

PERSONALITIES OF MATED PAIRS AND PARENTAL PROVISIONING
COORDINATION IN EASTERN BLUEBIRDS

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by
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Abstract

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Animal personality is characterized by consistent similar reactions by an individual across contexts and time. Although individual personality is known to influence fitness, the extent to which similarity of pair personality influences fitness in monogamous animals with a system of bi-parental care is not well studied. Previous research from my focal population demonstrated that eastern bluebirds (*Sialia sialis*) that are mated pairs display similar personalities (as measured by aggression toward conspecifics) and that those with similarity personalities produced higher-quality offspring in highly competitive environments. However, the mechanisms behind this trend are not well studied. In Chapter 2, I document that individual bluebirds also show repeatable behavior traits (animal personality) when measured as parental defense aggression and parental provisioning to offspring. Further, I show that mated pairs of bluebirds tend to display similar personalities. In Chapter 3, I demonstrate that parental coordination of parental provisioning behavior and, thereby, reproductive success is influenced by the local community of tree swallows (*Tachycineta*

bicolor), a novel (~40 years) and invasive interspecific competitor. Overall, my thesis suggests that pair behavior may allow parents to coordinate feeding behavior more equitably and that this can improve fitness in a context dependent way.

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Foreword

Chapters 2 and 3 of this thesis will be submitted to *Animal Behaviour*, a monthly peer-reviewed journal published by Elsevier on behalf of the Association for the Study of Animal Behaviour in collaboration with the Animal Behavior Society; it has been formatted according to the style guide for that journal.

Chapter 1

Individual and Mated Pair Personalities of Eastern Bluebirds in North Carolina

Recent research focusing on a diversity of animal species suggests that individual animals express limited behavioral flexibility (i.e. plasticity) and often display consistent differences in patterns of behavior within and across contexts- a phenomenon referred to as ‘animal personality’ (also referred to as ‘behavioral types’, ‘behavioral syndromes’, ‘coping styles’, or ‘temperament’ reviewed in Stamps & Groothuis, 2010; van Oers & Naguib, 2013). Some commonly measured behaviors include: aggression, boldness, exploration and neophobia (reviewed in Sih et al., 2004; van Oers & Naguib, 2013). Much of the early personality research focused on lab animals, or wild animals measured while animals were temporarily in captivity. Studying wild animals in the field and focusing on behaviors that have ecological relevance are more appropriate for asking evolutionary questions. Yet, field-based behavioral research is often limited when researchers measure individuals one time because incorporating a repeated measures design can yield valuable within-individual variance (Archard et al., 2012; Fürtbauer et al., 2015). By repeatedly measuring the behavior of wild animals under ecologically-relevant environmental conditions, researchers can increase our understanding of individual variation (reviewed in Westneat et al., 2015) and how personality traits respond to selection.

For species with bi-parental care, reproductive benefits can occur as a consequence of the behavioral compatibility within breeding partners (Spoon et al., 2006; Schuett et al., 2010). One aspect of mate compatibility is the behavioral similarity of mated partners (that is, the tendency for two individuals to behave like each other) (Spoon et al., 2006; Schuett et

al., 2010). Partners that are similar in nest defense and feeding strategies have been shown to achieve high fitness (Spoon et al., 2006; reviewed in Schuett et al., 2010, 2011). In zebra finches (*Taeniopygia guttata*) and great tits (*Parus major*), partner similarity positively influences reproductive success (Both et al., 2005; Schuett et al., 2011). Further, much past behavioral research has focused on how parents that provide bi-parental care may attempt to reduce their effort to conserve energy for future reproductive attempts. However, more recent studies have shown that offspring benefit when parents coordinate their provisioning efforts by synchronizing or alternating their visits to the nest (Mariette & Griffith, 2015). It is also possible that similarly behaved pairs achieve increased reproductive success because they are better able to coordinate the alternation of feeding trips, although, to date, no published research has demonstrated this trend.

Study Species

Eastern bluebirds (*Sialia sialis*) are common, socially monogamous passerines that breed throughout eastern North America (Gowaty & Plissner, 1998). Bluebirds are secondary cavity nesters of pine woodlands, agricultural edges and open grasslands, and readily breed in nestboxes. They are sexually dimorphic in plumage color: males exhibit brighter blue dorsal color and chestnut breasts; females are lighter with grayish-blue dorsal color and duller breasts. This dimorphism allows researchers to easily tell the mates apart during behavioral observation. Further, bluebirds are useful subjects to investigate the adaptive significance of animal personality and coordination of behaviors of mated pairs because they are seasonally socially monogamous and both parents provision offspring and defend the nest (Gowaty & Plissner, 1998). In the mountains of North Carolina, the breeding season lasts from late April to August, with pairs producing one to two broods per year. The female

constructs the nest, lays 3-6 eggs per nest, and incubates them for 14-16 days. Nestlings leave the nest cavity 16-22 days after hatching but fledglings continue to rely upon parental provisioning for another 2-3 weeks (Gowaty & Plissner, 1998). Bluebirds are mainly insectivorous. Males provide extensive parental care, and feed females during egg laying and incubation (Gowaty & Plissner, 1998). Males exhibit mate-guarding behavior and are philopatric (Gowaty & Plissner, 1998). Extra-pair fertilization is not uncommon while conspecific brood parasitism occurs infrequently (Gowaty & Plissner, 1998). Eastern bluebirds appear to be non-migratory in North Carolina, but the species is a partial migrant with more northern populations migrating to the southern United States.

Eastern bluebirds at my field site (Watauga County, North Carolina; 36.299 N, 81.676 W) and in an Oklahoma population show repeatable territorial aggressive behavior (i.e. low within-individual variation coupled with high between-individual variation; Harris & Siefferman, 2014; Burtka & Grindstaff, 2013). Further, Harris & Siefferman (2014) demonstrated that bluebird pairs with similar personalities fledged offspring with higher mass than dissimilar pairs, but this trend was most clear when the bluebirds experienced high levels of interspecific competition with tree swallows (*Tachycineta bicolor*). In an Oklahoma population, Burtka & Grindstaff (2015) showed that similarity of behavior among mated pairs predicts reproductive output.

