NO EVIDENCE OF TRADE-OFFS BETWEEN AGGRESSION AND PARENTAL PROVISIONING IN MALE SONG SPARROWS (MELOSPIZA MELODIA)

A thesis presented to the faculty of the Graduate School of Western Carolina University in
partial fulfillment of the requirements for the degree of Master of Science in Biology.

By

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ABSTRACT

NO EVIDENCE OF TRADE-OFFS BETWEEN AGGRESSION AND PARENTAL PROVISIONING IN MALE SONG SPARROWS (MELOSPIZA MELODIA)

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Differences in behaviors such as aggression and boldness can significantly influence fitness in many bird species by impacting factors such as territory quality, resource acquisition, and parental provisioning rates. This study aims to investigate the influence of individual variation in male aggressive behavior on reproductive success in a population of Song Sparrows (*Melospiza melodia*). Song Sparrows show significant individual variation in territorial aggression, but the implications of this variation are unclear. By measuring responses to conspecific playback experiments simulating territorial intrusion, individual provisioning rates, and offspring growth rates, we can investigate if there is a relationship between male aggression and reproductive success. This study found no relationship between male aggression and offspring growth rate. We also found no relationship between aggression and provisioning rate, and thus, no evidence of a trade-off between male aggression and parental care. Provisioning rates of males and females were found to be consistent across days, suggesting provisioning rate may be an individually distinctive trait. Provisioning rates were also significantly similar within pairs, suggesting that assortative mating or convergence of parental behaviors may be occurring. These findings highlight the need for large-scale, multi-year studies to clarify the relationship between

aggression and reproductive success, and to understand the mechanisms and significance of pair similarity in parental care in Song Sparrows.

INTRODUCTION

Individual variation in behaviors such as aggression and boldness can have significant impacts on fitness in many bird species including Great Tits (Dingemanse et al., 2004), House Wrens (Krieg & Getty, 2020), and Song Sparrows (Higgins et al., 2022; Scales et al., 2013); as well as other vertebrates such as rodents and felids (Smith & Blumstein, 2008). Male aggression, particularly, has been shown to have influence on mate selection (Krieg & Getty, 2020), resource acquisition (Dingemanse et al., 2004; Higgins et al., 2022; Scales et al., 2013), provisioning rates (Krieg & Getty, 2020), offspring growth rates (Krieg & Getty, 2020; Krippel et al., 2017), and overall reproductive success (Smith & Blumstein, 2008). In this study, we aim to investigate the influence of individual variation in male aggressive behavior on reproductive success within an urban population of Song Sparrows (*Melospiza melodia*). Song Sparrows are an ideal species for examining consequences of individual variation in aggression because they show consistent individual variation in aggression, based on their response to playback experiments simulating territorial intrusion, both within and between breeding seasons (Hyman et al., 2004; Nowicki et al., 2002).

Territoriality is an important factor in determining Song Sparrow reproductive success (Arcese & Smith, 1988) and studies have shown that, in cases with new territorial males, more aggressive male behavior was positively correlated with obtaining higher quality territories that had previously produced nests with larger clutches (Scales et al., 2013). Aggression has also been shown to be correlated with growth rate of chicks in a male’s territory (Krippel et al. 2017). Possible explanations for this observation could be that more aggressive males provision their offspring at higher rates than less aggressive males (Class and Moore 2010) or that aggressive males outcompete less aggressive males for territories with more food resources (Foltz et al., 2015). This demonstrates a reproductive benefit to higher levels of male aggression, which may be attributed to higher parental investment in offspring during egg laying, as well as after hatching.

Research has also found a strong association between dominance hierarchy (the ranking of individuals in a population from most dominant to least dominant) and foraging methods that influences foraging success (Liker & Barta, 2002). Less aggressive males have been observed to mainly engage in producing behaviors (i.e. where individuals will discover and feed from a new food patch). Alternatively, more aggressive males engage in scrounging more frequently (i.e. where individuals wait for producers to discover a food patch and feed from that). In turn, subdominant individuals had lower foraging success as the frequency of dominant individuals increased, leading to more aggressive, dominant individuals outcompeting subordinates for resources (Liker & Barta, 2002) and demonstrating a possible relationship between aggression and food acquisition. As a result, more aggressive males could have higher offspring growth rates due to outcompeting subordinates for food and having the ability to allocate less time towards foraging and more time towards parental care.

An alternative explanation for more aggressive males raising faster growing offspring could be more directly associated with female mate choice. Many studies on birds have noted a positive relationship between male quality and female parental investment (Diniz et al., 2015; Grunst et al., 2016; Petrie & Williams, 1993; Uller et al., 2005). Male Song Sparrows that exhibit higher aggression may have mates that invest more in eggs or in parental care, establishing an indirect positive relationship between male aggression and offspring growth rate.

The relationship between aggressive behavior and foraging behavior, higher territory quality, larger clutch size, and higher chick growth rates suggests a potential link between aggressive male behavior and higher fitness. If more aggressive males obtain higher quality territories and have greater foraging efficiency, we would expect more aggressive males to have more, better quality nest visits than less aggressive males – resulting in faster growing offspring (Class & Moore, 2010; Krippel et al., 2017). In this study, we measured territorial aggression, clutch size, chick growth rates, and both male and female provisioning rates in a population of Song Sparrows. If individual variation in aggressive behavior has significant functional implications, then we hypothesize that more aggressive males will have larger clutch sizes, faster growing offspring, and higher provisioning rates, resulting in higher reproductive success and overall fitness than less aggressive males.

METHODS

Study Population and Field Site

The study was conducted on a population of Song Sparrows on the campus of Western Carolina University, Cullowhee, NC (35°18’N, 83°11’W, elevation 640m) during the 2024 breeding season (late March to early August). The study site consists of buildings, roadways, and walkways surrounded by patches of lawn, shrubbery, and trees. The campus is bordered by high traffic roads and more densely forested habitat. A population of Song Sparrows with over 50 territories has been consistently observed within this site for over 15 years (Cook, 2023; Evans et al., 2010; Krippel et al., 2017; Myers & Hyman, 2016). Using a combination of baited Potter traps and mist-nets, we caught a total of 52 adults. We banded each individual with one uniquely numbered USFWS metal band and three plastic, colored bands to allow for consistent identification of the individual.

Nest Searches and Monitoring

We conducted nest searches every day by observing adult behavior for nest location cues, such as frequent visits to a particular spot or nest-building behavior, and systematic searches of possible nest sites. Once located, we monitored nests daily to accurately determine hatch date (hereinafter referred to as day 0).

Upon hatching, we used cameras (Lawmate PV-500NP-BUNDLE) to record parental activity on the nest. The cameras were fixed above the nest using a rebar stake anchored in the ground with a metal wire wrapped around the top of the rebar. The lens of the camera was secured to the metal wire such that we had a clear view of the nest cup from a distance of ~ 200-

250mm. Camera monitors were placed inside plastic Tupperware for protection and hidden among vegetation. Cameras were set up on day 0 to allow adults to acclimate to the novel object before recording behaviors. Recording took place approximately between 07:00-14:00h on days 1, 3 and 5 after hatch to document instances of food provisioning. We measured provisioning rates by calculating the average number of visits with successful food transfer from adult to chick per hour per nestling for each day. The hours used in the analysis (9:00-13:00) provided complete data from all nests. Data from earlier and later hours were excluded due to issues affecting camera performance (such as foggy lenses, battery issues, etc.).

Nestling Growth

To measure nestling growth rate, we visited nests on days 1, 3, and 5 after hatch to record the brood weight in grams. Nests that were parasitized by Brown-headed Cowbirds (*Molothrus ater*) were weighed twice per visit: with the cowbird and without. Weights with cowbird nestlings were excluded from the growth rate analysis.

