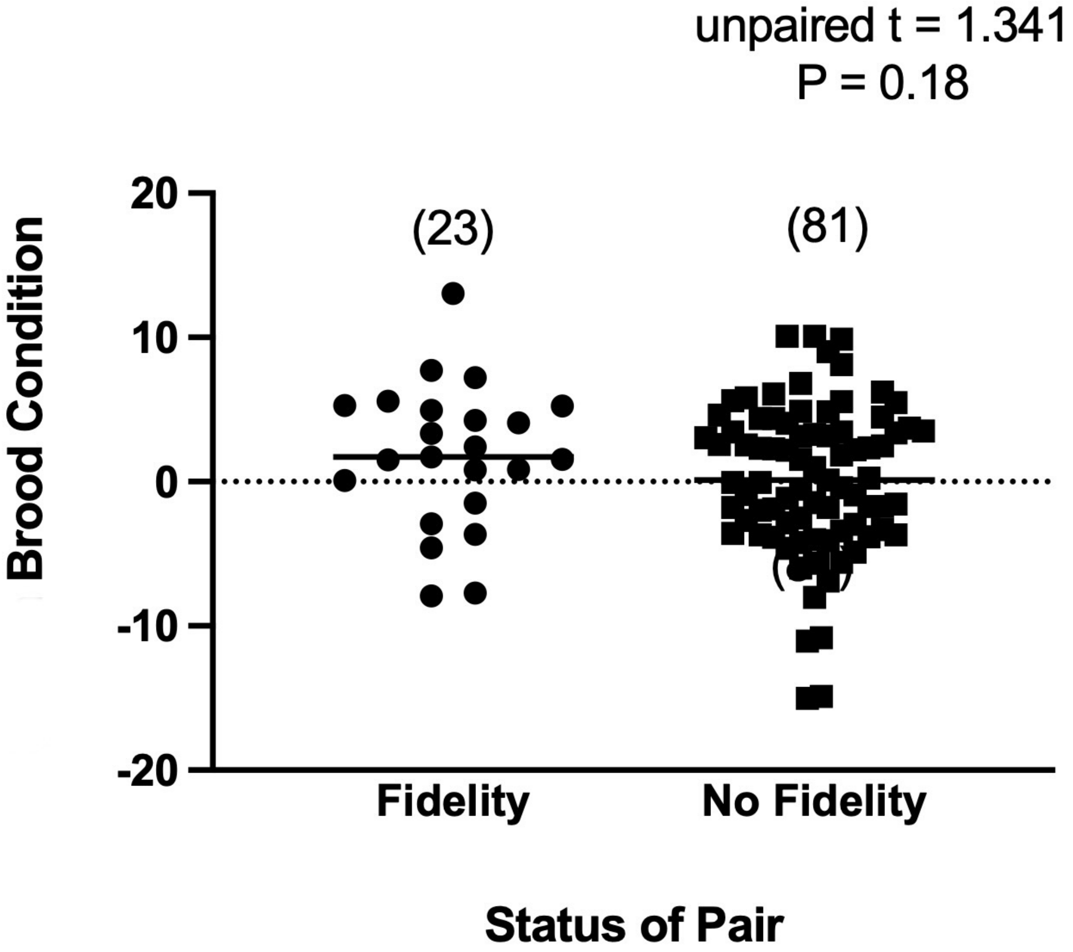

Figure 4. Brood condition of broods raised by pairs showing subsequent mate fidelity and those not showing subsequent mate fidelity. Sample size of each category shown in the brackets.