At my North Carolina site, the bluebird population has only recently experienced the arrival of tree swallows (*Tachycineta bicolor*) because this species is currently undergoing a natural range expansion and have bred locally for <40 years (Lee, 1993). At this site 300 nestbox site, occupancy for bluebirds is ~32% of nest boxes per breeding season (Albers et al., 2017). Tree swallows occupy ~31% of the nest boxes per breeding season and 22% of the

boxes used by bluebirds are occupied sequentially by bluebirds and then tree swallows (Albers et al., 2017). Swallows are often observed harassing breeding bluebirds which can lead to nest failure.

Thesis Objectives

This study builds on Harris & Siefferman's (2014) and Albers et al.'s (2017) previous work on a population of eastern bluebirds breeding in Watauga County, NC. In Chapter 2, I present results of three research objectives. First, I show repeatability of offspring provisioning rates and parental defense aggression of male and female bluebirds. I focus on parental nest defense behavior and provisioning because both are important aspects of reproductive investment and integrate offspring and parental fitness (Kokko & Jennions, 2008). Second, I establish that parental defense and parental provisioning behaviors do not covary significantly within individuals and thus do not represent a behavioral syndrome. Finally, I compare behaviors of mated pairs and demonstrate that mated pairs display similar nest defense behaviors and parental provisioning behaviors. In Chapter 3, I present results of three more research objectives. First, I show that parents coordinate provisioning such that they alternate nest visits more often than would be expected based on each parent's provisioning rates. Second, I demonstrate that parental coordination influences nestling growth rates; I find that parents with greater coordination should rear faster growing offspring. Third, I show that the density of interspecific competitors (tree swallows) influences the extent to which parental coordination impacts their reproductive success.

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Chapter 2

Animal Personality in bluebirds as measured by parental provisioning and defense: Evidence of similarity of personality of mated pairs

ABSTRACT

Recent studies of animal behavior have found that, in many species, individuals display repeatable behaviors across environmental contexts, and thus exhibit personality. Yet much work focusing on animal personality has been conducted under laboratory conditions and little is known about the significance of animal personality the wild. In monogamous animals that exhibit biparental care, reproductive success can be influenced by both personality and the similarity in pair personality. Thus, personality traits associated with parental care behaviors could be an indicator of mate quality and driven by sexual selection. Past research with this population of eastern bluebirds (*Sialia sialis*) demonstrates that mated pairs with similar territorial behavior are more successful parents. Here, I focus on personality traits that are associated with parental effort: provisioning behavior and parental defense aggression. I demonstrate that both male and female eastern bluebirds display significantly repeatable offspring provisioning and anti-predator nest defense behaviors. Further, I found no evidence of behavioral syndromes, as parental provisioning and nest defense did not covary significantly within individuals. However, like territorial defense aggression, I also found birds in pair bonds display significantly similar provisioning rates and parental defense aggression.

INTRODUCTION

Animal personality is characterized by consistent similar reactions by an individual across contexts and time. Numerous studies have shown that animals display individual personalities, and that these personalities impact their individual fitness (Wilson, 1998; Sih et al., 2004; Réale et al., 2007; Stamps & Groothuis, 2010). Animal personality studies have focused on behaviors such as exploration (Both et al., 2005), provisioning of offspring (Burtka & Grindstaff, 2015; Duckworth, 2006; Westneat et al., 2011), and aggression (Burtka & Grindstaff, 2013, 2015; Duckworth, 2006; Harris & Siefferman, 2014).

Aggression can be expressed in territorial disputes against conspecifics (Duckworth, 2006; Harris & Siefferman, 2014), or interspecific competitors (Burtka & Grindstaff, 2013; Duckworth, 2006), or anti-predator defense (Redmond et al., 2009).

Within individuals, these differing types of aggressive behaviors may covary, and perhaps even with other types of behaviors, such as provisioning (Duckworth, 2006). Individuals that are more aggressive, bold, or quick to explore are considered proactive, whereas more passive individuals are classified as reactive (Sih et al., 2004). When multiple behaviors are correlated within an individual, this is considered a behavioral syndrome (i.e. proactive or reactive) (Sih et al., 2004).

It is possible that sexual selection acts on animal personality (Schuett et al., 2010). Behavioral repeatability in parental care behaviors could be an indicator of mate quality and driven by sexual selection (Schuett et al., 2010). A few studies have shown that mated individuals tend to display similar personalities (Both et al., 2005; Burtka & Grindstaff, 2015; Harris & Siefferman, 2014; Spoon et al., 2006). Moreover, some have shown that pairs with similar personalities tend to have greater success compared dissimilar pairs. Great tit

(*Parus major*) pairs that display similar exploratory behavior outside of the breeding season fledge heavier nestlings (Both et al., 2005). Likewise, Spoon et al. (2006) performed controlled aviary-based experiments that show pairs of Cockatiels (*Nymphicus hollandicus*) that are behaviorally similar rear more nestlings to independence compared to pairs that exhibit dissimilar behavior.

Previous research has found that bluebirds (*Sialia sp.*) exhibit repeatable aggressive behavior as a measure of personality (Burtka & Grindstaff, 2013, 2015; Duckworth, 2006; Harris & Siefferman, 2014), as well as provisioning behavior (Burtka & Grindstaff, 2015). Eastern bluebirds (*Sialia sialis*) are an excellent model organism for this type of study because they are a secondary cavity nesting species that readily nests in human-constructed nestboxes. They are also seasonally socially monogamous and both parents provision offspring and defend the nest (Gowaty & Plissner, 1998). Here, I investigate repeatability offspring provisioning rates and parental defense aggression of male and female bluebirds. I focus on parental nest defense behavior and provisioning because both are important aspects of reproductive investment and integrate offspring and parental fitness (Kokko & Jennions, 2008). I establish whether these behaviors covary within individuals, and finally, determine if mated pairs display similar personalities. This research question was motivated by previous research that documented repeatable territorial defense behavior within individuals and that mated pairs showed similar territorial defense behaviors (this population, (Harris & Siefferman, 2014); an Oklahoma population, (Burtka & Grindstaff, 2013)).