Aggression Assays

We measured aggression with playback experiments using the same methods as Krippel et al. (2017). We broadcasted conspecific songs to simulate territorial intrusion and measured the distance of the territory owner to the playback speaker. Each experiment lasted 9 min; song was broadcasted for a total of 6 min, with 3 min of silence afterward. We recorded the focal male’s distance from the speaker every 5 sec for the entire 9 min. Distance was binned into 0-2 m, 2-4 m, 4-8 m, and 8-12 m, which were marked with flagging to allow for consistent measurement. We then calculated average distance to the speaker to act as an aggression score for each male. Previous research has found that, in Song Sparrows, average distance to the speaker is a significant predictor of attack and can be used as a valid measure of aggression (Searcy et al., 2006). Males with low average distance to the speaker were considered aggressive. We performed assays during the hours of peak territorial defense (06:00-10:00h). In order to avoid possible seasonal variation in aggression, we conducted assays between mid-May through June, during the females’ fertile stage (Moser-Purdy et al., 2017).

STATISTICAL ANALYSES

All statistical analyses were conducted using R Statistical Software (version 4.3.2; R Core Team 2023). We log transformed data when necessary to meet the assumptions required for statistical analyses.

Aggression and Growth Rate

To calculate nestling growth rates, we divided the total brood weight by the number of nestlings to obtain an average weight per nestling for each day. We then measure growth rates by calculating the slope of a regression line of mass on age.

To investigate the relationship between male aggression and nestling growth rate, we fitted a linear mixed-effects model, accounting for random effects due to hatch date (Julian date). We used a Welch's two sample t-test to measure the relationship between aggression and nest success to day 5. To assess the relationship between male aggression and clutch size, we used Pearson's correlation.

Aggression and Provisioning

We examined the relationship between male aggression and average provisioning rate using a linear mixed-effects model. Additionally, to determine if pairs with higher total day 1 provisioning rates had faster growing offspring, we used a linear regression analysis.

To explore the relationship between provisioning similarity within pairs and offspring growth rate, we first calculated the Euclidean distance (a measure of dissimilarity) between male and female provisioning rates and then performed a linear regression analysis. Similarly, we assessed the relationship between provisioning similarity and clutch size using Euclidean distance and a linear regression model.

Provisioning Repeatability

We calculated repeatability of provisioning rates across days 1, 3, and 5 using the Lessells and Boag repeatability ANOVA.

Provisioning Similarity

To test if high provisioning males tended to pair with high provisioning females, we used Pearson’s correlation.

Ethical Note

All protocols were approved by the Institutional Animal Care and Use Committee of Western Carolina University (IACUC Protocol # 2024-01-29-04). All bird banding and trapping was conducted under a US Department of the Interior Federal Bird Banding Permit (Permit # 23626).

RESULTS

Aggression and Nestling Growth

Aggression did not show a significant linear relationship with nestling growth rate (Linear Mixed-Effects Model, $p = 0.9694$, $\beta = - 0.0008$, SE = 0.0214, $t_{11.96} = - 0.039$, Fig. 1, Table 1). Additionally, there was no detectable relationship between male aggression and nest success (t-test, 5.41 ± 0.4493 vs 7.10 ± 0.5346, $\overline{x}$ difference = 1.69, 95% CIs: - 0.99 to 0.52, $t = - 0.8420$, df = 4.4228, $p = 0.4429$, Fig. 2).

Aggression and Clutch Size

There was no relationship between male aggression and the number of eggs laid; hatched and unhatched (Pearson's Correlation, Pearson's $r = - 0.0236$, $p = 0.9261$, $t = - 0.0943$, Fig. 3, Table 2).

Aggression and Provisioning Rate

Aggression did not show a significant linear relationship with male average provisioning rate (Linear Mixed-Effects Model, $p = 0.9967$, $\beta = 0.0079$, SE = 0.0185, $t_{0.001} = 0.431$, Fig. 4, Table 3). Male aggression also did not show a significant linear relationship with female provisioning rate (Linear Mixed-Effects Model, $p = 0.6042$, $\beta = 0.0240$, SE = 0.0457, $t_{21} = 0.526$).

Provisioning Repeatability

The repeatability measure indicated significant repeatability for male provisioning between days 1, 3, and 5 (Lessells and Boag Repeatability ANOVA, $R = 0.5930$, $F_{8,18} = 5.37$, p <

0.01, Fig. 5, Table 4) and female provisioning between days 1, 3, and 5 (Lessells and Boag Repeatability ANOVA, R = 0.5353, $F_{7,16} = 4.46$, $p < 0.01$, Fig. 6, Table 4).

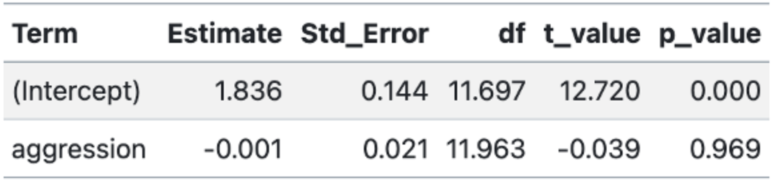
Pair Total Provisioning and Nestling Growth

Pearson's Correlation revealed a strong correlation of day 1 provisioning rates within pairs (Pearson's Correlation, Pearson's r = 0.5907, $p < 0.05$, t = 2.7392, Fig. 7, Table 5). However, total day 1 provisioning rates of pairs had no significant linear relationship with offspring growth rate (Linear Regression, p = 0.2218, $\beta = 0.0752$, SE = 0.0581, $t_{11} = 1.295$, Fig. 8, Table 6).

Pair Provisioning Similarity and Reproductive Success

There was no significant relationship between similarity scores of male and female provisioning proportions (calculated as Euclidean distance) and nestling growth rate (Linear Regression, p = 0.6264, $\beta = - 0.1525$, SE = 0.3045, $t_{11.96} = - 0.501$, Fig. 9, Table 7). Furthermore, there was no significant relationship between similarity scores of male and female provisioning proportions and clutch size (Linear Regression, p = 0.8969, $\beta = - 0.0501$, SE = 0.3774, $t_{11.96} = - 0.133$, Fig. 10, Table 8).

Table 1. Mixed-effects model for nestling growth and aggression.



Term	Estimate	Std_Error	df	t_value	p_value
(Intercept)	1.836	0.144	11.697	12.720	0.000
aggression	-0.001	0.021	11.963	-0.039	0.969