Discussion

Contrary to my prediction, there was no significant difference in brood condition between nests that led to mate fidelity in a subsequent breeding attempt and those that did not. Despite the lack of statistical significance, mean brood condition followed the predicted trend; pairs that remained together for a subsequent nesting attempt appeared to have nestlings in better condition than pairs that separated after that nesting attempt. Past literature has shown that brood condition can be a predictor of subsequent mate fidelity or separation in monogamous bird (e.g., Dubois and Cézily, 2002; Ens et al., 1996). Desrochers and Magrath (1996) showed this direct relationship in their study of European Blackbirds (*Turdus merula*), where the pairs prior breeding success had a significant positive influence on their fidelity, with pairs experiencing breeding failure choosing to separate after the unsuccessful breeding attempt. However, other studies such as that by Coss et al (2019) on Eastern Bluebirds (*Sialis sialis*) determined that nestling condition had no strong effect on the occurrence of mate fidelity within their population. Similarly, in Hair-crested Drongos (*Dicrurus hottentottus*), researchers found that nestling body condition did not affect mate retention within the population (Lv et.al., 2016). This could suggest that body condition of individual nestlings is less important when deciding to remain with a mate than how many nestlings actually fledge, which is a more quantifiable measurement of reproductive success (Dubois and Cézilly, 2002).

The sample size of fidelity nests was limited to only the first nests raised by a pair instead of analyzing all the nests raised by faithful pairs that led to continued partnership over more than two breeding attempts within this study. These additional fidelity nests would likely have nestlings in better condition than was found in the first nests raised by the pair, because of the increased coordination and cooperation between parents due to their experience raising nestlings together (Black, 1996; Coss et al., 2019.; Choudhury, 1995; Llambías et al., 2008; Sánchez-Macouzet et al., 2014; Williams and McKinney 1996). Additional nests raised by faithful breeding pairs were intentionally left out of this study to avoid pseudo-replication and so that the effect of brood condition on a first attempt could be measured without the effects of the experience gained during a partnership. However, if these nests had been included in the overall fidelity category when compared against the no fidelity nests, perhaps the mean brood condition would have improved, leading to a significant difference between the two categories.

A variable other than brood condition might have a greater effect on the occurrence of mate fidelity in this population. "Year" accounted for some amount of variance (4.26%) within the relationship between brood condition and mate fidelity occurrence, but there was still a variance level of 22.04% after accounting for the known random effects. This finding suggests that there are other factors that are influencing mate retention in this population. These factors may include parental age and condition, fledging success, and offspring provisioning rates, all of which have been found influence mate fidelity in populations of other monogamous bird species (Bart, 1990; Choudhury, 1995; Coss et al., 2019; Desrochers and Magrath, 1996; Ens et al., 1996). There remains the possibility the rather than separating, one of the mates may died or chose to breed elsewhere in some cases. Future studies on this population should survey the band combinations of not only the breeding pairs within nest boxes, but also the Starlings nesting in natural cavities on the study site. Similarly, it would be important to determine if the mate that separated was identified in future years, ruling out death or study site dispersal. Still, although not statistically significant, the results did follow the direction predicted.

Wilson et al. (2022) proposed that individuals who find themselves in a more fluid social environment (an area in which new breeding partners are introduced more often compared to a static environment consisting of the same birds) were more likely to separate from their previous partner in favour of a new mate. Therefore, environments with higher social fluidity increased the likelihood of finding a more compatible mate (Wilson et al., 2022). Our study site is situated in an area with a large population of European Starlings both on campus and directly outside of it. This species is semi-colonial and highly gregarious. While the adults banded on the study site typically show a high degree of philopatry to the nesting site, there are many starlings that visit the study site looking for nesting sites, food and nesting materials, thereby making the environment one of high social fluidity, and potentially decreasing the occurrence of fidelity among this study population.

In future studies, in may be beneficial to measure many different individual traits and behaviours to determine which variables have the strongest effect on mate retention. By studying multiple potential influences at once, a complete picture can be made of which variables lead to mate fidelity. Studying mate fidelity in tandem with another important type of fidelity, namely nest-site fidelity could help determine if perhaps mate fidelity is the by-product of individuals simply preferring to mate in the same territory they held previously. There is evidence that individuals with high nest site fidelity are predisposed to having a higher rate of mate fidelity (Jeschke and Kokko, 2008). Finally, Dubois and Cézilly (2002) suggest that reproductive success be defined on a species-by-species basis, as past studies have tried to use the same standard of a successful reproductive for attempt for all avian species, with success being defined as raising one nestling to fledge. This interpretation of breeding success can skew the results of studies that focus on birds raising larger broods, where raising only one nestling would not be necessarily successful. By defining reproductive success to better fit each individual species, more conclusive results can be produced when comparing breeding success and its effect on the occurrence of mate fidelity and should be taken into account in future studies (Dubois and Cézilly, 2002).