METHODS

General Field Methods

I studied the breeding behavior of eastern bluebirds at 200 nestbox field site in Watauga County, NC, during 2015, the boxes were erected and have been monitored since 2009. I monitored nest building, egg laying, and hatching. I captured adult bluebirds in the nestbox using trapdoors and banded them with a numbered USGS aluminum band, along with three colored plastic bands for identification.

Provisioning

I recorded offspring provisioning using video cameras placed at least 2 m away from the nestbox. To determine the extent to which parental provisioning is repeatable, I recorded each nest twice, first when nestlings were between 3 and 7 days old, and again when nestlings were between 9 and 13 days old (hatch day = 1 day old). Each observation lasted 2 hours. I recorded the total number of visits to the nest for each parent and calculated the provisioning rate (visits/h).

Aggression

Nest defense was measured by performing Simulated Predation Events (SPEs) using a model crow hung above the nestbox and a small speaker to broadcast American Crow (*Corvus brachyrhynchos*) and nestling bluebird calls. To determine repeatability of response to SPE I performed two events per nest when nestlings were between 10 and 14 days old. I recorded the number of times each bird attacked the model crow within each 10 min trial.

Statistical Methods

I analyzed repeatability of provisioning behavior using a Linear Mixed Model (LMM) based repeatability model, and calculated repeatability of aggression using a

Generalized Linear Mixed Model (GLMM) approach with the “rptR” package (Stoffel et al., 2017) in R Statistical Software v. 3.4.0 (R Core Team, 2015). I used IBM SPSS v. 24 (IBM Corp., 2017) to perform Spearman’s and Pearson’s correlations to determine covariation of provisioning and nest defense aggression behavior within individuals and pair similarity. I analyzed attack data from SPEs using non-parametric methods because the count data had a zero-inflated Poisson distribution that could not be normalized by transformation.

RESULTS

Repeatability of Behavior

I found significant repeatability in provisioning behavior ($R = 0.353$, $p = 0.011$, $n = 46$; Figure 1, 2. Table 1). Nest defense behavior (number of dives) was also significantly repeatable ($R = 0.550$, $p < 0.001$, $n = 64$; Figure 3, 4. Table 1). Controlling for sex did not affect repeatability for either provisioning ($R_{\text{adj}} = 0.359$, $p = 0.010$, $n = 46$; Table 1) or nest defense behavior ($R_{\text{adj}} = 0.555$, $p < 0.001$, $n = 64$; Table 1).

Covariation of Behaviors Within Individuals

I found no significant correlation between provisioning rate and number of dives among males (Spearman’s $\rho = -0.117$, $p = 0.438$, $n = 38$) nor among females (Spearman’s $\rho = -0.258$, $p = 0.118$, $n = 38$).

Pair Similarity

The average provisioning rates of mated pairs were significantly positively correlated (Pearson’s $\rho = 0.442$, $p = 0.002$, $n = 45$; Figure 5). Further, there was a marginally

significant positive correlation between the number of nestling defense dives among mated pairs (Spearman's $\rho = 0.302$, $p = 0.055$, $n = 40$; Figure 6).

DISCUSSION

In this study, I demonstrated that both male and female eastern bluebirds display repeatable provisioning and nest defense behavior; however, these behaviors do not appear to covary within individuals (no evidence of behavioral syndromes). I also found that mated pairs show tendencies to display similar personalities- both in terms of offspring defense aggression and parental provisioning behaviors. Repeatability in both parental provisioning and defense behavior suggest these birds have predictable behavior; because mated pairs show similarity in personalities, it is possible that personality influences mate choice and is driven by sexual selection (Schuett et al., 2010).

Repeatability of provisioning and defense behaviors indicates that these birds display individual personalities and my results corroborate those of Harris & Siefferman (2014) and Burtka & Grindstaff (2013) who studied eastern bluebirds and that of Duckworth (2006) who studied western bluebirds (*Sialia mexicanus*). I found no difference in the degree to which males and females exhibit repeatable behaviors. Previous research measuring personality of eastern bluebirds measured response of breeding birds to simulations of territorial intrusions of either conspecifics (this population, Harris & Siefferman, 2014) or of an invasive competitor species (an Oklahoma population, Burtka & Grindstaff, 2013) and found females to be more repeatable than males. The discrepancy in sex-specific repeatability could be because I measured parental defense aggression, not territorial aggression.

Relatively little research has investigated repeatability of provisioning and only a few studies have considered provisioning to be a personality trait (Burtka & Grindstaff, 2015; Westneat et al., 2011; Wetzel & Westneat, 2014). I found that both sexes showed repeatable provisioning behavior, whereas studies of parental care in eastern bluebirds found males to exhibit greater repeatability in provisioning behavior than females (Burtka & Grindstaff, 2015). In an Oklahoma population, males exhibited significantly repeatable provisioning rates and visit duration, while only provisioning rate of females was repeatable (Burtka & Grindstaff, 2015). Studies of house sparrows, (*Passer domesticus*), also show that males to display more repeatable parental care behaviors (Nakagawa et al., 2007; Schwagmeyer & Mock, 2003). If males are predictable, male parental care behavior in one breeding attempt could be used by females to predict future investment by males and thus should be used in mate choice (Nakagawa et al., 2007).