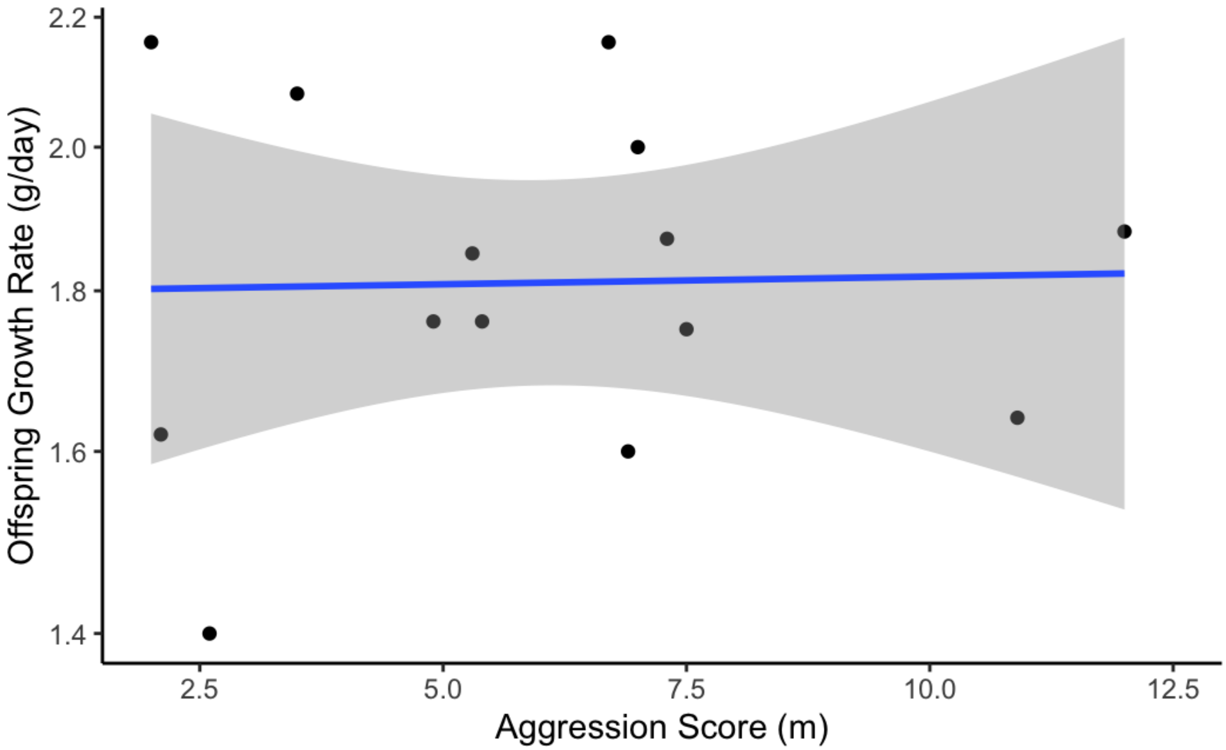


Figure 1. Nestling growth rate shows no significant relationship with aggression (Linear Mixed-Effects Model, p = 0.9694, β = - 0.0008, SE = 0.0214, $t_{11.96}$ = - 0.039).

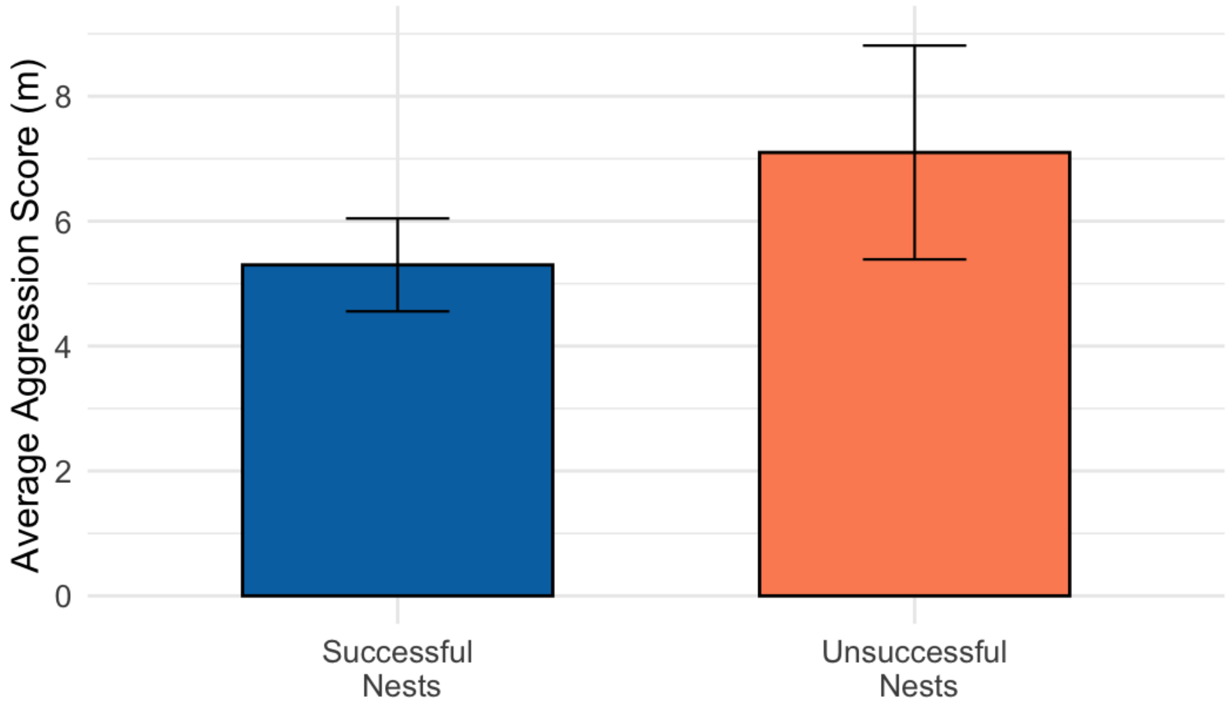


Figure 2. There was no significant relationship between male aggression and nest success (T-Test, 5.41 ± 0.4493 vs 7.10 ± 0.5346, $\bar{x}$ difference = 1.69, 95% CIs: - 0.99 to 0.52, *t* = - 0.8420, df = 4.4228, p = 0.4429).

Table 2. Pearson's correlation for clutch size and aggression.

	Pearson_Correlation	t_statistic	p_value
Clutch Size & Aggression	-0.024	-0.094	0.926

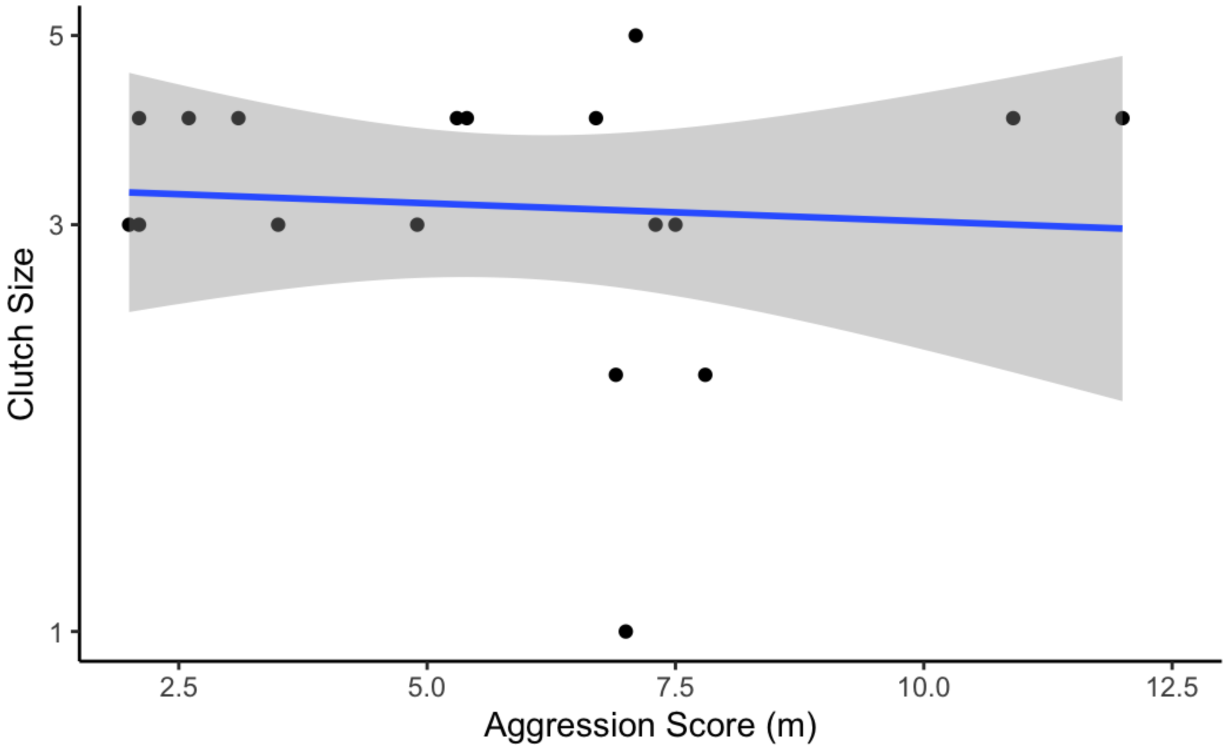
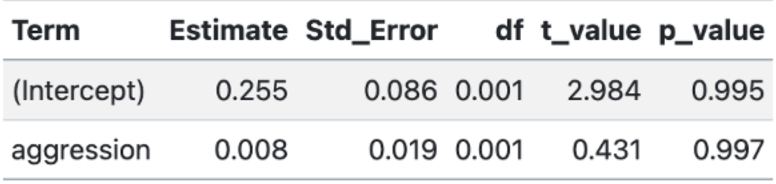


Figure 3. There was no significant correlation between male aggression and the number of eggs laid (Pearson's Correlation, Pearson's r = - 0.0236, p = 0.9261, t = - 0.0943).