In conclusion, there was no significant relationship between brood condition and mate fidelity occurrence among this focal population of European Starlings. Mate fidelity occurred in about 19% of all broods raised on this study site. The potential difference in brood condition that leads to fidelity and that which leads to separation is still worth examining further, perhaps alongside other types of fidelity such as that for nest sites. Quantifying which traits and behaviours influence mate fidelity occurrence would further our understanding of the breeding behaviours of passerines and provide valuable information on what birds consider when deciding to remate with their previous partner or separate in hopes of finding a "better" individual with whom to breed.

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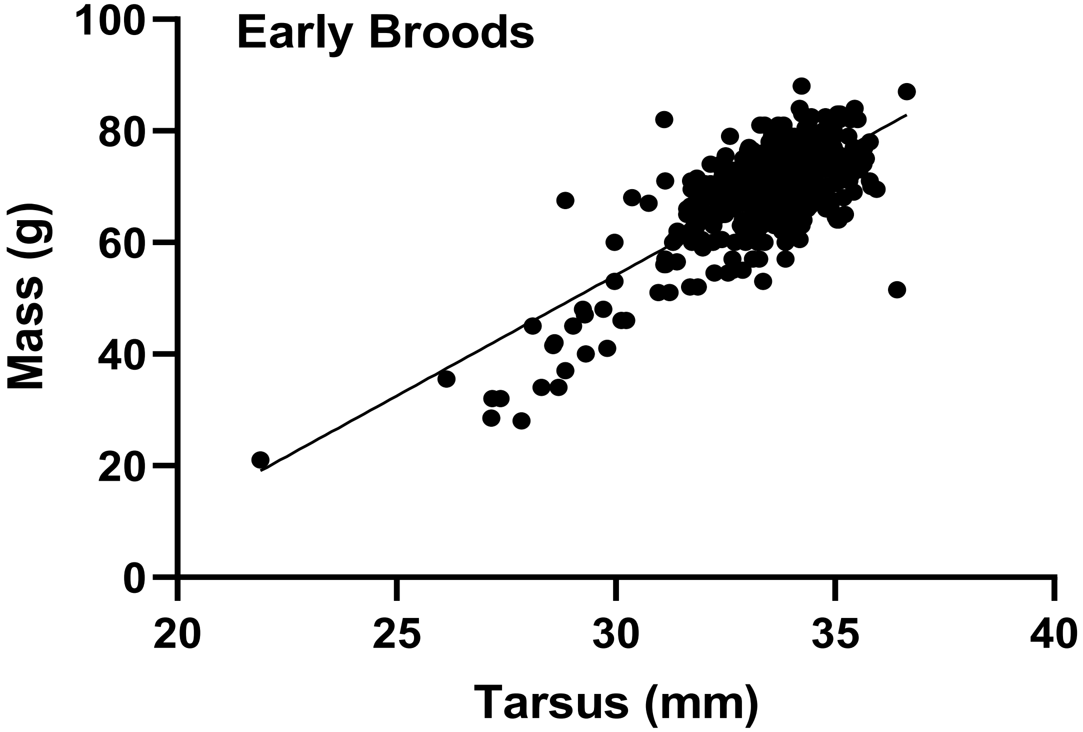
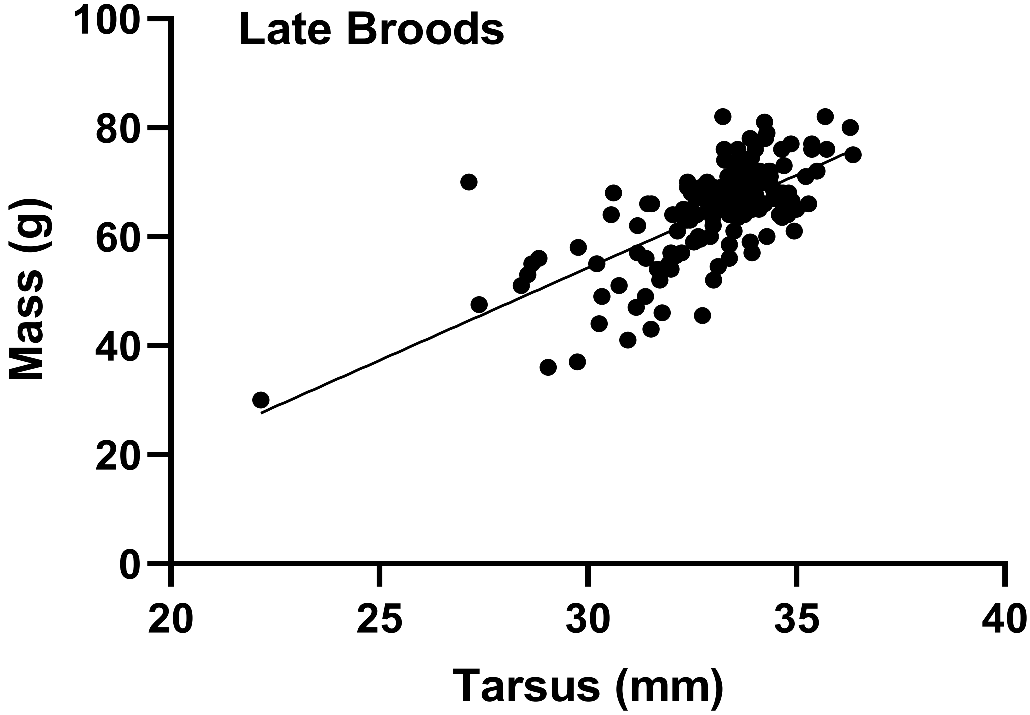
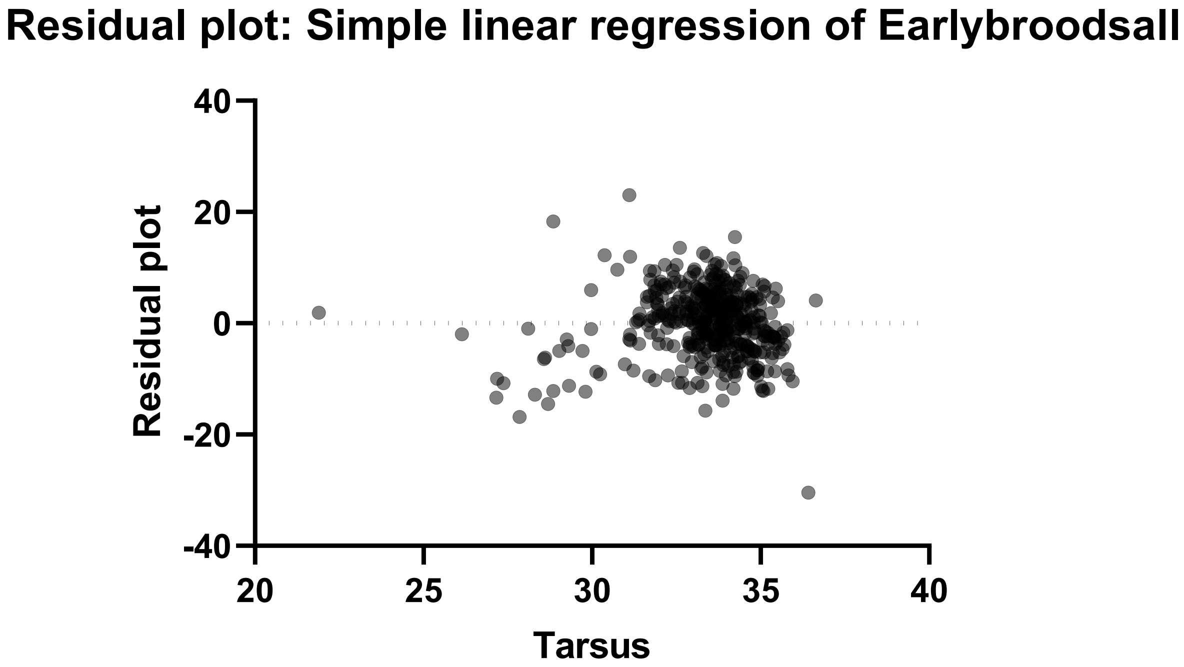
Supplemental Information