Individual personality may impact mutual mate choice. I found that mated pairs tended to behave similarly both during offspring provisioning and nest defense. There was a stronger trend towards similarity in provisioning than in aggression; however, this could be due to lack of statistical power, and increased sample size could provide a clearer trend. Similarity in pair behavior has been found to have positive effects on offspring size at fledging (Both et al., 2005; Harris & Siefferman, 2014; Schuett et al., 2011). Such reproductive benefits could be due to increased potential for cooperation between parents with similar personalities. Further, coordination of offspring care can reduce parental activity near the nest which leads to reduced predation (Bebbington & Hatchwell, 2016). However, even though individuals displayed repeatable behavior that tended to match their partner, birds may simply adjust their behavior to match that of their partner instead of choosing

mates based upon similarity of personalities (Schuett et al., 2011). To make this distinction, individual behavior would need to be observed outside of the breeding season or over a long period of time and/or multiple partners to determine the degree to which personality is consistent in various contexts. To date, most animal personality research has been conducted under laboratory conditions, and, despite its limitations, this work highlights the significance of measuring animal personality the wild.

Although birds were repeatable and exhibited similar behavior to their mates, I found no evidence of behavior syndrome – a statistical association between parental defense aggression and parental provisioning. In western bluebirds, males that defend the nest the most aggressively towards conspecifics provision their mates less often during incubation (Duckworth, 2006). Among blue tits (*Cyanistes caeruleus*), males that display the greater territorial aggression feed offspring less often (Mutzel et al., 2013). Negative associations between territoriality and provisioning are expected if both are testosterone mediated. Indeed, in many species, experimentally heightened testosterone levels encourage territorial aggression and suppress parental behaviors (Ketterson et al., 1992; Wingfield, 1985).

This study confirms that eastern bluebirds display repeatable individual differences in both provisioning and nest defense behavior, and that mated pairs tend to exhibit similar personalities when rearing offspring. Future work with this population will focus on the mechanisms by which similarity in mated pair behavior leads to higher offspring growth-how pair similarity influences provisioning coordination or synchrony.

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TABLES

Table 1. Repeatability values of offspring provisioning rate and nest defense aggression of eastern bluebirds. Adjusted repeatability values include sex as a fixed effect. Confidence intervals of provisioning data are 95%, and 97.5% CI for nest defense.

<i>Variable</i>	<i>Repeatability R</i>	<i>Adjusted R</i>	<i>SE</i>	<i>CI</i>	<i>p</i>	<i>n</i>
<i>Provisioning Rate</i>	0.353	0.359	0.128	0.084, 0.572	0.011	46
<i>Nest Defense</i>	0.550	0.555	0.147	0.176, 0.771	<0.001	64

FIGURES

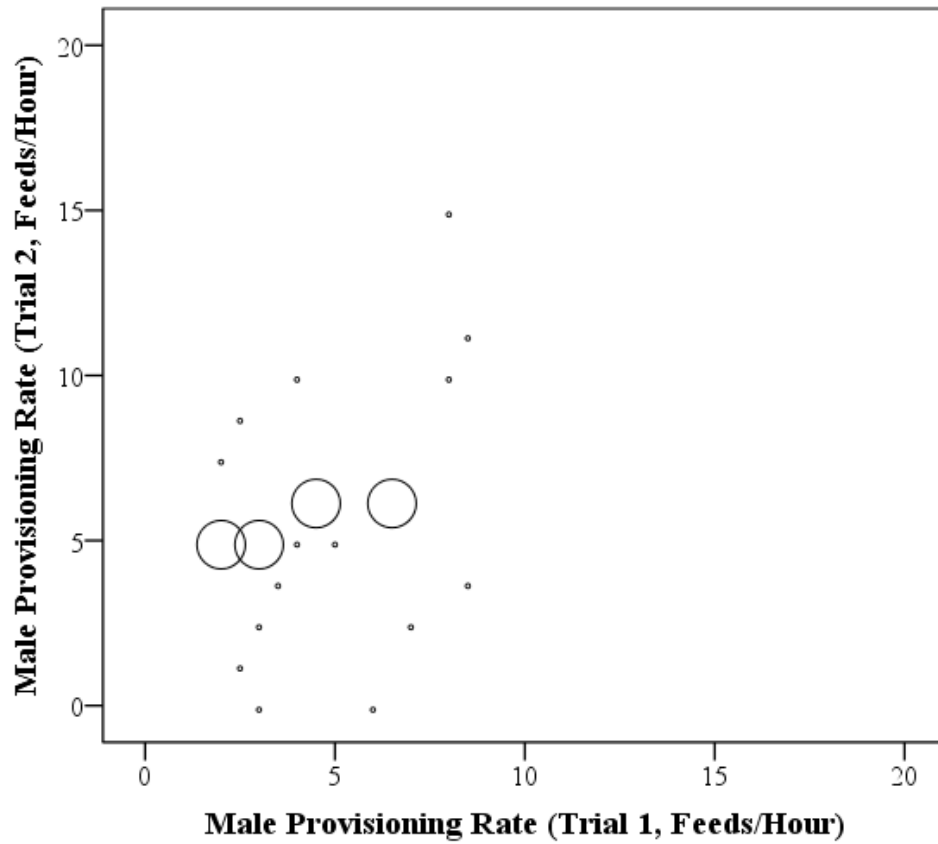


Figure 1. Comparison of provisioning rate (feeds/hour) to offspring during trial 1 and trial 2 (n=23) among male eastern bluebirds. Marker size indicates number of overlapping points; large circles (n=2), small circles (n=1).