Table 3. Linear mixed effects model for male average provisioning rate and aggression.



Term	Estimate	Std_Error	df	t_value	p_value
(Intercept)	0.255	0.086	0.001	2.984	0.995
aggression	0.008	0.019	0.001	0.431	0.997

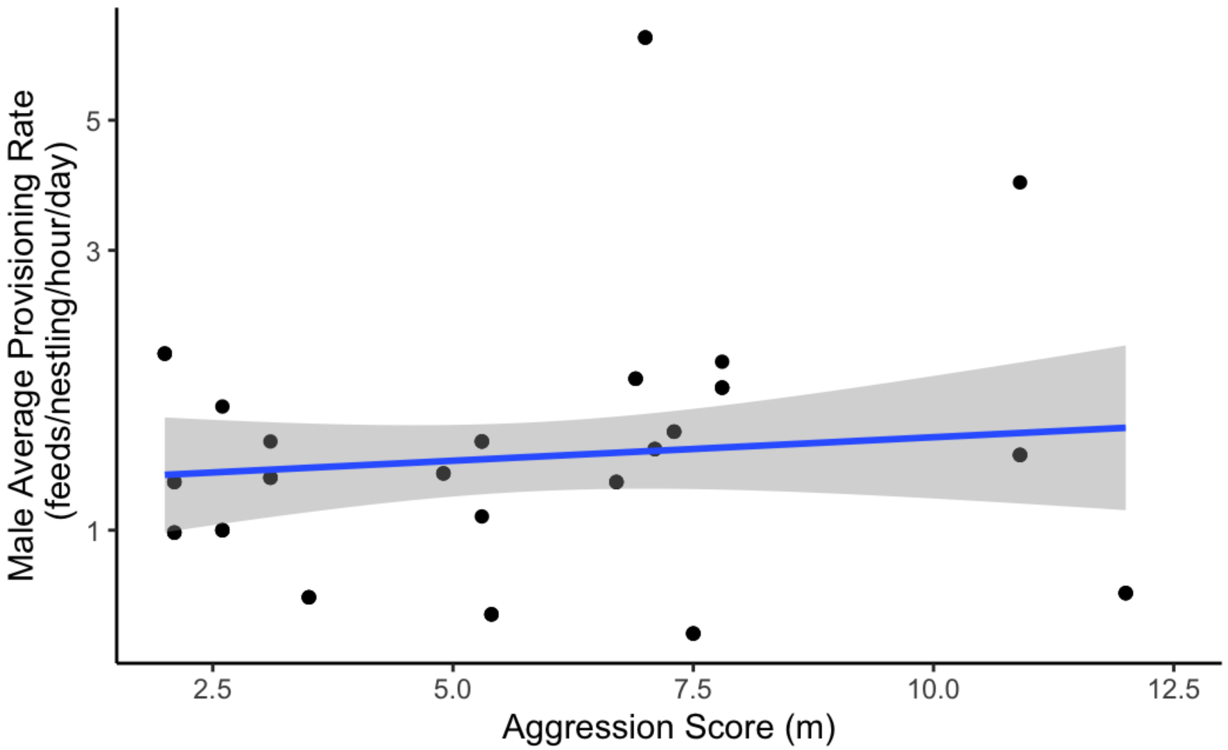
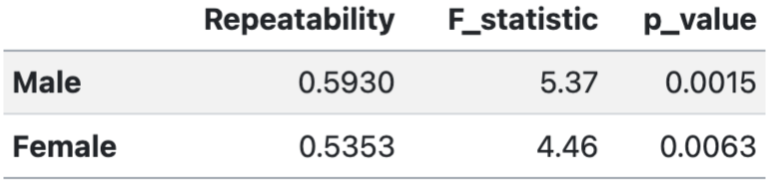


Figure 4. Male average provisioning rate shows no significant relationship with aggression (Linear Mixed-Effects Model, p = 0.9967, β = 0.0079, SE = 0.0185, $t_{0.001}$ = 0.431).

Table 4. Lessells and Boag repeatability ANOVA for male and female provisioning rate repeatability.



	Repeatability	F_statistic	p_value
Male	0.5930	5.37	0.0015
Female	0.5353	4.46	0.0063

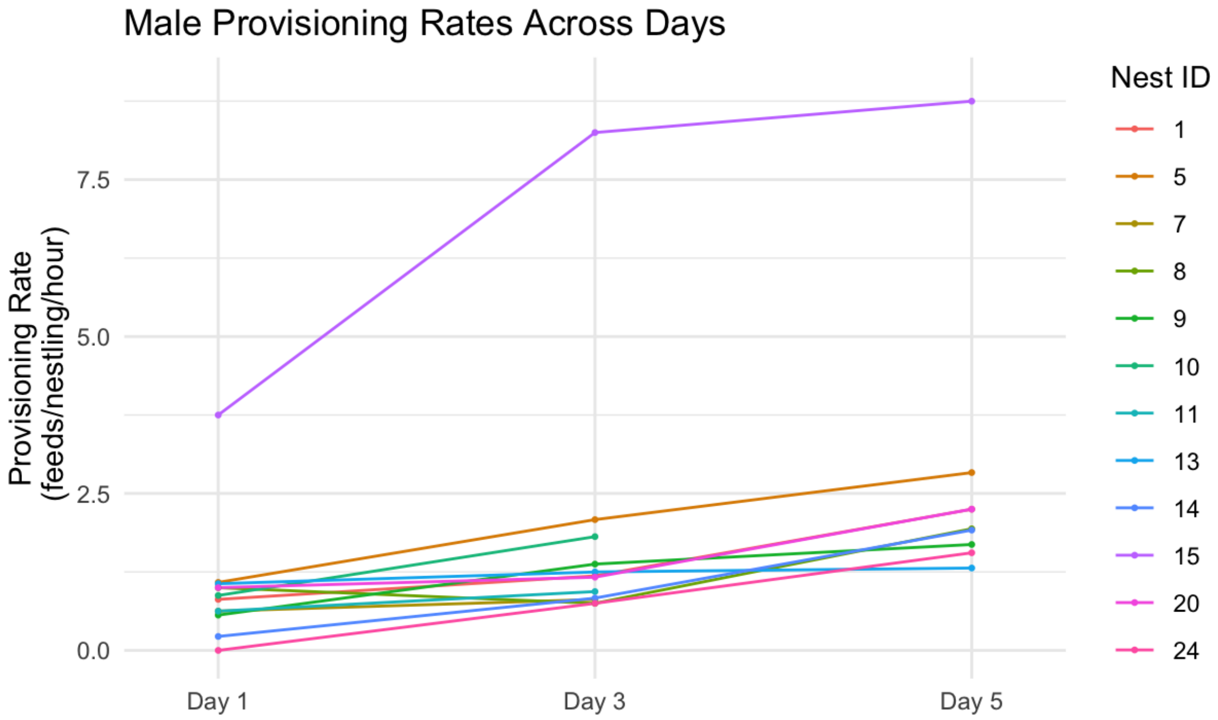


Figure 5. Male provisioning rates show strong repeatability across days (Lessells and Boag Repeatability ANOVA, R = 0.5930, $F_{8,18} = 5.37$, $p < 0.01$).