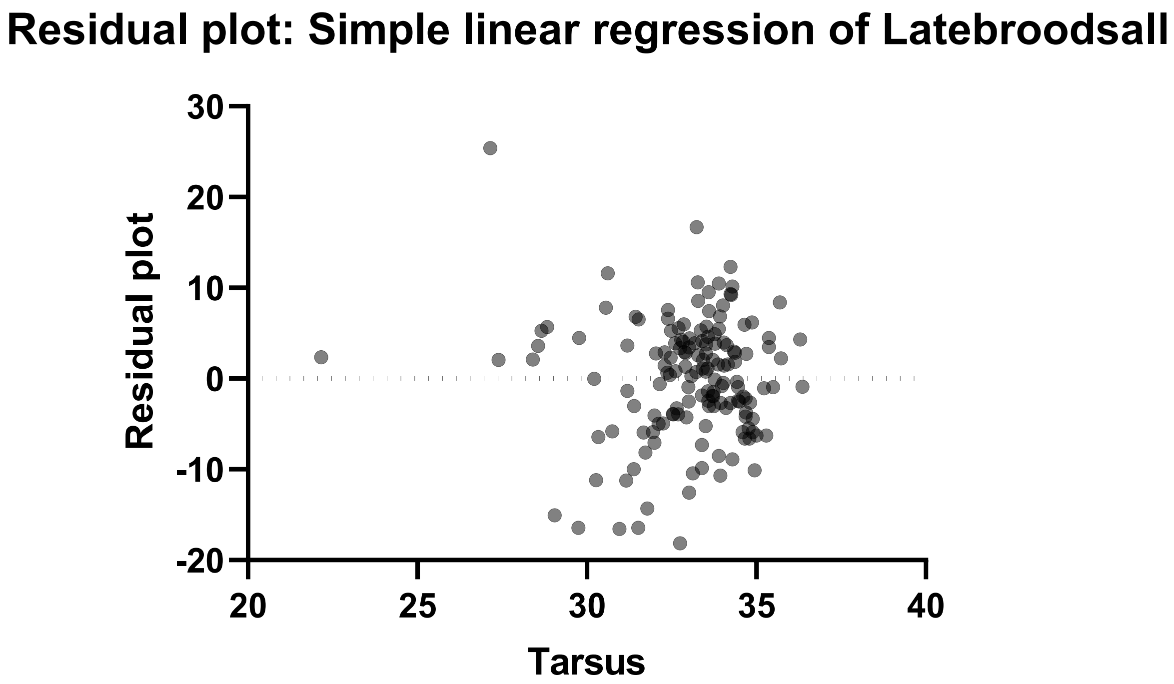
Supplementary Figure 1: Linear regression of mass (g) vs tarsus (mm) to calculate nestling condition for early brood nests from 2007-2022 (r^2=0.5726; n =426).



Supplementary Figure 2: Linear regression of mass (g) vs tarsus (mm) to calculate nestling condition for late brood nests from 2007-2022 (r^2=0.4819; n =153).



Supplementary Figure 3: Residual plot of a simple linear regression of mass (g) vs tarsus (mm) for early brood nests (laid late April-early May).



Supplementary Figure 4: Residual plot of a simple linear regression of mass (g) vs tarsus (mm) for early brood nests (laid early-mid June).