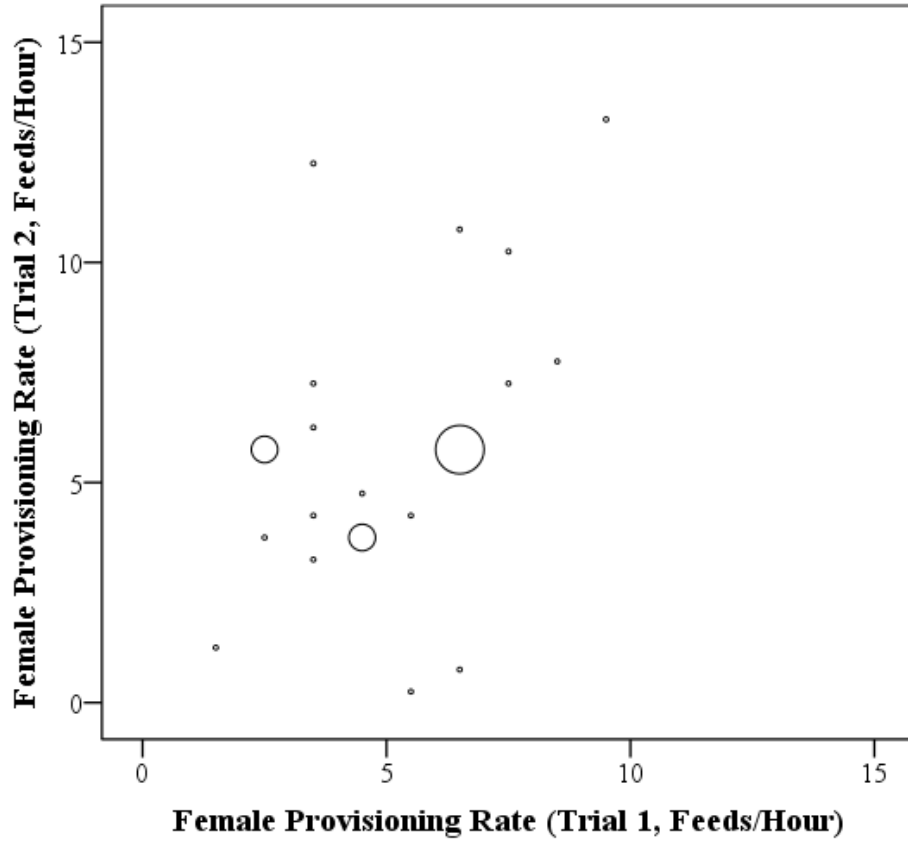


Figure 2. Comparison of provisioning rate (feeds/hour) to offspring during trial 1 and trial 2 (n=23) among female eastern bluebirds. Marker size indicates number of overlapping points; large (n=3), medium (n=2), small (n=1).

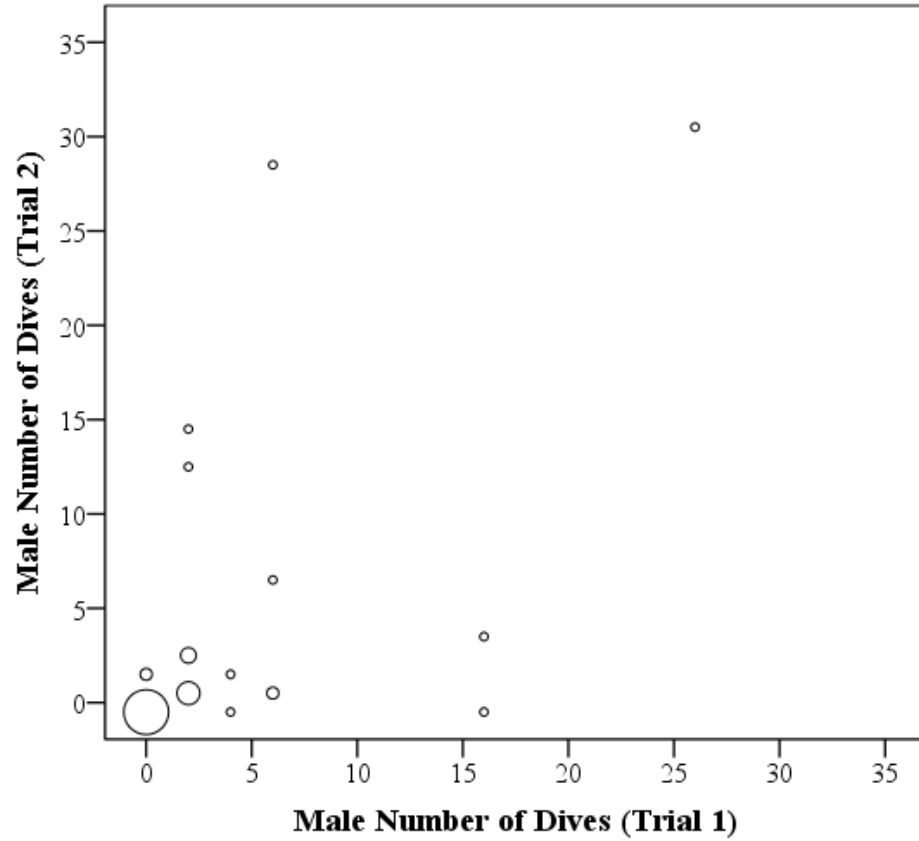


Figure 3. Comparison of number of dives during trial 1 and trial 2 (n=32) among male eastern bluebirds. Marker size indicates number of overlapping points; large (n=11), medium-large (n=5), medium (n=3), medium-small (n=2), small (n=1).