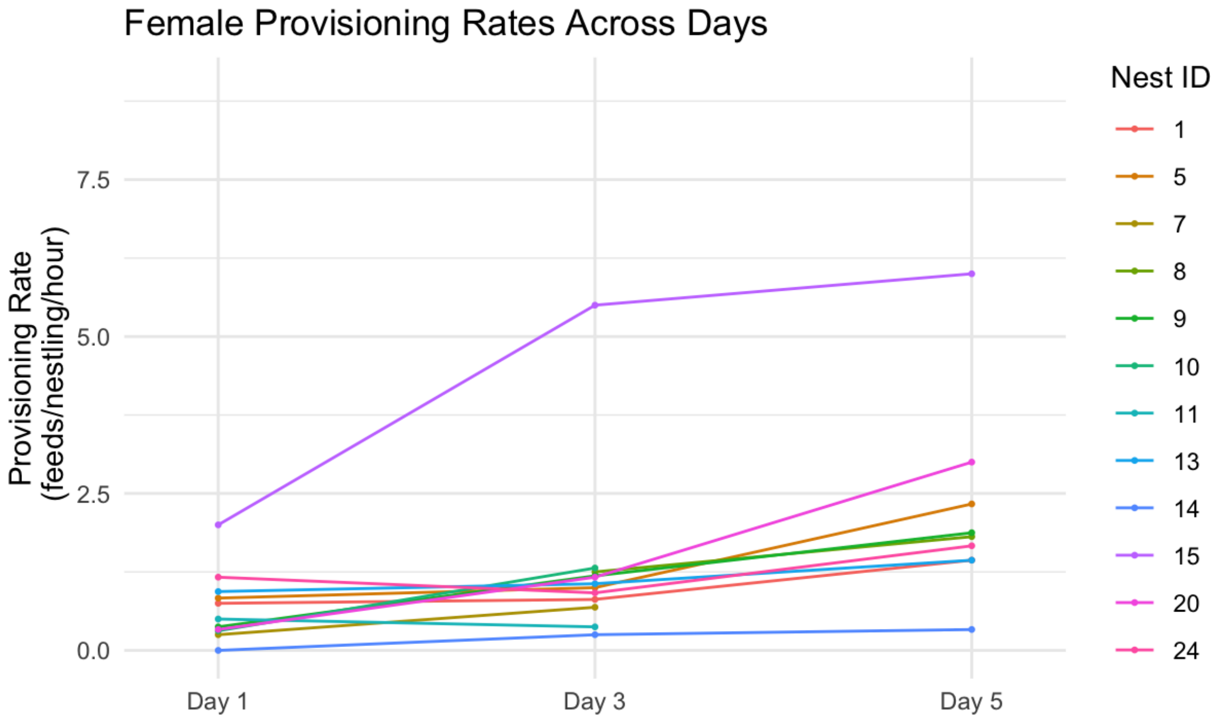
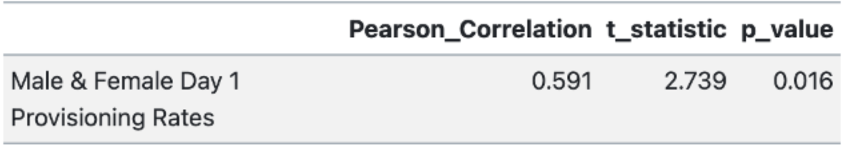


Figure 6. Female provisioning rates show strong repeatability across days (Lessells and Boag Repeatability ANOVA, R = 0.5353, $F_{7,16} = 4.46$, $p < 0.01$).

Table 5. Pearson's correlation for male and female day 1 provisioning rates.



	Pearson_Correlation	t_statistic	p_value
Male & Female Day 1 Provisioning Rates	0.591	2.739	0.016

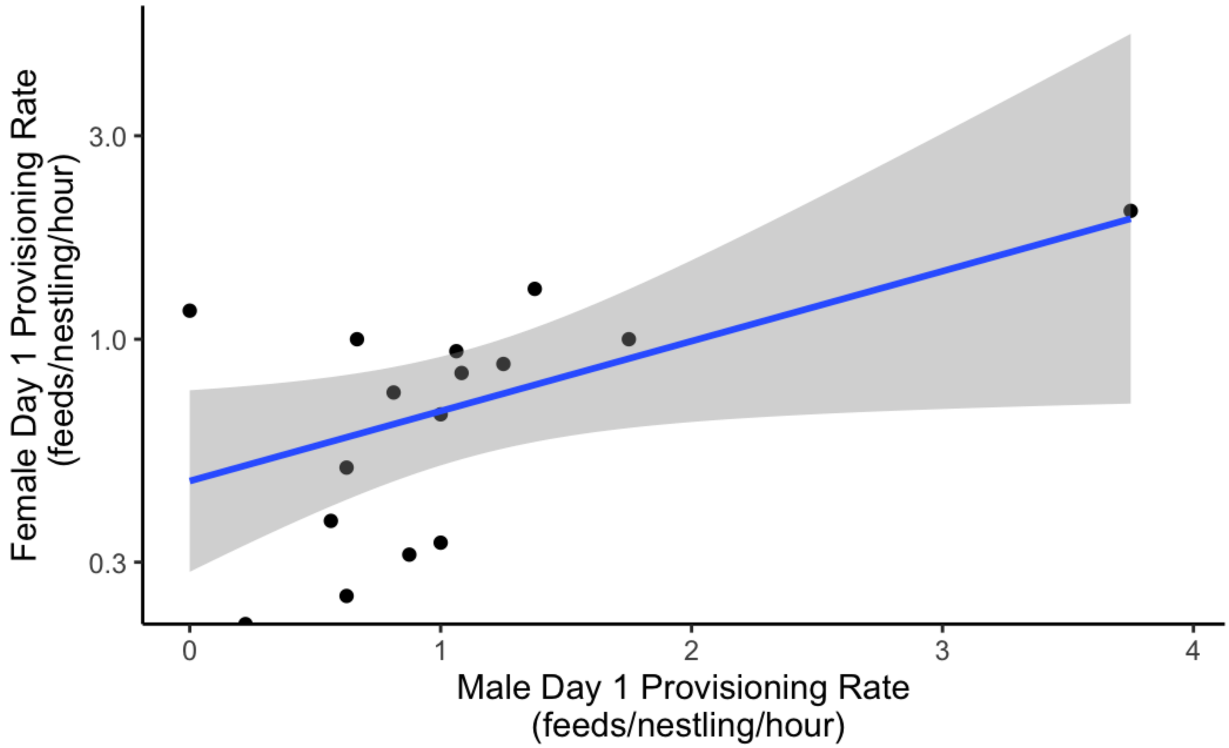


Figure 7. Day 1 provisioning rates show strong consistency between males and females within a pair (Pearson's Correlation, Pearson's r = 0.5907, p < 0.05, t = 2.7392).

Table 6. Linear regression for pair day 1 provisioning rate and offspring growth rate.

Term	**Estimate**	**Std_Error**	**t_value**	**p_value**
(Intercept)	0.971	0.058	16.692	0.000
Day 1 Total Provisioning Rate	0.075	0.058	1.295	0.222

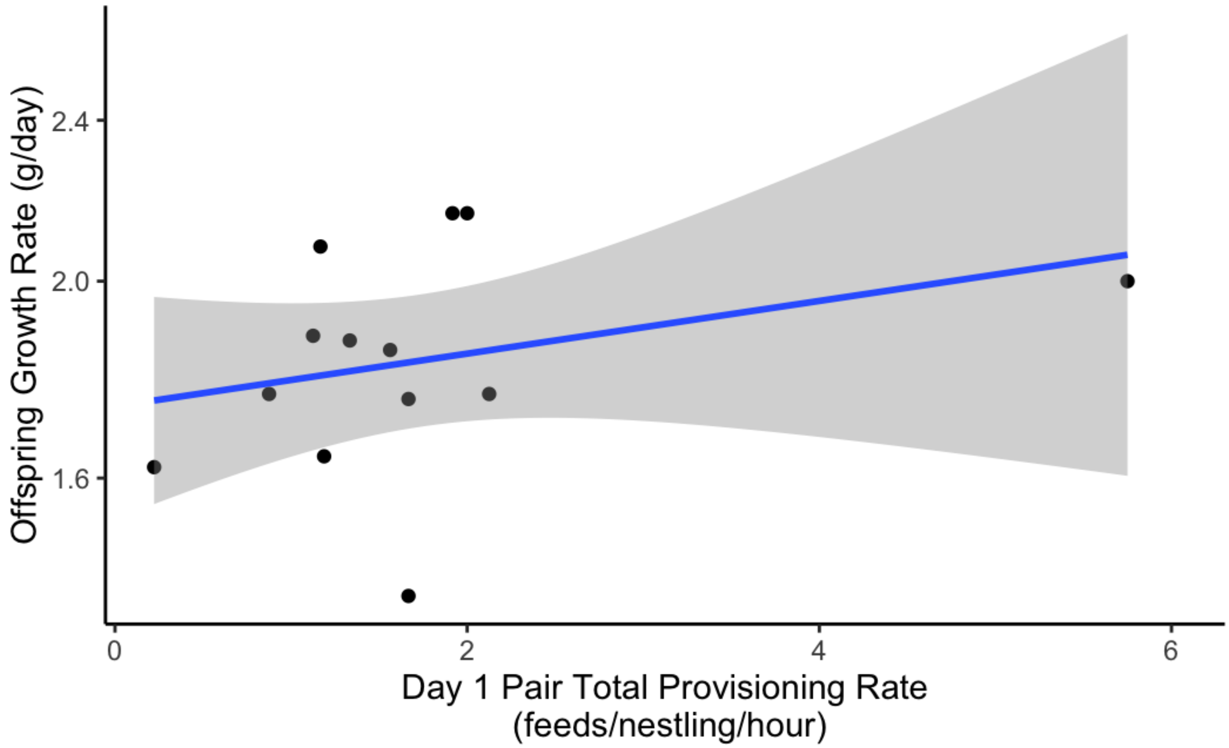
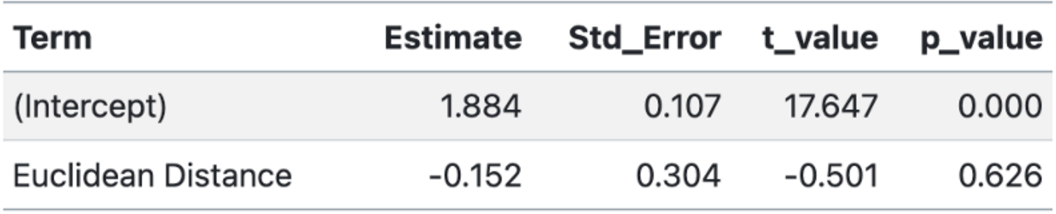


Figure 8. Pair total day 1 provisioning rate shows no significant linear relationship with offspring growth rate (Linear Regression, $p = 0.2218$, $\beta = 0.0752$, SE = 0.0581, $t_{11} = 1.295$).

Table 7. Linear regression for pair provisioning similarity (Euclidean distance) and growth rate.



Term	Estimate	Std_Error	t_value	p_value
(Intercept)	1.884	0.107	17.647	0.000
Euclidean Distance	-0.152	0.304	-0.501	0.626

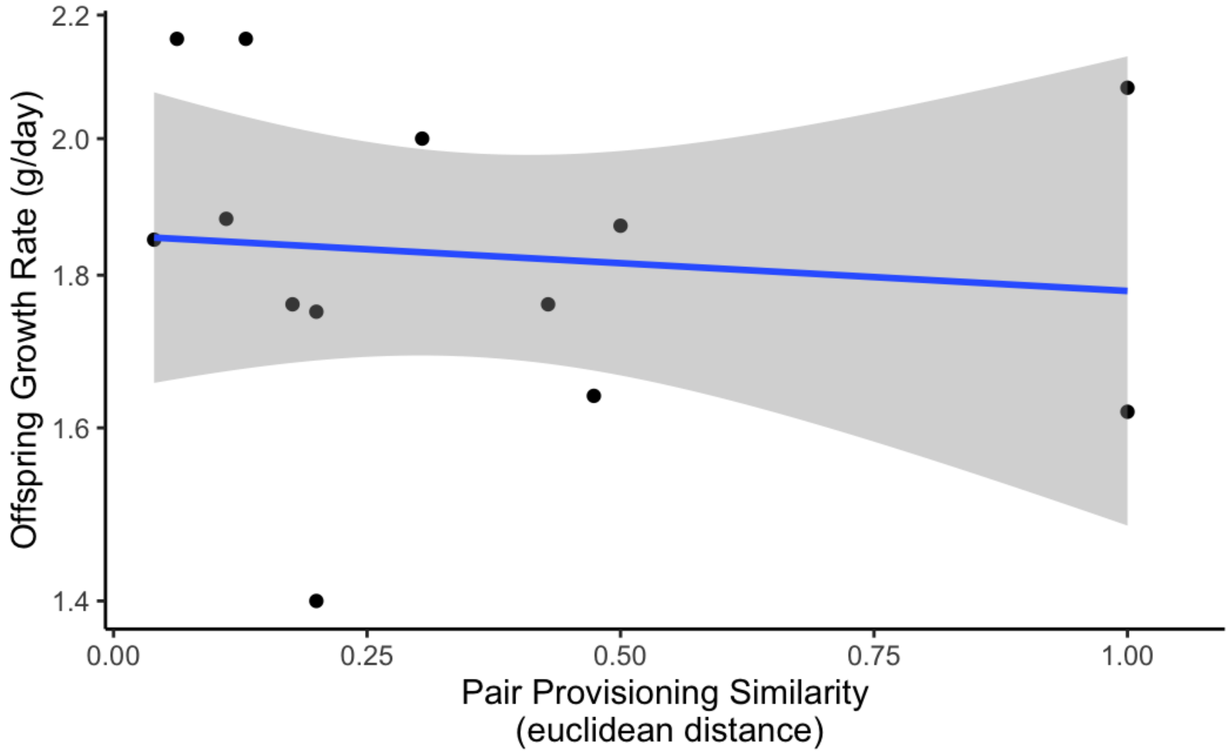
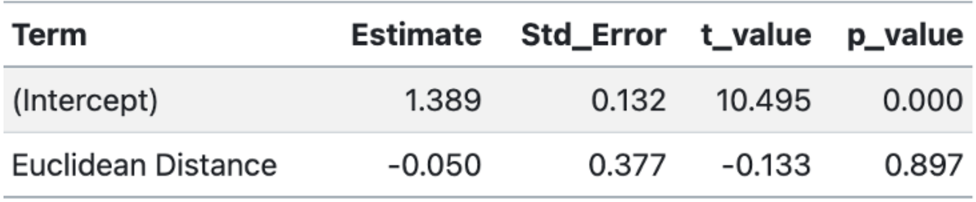


Figure 9. There was no significant relationship between pair provisioning proportional similarity and offspring growth rates (Linear Regression, p = 0.6264, β = - 0.1525, SE = 0.3045, $t_{11.96}$ = - 0.501).

Table 8. Linear regression for pair provisioning similarity (Euclidean distance) and clutch size.