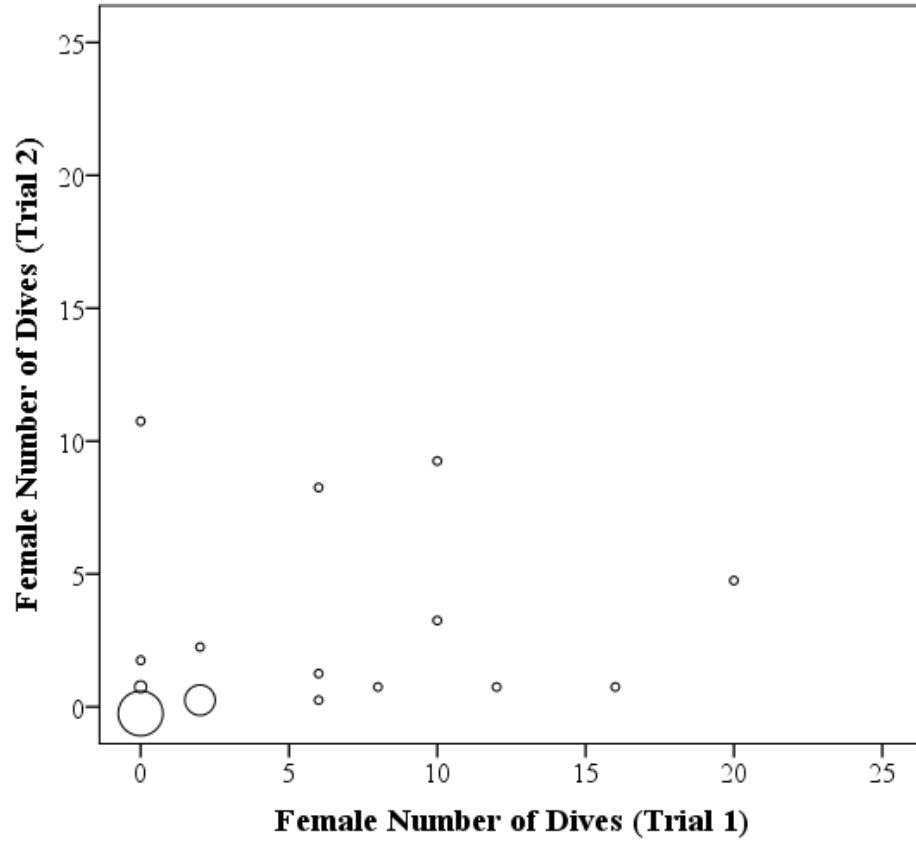


Figure 4. Comparison of number of dives during trial 1 and trial 2 (n=32) among female eastern bluebirds. Marker size indicates number of overlapping points; large (n=11), medium-large (n=7), medium-small (n=2), small (n=1).

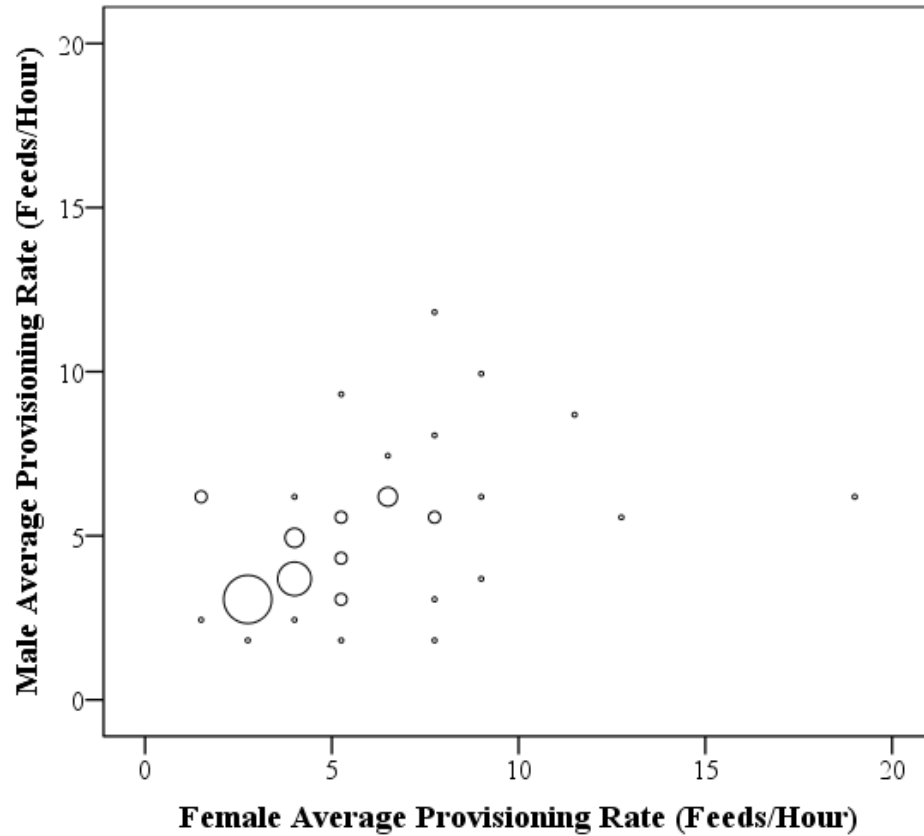


Figure 5. Comparison of provisioning behavior (feeds per hour) of mated pairs of eastern bluebirds (data points represent the average of the two video recordings of provisioning behavior per individual) (n=40) Marker size indicates number of overlapping points; large (n=12), medium-large (n=8), medium-small (n=4), small (n=2), smallest (n=1).

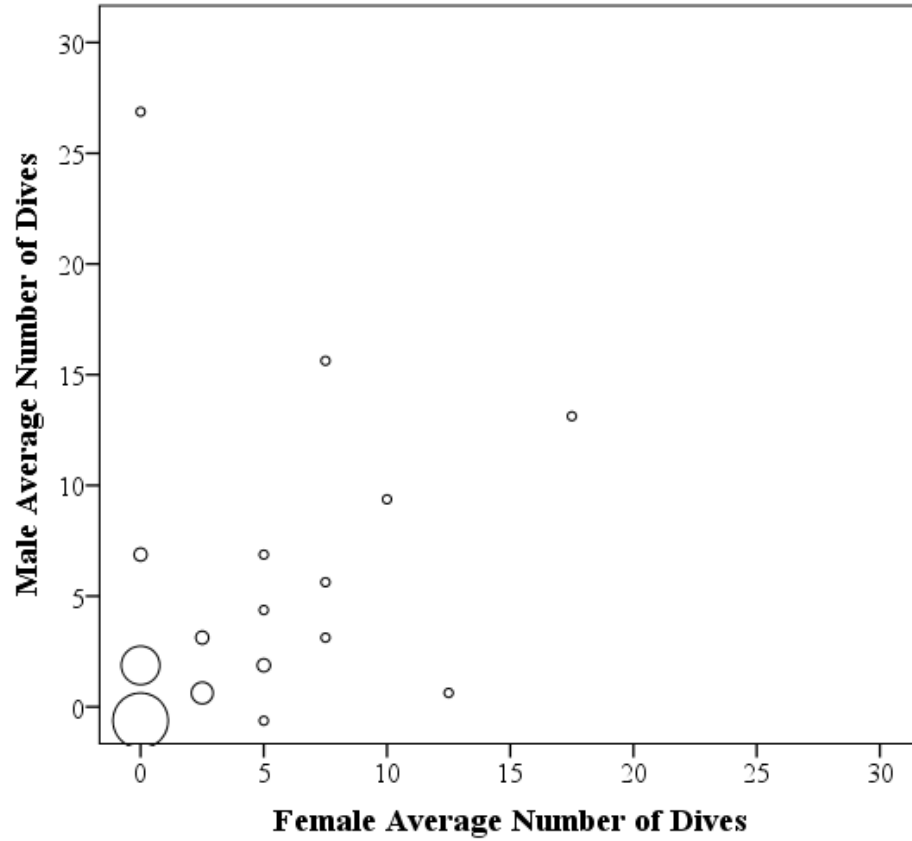


Figure 6. Comparison of aggressive behavior (diving response to SPE) of mated pairs of eastern bluebirds (data points represent the average of the two SPE per individual) (n=45) Marker size indicates number of overlapping points; large (n=7), medium-large (n=5), medium (n=3), medium-small (n=2), small (n=1).

Chapter 3

Interspecific competition influences the adaptive significance of provisioning coordination between breeding partners

ABSTRACT

Cooperation between parents in species with biparental care can reduce sexual conflict and increase reproductive success. Environmental variation can influence the need for, and benefits of, parental cooperation. In this study site, tree swallows (*Tachycineta bicolor*) are a recent (<40 years) and aggressive nestbox competitor with eastern bluebirds (*Sialia sialis*). Here, I measure the benefits of partner coordination of offspring provisioning behavior when the strength of interspecific competition varies spatially. First, I demonstrate that eastern bluebird pairs alternate provisioning trips more than would be expected by chance. Second, I demonstrate that partner alternation is positively associated with provisioning rates and beneficial to nestling growth only in areas of high interspecific competition for nest cavities. This study provides an important new perspective on the resolution of negotiations between breeding partners; environmental variation could influence the benefits of parental cooperation in a wide variety of animals.

INTRODUCTION

Trivers (1972) argued that, in species with biparental care, individuals can save energy for future reproductive attempts by decreasing their parental effort. However, for this strategy to work, their partner must increase effort, and therefore the hard-working parent should have less energy to invest in future offspring. To avoid expending more energy than

necessary, partners may organize provisioning visits. For example, wild pairs of zebra finches (*Taeniopygia guttata*) that synchronize provisioning visits by arriving at the nest at the same time can equalize their parental effort (Mariette & Griffith, 2012). Likewise, great tits (*Parus major*) keep track of when their partner visits the nest and tend to alternate provisioning visits (Johnstone et al., 2014). For partner synchrony or alternation to occur, birds must keep track of their partners; indeed, zebra finches not only synchronize their provisioning visits, but also forage together (Mariette & Griffith, 2015). However, the extent to which offspring benefit from increased parental coordination is still unclear. Some studies show no effects of increased coordination on nestling quality or fledging success (Iserbyt et al., 2017; van Rooij & Griffith, 2013), while others have found positive effects on nestling growth (Mariette & Griffith, 2015) or higher fledging rates (Mariette & Griffith, 2012).

Environmental variables, like level of competition or food availability could influence both the need for the parental coordination and the benefits of parental coordination for dependent young. Partners' coordination during parental care may reflect their coordination in other situations: mates may defend their territory or nest against intruders or predators (Curio & Regelman, 1986; Black, 2001; Krams et al., 2006).

The goals of this study were threefold. First, I tested the hypothesis that parents coordinate provisioning such that they alternate nest visits more often than would be expected based on each parent's provisioning rates. Second, I hypothesized that parental coordination influences nestling growth rates, with the expectation that parents with greater coordination should rear faster growing offspring. Third, I tested the hypothesis that the density of interspecific competitors for nesting sites could influence the degree to which

parents coordinate feeding to offspring, how parental coordination translates to nestling growth, and reproductive success of bluebird pairs.

METHODS

Study Species

Eastern bluebirds (mass ~30g) are a secondary cavity nesting species that readily nest in human-constructed nestboxes. They are seasonally socially monogamous and both parents care for the young and defend the nest (Gowaty & Plissner, 1998). This research is intended to build upon previous work in this population of eastern bluebirds breeding in Watauga County, NC. Harris & Siefferman (2014) demonstrated that, in zones of high interspecific competition with tree swallows (*Tachycineta bicolor*), bluebird pairs that displayed similar levels of aggression fledged offspring with higher mass than dissimilar pairs. Tree swallows (mass: ~20g) and have recently expanded their breeding range to the southeastern United States (~40 years; Lee, 1993). At this western North Carolina field site, they often outcompete bluebirds for nesting cavities (45% usurped in 2015, pers. obs.; Harris & Siefferman, 2014). Tree swallows are semi-colonial nesters that forage within a 300 m radius of their nest on emergent aquatic insects (McCarty & Winkler, 1999). Although bluebirds and tree swallows co-occur in the northeastern North America, for southeastern breeding bluebirds, tree swallows represent a relatively new interspecific competitor, thus allowing for the unique opportunity to investigate the effects of an invasive-like competitor on a native species. This recent increase in interspecific competition may select for pair behavior in parental defense behaviors (Harris & Siefferman 2014) and in coordination of parental provisioning.

General Field Methods

I monitored nest building, egg laying, hatching, and fledging success of eastern bluebirds and tree swallows in Watauga County, NC during the breeding season of 2015. I measured nestling mass (± 0.1 g) when bluebird nestlings were 2, 5, 8, 11, and 14 days old (day 1=hatch day). Nestling bluebird growth asymptotes at 13 days old (Pinkowski, 1975), therefore, the mass of the nestlings at 14 days old is indicative of mass at fledging (Gowaty & Plissner, 1998). Adult bluebirds were captured in the nestbox using trapdoors and banded with a numbered USGS aluminum band, along with three colored plastic bands for identification. Nestlings were also fitted with a USGS aluminum band at 8 days old.