Term	Estimate	Std_Error	t_value	p_value
(Intercept)	1.389	0.132	10.495	0.000
Euclidean Distance	-0.050	0.377	-0.133	0.897

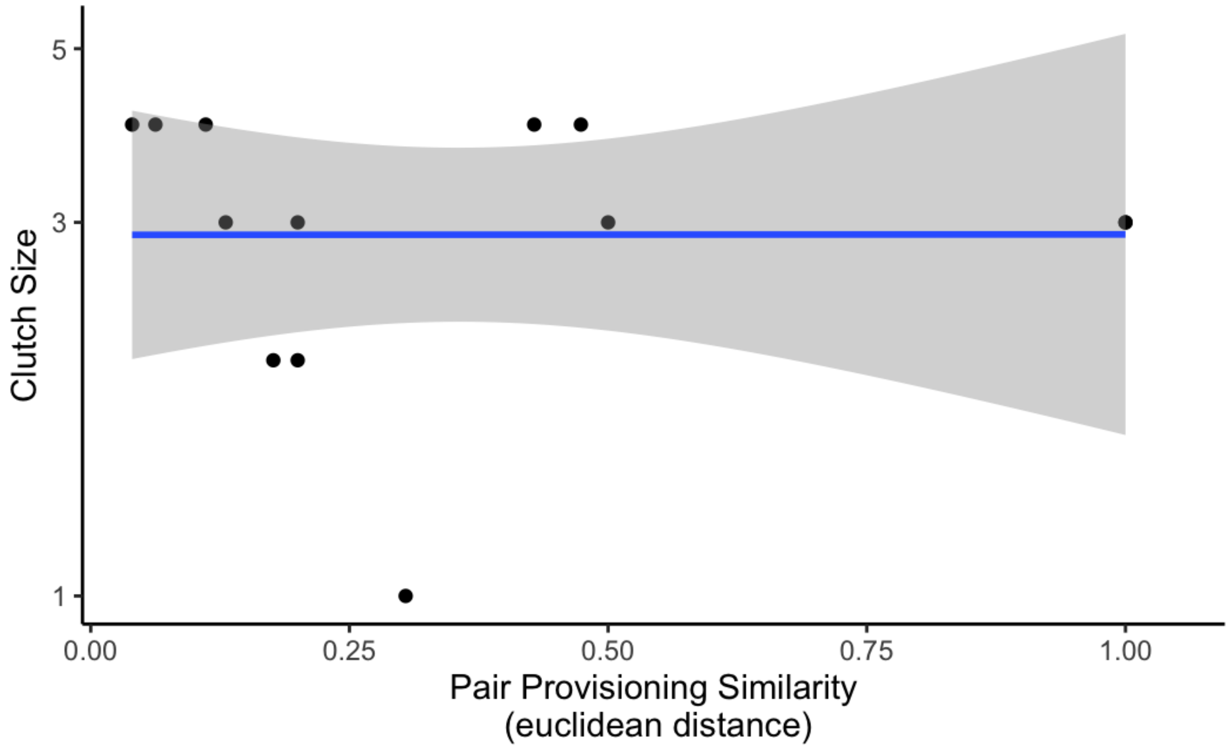


Figure 10. There was no significant relationship between pair provisioning proportional similarity and clutch size (Linear Regression, p = 0.8969, β = - 0.0501, SE = 0.3774, $t_{11.96}$ = - 0.133).

DISCUSSION

Aggression and Offspring Growth Rate

We found no relationship between male aggression and offspring growth rate. However, previous studies on the same population found that male aggression had a significant positive impact on nestling growth (Krippel et al., 2017). Possible explanations for the difference in results could be small sample sizes, variation in the particular males studied, and/or environmental differences from year to year.

Although both studies had small sample sizes, they were similar in size (n = 18, current study; n = 22, Krippel 2017), making small sample size an unlikely explanation for the discrepancy. Another possibility is that environmental conditions may have impacted results year-to-year. For example, precipitation during the 2024 breeding season was the second lowest recorded in the past 10 years (Menne et al., 2012). Additionally, anthropogenic habitat disturbance, such as removal of bushes or heavy construction, may have led to differences between years in resource availability or nesting habitat availability and quality, which potentially masked or impacted the relationships between aggression, nestling growth, and provisioning rates (Stojanovic et al., 2021; Tremblay et al., 2005). Territorial aggression exhibits a degree of plasticity and aggression is adjusted in response to environmental conditions such as food availability (Foltz et al. 2015). Territorial intrusion pressure may also differ for individuals and from year to year, which could result in variation in territorial aggression (Arcese 1987). These studies demonstrate possible environmental impacts on aggressive behaviors that were not accounted for in this study. However, it is worth noting that aggression is consistent from year to year in our population (Krippel et al. 2017). If aggression remains consistent from year to year for individuals, but food supply availability for nestlings change, then the relationship between aggression and offspring growth could change from year to year. Larger-scale studies are required to verify a relationship between male aggression and offspring growth rate in Song Sparrows.

Aggression and Provisioning

Previous studies found a relationship between territorial aggression and chick growth rate, and we anticipated that differences in growth rate might have resulted from differences in provisioning behaviors. We expected males with higher aggression to have higher provisioning rates, resulting in faster growing offspring (Krieg & Getty, 2020; Krippel et al., 2017). We found no relationship between male aggression and provisioning rate.

Though we found no benefit to higher territorial aggression, we also found no fitness cost to aggression. Many studies report costs to aggression which can result in reduced parental investment (Duckworth, 2006), reduced offspring quality (Rosvall, 2011), and other costs (reviewed in Ord 2021). The consequences of variation in territorial aggression in our population of Song Sparrows remains unclear. Our findings are similar to those from Szász et al. (2019) on Collared Flycatchers (*Ficedula albicollis*) which also found no relationship between aggression level and provisioning rates in males. Previous studies have hypothesized a trade-off between territorial defense and parental care in males, where more aggressive males provide less parental care in competitive environments (Pryke & Griffith, 2009; Saino & Møller, 1995). While the presence of behavioral polymorphism suggests a trade-off to aggressive behaviors, we found no evidence of such trade-off. Many studies have suggested the trade-off between male aggression and parental investment is offset by extra-pair copulations (Stoehr & Hill, 2000; Tuttle, 2003). However, other studies, including work on this population of Song Sparrows, has found no relationship between male aggression and extra-pair paternity (Duckworth, 2006; Krippel et al., 2017).

Reduced predation risk in urban habitats, such as our study site, may have an influence on individual provisioning rates. In our study we did not assess predation risk, however many studies show evidence that nest predation decreases in urban habitats (Eötvös et al., 2018; Fischer et al., 2012; Lane et al., 2023). When nest predation risk is low, less aggressive males may experience more security and have fewer risks associated with visiting the nest; risks that more aggressive males can afford to neglect, such as attracting a predator. Evidence of increased nest predation negatively impacting provisioning rates has been found in a number of studies (Ghalambor, 2002; Mouton et al., 2020; Mutzel et al., 2019; Şahin Arslan & Martin, 2024; Skutch., 1949). This increased sense of safety could allow the less aggressive males in our urban study site to visit the nest more often than in environments with higher predation risk, leading to no significant relationships between provisioning and aggression.

The relationship between aggression and provisioning behavior may be more nuanced than previously anticipated. Variations of provisioning rates in Collared Flycatchers were associated with other factors such as age and prey availability (Cauchard et al., 2021). Provisioning rates increasing with age may be attributed to older males trying to maximize their last reproductive output by contributing greater parental effort in the later years of their lifespan (Froy et al., 2013). Additionally, young birds with limited provisioning experience may also contribute to this trend, as their initial inexperience in parental care may result in lower offspring investment, which could potentially increase as proficiency is gained over time. Research has found that inexperienced females tend to rear smaller offspring compared to more experienced females. This could be a result of foraging inexperience and, therefore, inefficiency. In experimentally manipulated conditions of Collared Flycatchers, lower weights and shorter tarsi of chicks were prominent in nests of inexperienced females, suggesting that younger, novice females may exhibit reduced foraging efficiency (Cichoñ, 2003).

Environmental conditions may have a significant influence on foraging success, and therefore provisioning rates and offspring quality, as well. This has been shown in Collared Flycatchers, where nestlings raised under poor feeding conditions developed smaller tarsi than their full siblings raised under optimal feeding conditions, indicating a reflection of nutritional conditions during growth rather than heritability (Merilä, 1997). Variation of environmental conditions between years may also impact an individual's ability to locate preferred prey, and therefore, lead to lower provisioning rates. Research has shown that, across bird species, habitat characteristics – such as the types and density of vegetation – are important selective forces in determining foraging behavior and resource exploitation (Robinson & Holmes, 1982). In a heavily modified habitat, like our study site, frequent changes in vegetation may result in reduced foraging success or efficiency. White-throated Sparrows (*Zonotrichia albicollis*) have been found to focus their efforts on foraging sites where prey are most detectable rather than where they are most abundant (Getty & Pulliam, 1993). Recurrent landscaping at our study site may cause foraging areas with high prey densities to shift frequently, requiring new information to be acquired before foraging proficiency can be regained in the altered environment.

Others studies have found males with higher aggression have lower provisioning rates (Barnett et al. 2012; Mutzel et al. 2013) suggesting that aggressive males have access to better territories, differences in foraging techniques, or energy allocation. If more aggressive males invest more time exhibiting nest defense behaviors, they may compensate through alternative foraging methods, such as scrounging. If more aggressive males have better foraging success based on these different foraging tactics, they may obtain higher quality food during each foraging session, reducing the need for frequent visits to the nest without forfeiting offspring quality (Liker & Barta, 2002). Evidently, the relationship between aggressive behaviors and provisioning effort is highly complex, emphasizing the need for more nuanced investigation.

Provisioning Repeatability

We found that both male and female provisioning rates are significantly repeatable between days 1 and 3 after hatch. A similar pattern was revealed for days 1 and 5, though it was not statistically significant. A previous study measuring provisioning repeatability within the same brood across multiple days found significant repeatability for both males and females of Eastern Bluebirds (*Sialia sialis*) (Burdick, 2018). Research on House Sparrows (*Passer domesticus*) reported significant repeatability of male provisioning behaviors across broods (Schwagmeyer & Mock, 2003). In a 10-year study on Blue Tits (*Cyanistes caeruleus*), provisioning rates were found to exhibit small-to-moderate repeatability across years (Santema et al., 2024). In contrast, a study on Manx Shearwaters (*Puffinus puffinus*) found no repeatability of provisioning across multiple years (Gray et al., 2005). When adjusting for factors such as seasonality – which typically results in a reduction of individual provisioning rates due to declining resource availability – 37.5% of provisioning variation was due to persistent differences in males rather than environmental conditions (Schwagmeyer & Mock, 2003). Additional studies have found significant heritability of provisioning rates, indicating they are influenced by genetic factors and a stable aspect of individual behavior (Krist et al., 2024). The consistency seen in provisioning rates in many studies, across days, broods and years further suggests that provisioning rate can be an individually distinctive trait in birds.

Provisioning Similarity

Within-pair similarity analyses show significant similarity of provisioning rates between males and females. Males contributed slightly greater proportions of parental care than females for the majority of nests, consistent with the findings of other studies on songbirds (Cauchard et al., 2021; Johnson & Best, 1982; Nordlund & Barber, 2005; Reed et al., 2007). Sexual conflict theory suggests that males are more inclined to prioritize alternative behaviors over parental care when such activities allow a fitness advantage, leading to increased female parental investment as they compensate for the reduced male contribution (Mutzel et al., 2013; Paredes et al., 2005). We did not find any evidence of compensatory parental care, which would've presented itself as females contributing a significantly greater proportion of parental care than males.

Provisioning rate similarities could be a response to nestling begging effort or possibly evidence of assortative mating. Many studies have demonstrated similar feeding rates between mated pairs in a variety of species (Alatalo et al., 1988; Breitwisch et al., 1986; Burdick, 2018; Leffelaar & Robertson, 1986). Research has found strong associations between nestling begging intensity and parental provisioning rates (Mondloch, 1995; Price, 1998). Further investigation of parental response to manipulated nestling begging behaviors in Song Sparrows could supplement these findings and provide explanation for pair provisioning similarities.

However, parental effort is not always influenced by offspring begging behaviors (Clark & Lee, 1998; Santema et al., 2017). A study on Great Tits (*Parus major*) found that experimentally increasing the provisioning rate of one parent results in an increased provisioning rate of the corresponding parent, regardless of chick begging behavior (Hinde, 2006). This suggests that parental provisioning effort may be more strongly influenced by the corresponding mate's behaviors rather than offspring-driven cues.

Our study found no evidence of within-pair provisioning similarities influencing reproductive success, which was measured using two factors: growth rate and clutch size. Pair provisioning rate similarity could be behavioral convergence (adjustment of an individual's behavior relative to their mate's behavior) or an incidental outcome of assortative mating driven by a characteristic other than provisioning behavior, thus leading to high similarity but no direct relationship to reproductive success. Alternatively, females may select for males that exhibit traits indicating more similar parental investment to ensure reduced sexual conflict, while males may flaunt those indicators of parental investment to attract mates. If courtship displays provide information about parental care in male Song Sparrows, females may recognize these cues and select for males with similar traits to their own, consistent with the assortative mating hypothesis. Many have proposed that females may vary in their preference for specific behavioral types of mates (characterizations of an individual's consistent behavior) based on their own (reviewed in Schuett et al. 2010; Munson et al. 2020). This would account for the persistent variation in male Song Sparrow behaviors.

Additionally, pair provisioning synchrony (pairs arriving at the nest to feed within 2 min of each other) and coordination (pairs alternating visits) have been shown to reduce sexual conflict and have positive effects on reproductive success in birds (Bebbington & Hatchwell, 2016; Mariette & Griffith, 2015). It is worth noting, throughout this study, personal observation of Song Sparrow vocalizations on the nest were frequent and seemingly associated with provisioning coordination, which has been observed in song birds (Ferree et al., 2021; Mcdonald & Wright, 2008). Future studies could investigate the function of these vocalizations at the nest in Song Sparrows, in terms of reproductive success.

Other studies examining similarities in personality within pairs of birds show an influence on reproductive success through nesting defense. A study on Eastern Bluebirds found that pairs with more similar responses to simulated territorial intrusions fledged heavier offspring. This pattern may be explained by a trade-off in energy investment where a coordinated aggressive response by pairs allows for less time spent defending, resulting in more time to provision (Harris & Siefferman, 2014). Furthermore, when measuring nest defense behaviors, a similar study on Eastern Bluebirds found that mates with similar defense strategies produced more fledglings (Burtka & Grindstaff, 2015). Moreover, a previous study on our population of Song Sparrows found high similarity in nest defense boldness in the presence of fledglings for males and females within pairs, providing further evidence that Song Sparrows exhibit behavioral convergence or assortative mating (Cook, 2023). These studies suggest that behavioral convergence or assortative mating might help synchronize both reproductive efforts and broader behavioral patterns, contributing to more effective cooperation and less conflict between mates. Additional studies monitoring the number of nestlings that successfully fledge would be beneficial to further examine the intricacies of within-pair similarities and reproductive success.

Behavioral similarity between mates in activities seemingly unrelated to reproduction may play an important role in reducing conflict and improving reproductive success. A study on Chestnut Thrushes (*Tardus rubrocanus*) found evidence that pairs with more similar activity traits (hopping, walking, flying) had lower levels of sexual conflict over provisioning and higher total provisioning rates (Lou et al., 2021). These findings highlight how behavioral similarity in activities that are not directly related to reproduction can influence reproductive success.

Conclusion

Our study investigated the reproductive consequences of aggression in male Song Sparrows, specifically regarding parental investment. While we found no relationship between male aggression and offspring growth rate or provisioning rate, we acknowledge that single-year studies may not fully reflect the complex interactions between these variables. Previous research has reported a positive link between aggression and nestling growth, suggesting environmental fluctuations may account for differences in the relationships between aggression, provisioning, and growth rate year to year (Krippel et al., 2017). We found no evidence of a trade-off between male aggression and parental care, nor evidence of compensatory care from females. Additionally, individual provisioning rates were consistent across days and mates exhibited similar provisioning behaviors, suggesting provisioning rate may be an individually distinctive trait and that assortative mating or convergence of behaviors may be occurring, perhaps to ensure reduced sexual conflict. These results highlight the need for larger scale, multi-year studies to better understand the relationship between aggression and reproductive success, and the mechanisms and significance of pair similarity in parental care in Song Sparrows.

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