Provisioning

I recorded offspring provisioning using video cameras placed at least 2m away from the nestbox. I took videos of each nest twice, first when nestlings were between 3 and 7 days old, and again when nestlings were between 9 and 13 days old (hatch day = 1 day old). Each observation lasted 2 hours. I recorded the total number of visits to the nest for each parent and calculated the provisioning rate (visits/h). Observed and expected alternation values were calculated using male and female nest visit order following the methods of Iserbyt et al. (2017).

Interspecific Competition

I quantified interspecific competition as the number of active swallow nests within that 300m radius of the focal bluebird nest using Point Distance Tool in ArcGIS 10.4.1

(ESRI, 2016). I then categorized competition as low (0-1 swallow nests) or high (2 or more swallow nests).

Statistical Methods

Statistical analyses were conducted using SPSS v.24 statistical software (IBM Corp., 2017). Using General Linear Mixed Models (LMM), I investigated the effects of brood size, competition, and alternation (predictors) on provisioning rate (dependent variable) with nest identity and individual identity as random effects to account for non-independence within mated pairs and repeated measures of individuals. I then performed LMMs on nestling growth rate using nestling identity as random effects to investigate the effects of nestling age, brood size, competition, average provisioning rates of parent birds, and average alternation (predictors) on nestling mass (dependent variable).

RESULTS

Evidence of Partner Alternation

Using a paired t-test, I determined that observed alternation values were significantly higher than expected values during both provisioning observations (Week 1: $t = -9.763$, $df = 33$, $p < 0.001$; Week 2: $t = -6.332$, $df = 29$, $p < 0.001$).

Effect of Competition on Bluebird Nest Parameters

Using an independent samples t-test grouped by competition level, I found that competition had no significant effect on initial clutch size ($t = -0.360$, $df = 45$, $p = 0.720$) or brood size ($t = 1.836$, $df = 45$, $p = 0.073$). In low competition areas the number of offspring

fledged ($t = 2.199$, $df = 45$, $p = 0.033$) was significantly greater than in areas of high competition. There was no significant difference between fledging mass of nestlings in low or high competition areas ($t = 0.036$, $df = 149$, $p = 0.972$).

Average alternation values were not significantly different between high and low competition pairs ($t = -0.454$, $df = 42$, $p = 0.848$). Likewise, there was no significant effect of competition level on average provisioning rate of males ($t = 1.050$, $df = 43$, $p = 0.300$), females in low competition, however, had a significantly higher provisioning rate than their counterparts in high competition areas ($t = 2.048$, $df = 43$, $p = 0.047$). There was, therefore, a trend towards reduction of overall pair average provisioning rate in areas of high competition ($t = 1.921$, $df = 43$, $p = 0.061$; Figure 1).

Effect of Competition and Partner Alternation on Provisioning Rates

Parental provisioning rate increased with brood size (Table 1, Figure 2). The LMM showed a significant interaction between competition level and alternation on parental provisioning rates ($F = 5.631$, $df = 124.3$, $p = 0.019$). Thus, I split the data by competition level. There was a positive trend in high competition nests wherein alternation increased with provisioning rate (Table 1, Figure 3b). Alternation did not have a strong relationship with provisioning rate in low competition areas (Table 1, Figure 3a).

Effect of Competition on Nestling Growth Rates

I found a significant negative relationship between nestling growth rate and brood size (Table 2, Figure 4). There was a significant interaction between competition level and average pair provisioning rate on nestling growth rate ($F = 8.310$, $df = 202.6$, $p = 0.004$), I

therefore split the data by high and low competition for further analysis. Average pair provisioning rate had a significant positive relationship with nestling growth rate in high competition areas, but there was no significant effect of average pair provisioning in low competition areas

(Table 2, Figure 5). There was a significant positive relationship between average alternation and nestling growth rate in both low and high competition, though the trend is stronger in nestlings raised in high competition environments (Table 2, Figure 6).

DISCUSSION

In this population of bluebirds, parents alternated provisioning trips more often than would be expected by random chance, this suggests that parents may be adopting strategies to cooperate and match their partner's effort (Johnstone et al., 2014). In this western NC population, tree swallows are a relatively new nest competitor as they were only rarely seen in the area and only during migration prior to about 1970 (Lee, 1993). Competition is fierce as 45% of the bluebird cavities are usurped by tree swallows (Albers et al., 2017). The competitive environment has clear effects on how parental provisioning strategies influenced nestling growth. When eastern bluebirds nest in areas with high densities of tree swallow competitors, their reproductive success is jeopardized. Adult bluebirds provision their offspring less often, which leads to slower nestling growth and fewer nestlings surviving to fledging age; though those that do survive reach similar fledging mass to those in low competition areas. Finally, when breeding among high densities of tree swallows, nestlings of partners that provision more often and alternate provisioning trips with their partner

experience increased growth rates, suggesting that paying attention to partner behavior increases both parents' investment in the young.

Although tree swallow competition may be exacerbating the effects of sexual conflict and thus promoting the benefits of partner coordination, the literature suggests that the benefits of coordinated parental care on offspring growth may be widespread. Similar studies on coordinated provisioning efforts have found mixed results on its effects on reproductive success; studies with long-tailed tits (*Aegithalos caudatus*) (van Rooij & Griffith, 2013), and Fife fancy canaries (*Serinus canaria domesticus*) (Iserbyt et al., 2017) found no relationship between reproductive success and parental coordination; while parental coordination has affected reproductive success in zebra finches (Mariette & Griffith, 2012, 2015), and long tailed finches (Bebbington & Hatchwell, 2016). Mariette & Griffith (2015) did not see a direct relationship with nest visit synchrony, but instead found that nestlings of pairs that foraged synchronously were heavier than nestlings of pairs that foraged together less often. It is therefore likely that other forms of parental cooperation may have more pronounced effects on reproductive success in species with varying life histories.

Tree swallows arrive from migration and settle after the bluebirds have paired for the season. Therefore, greater alternation of bluebird pairs breeding among high densities of tree swallows is likely to be a facultative behavioral response, rather than a fixed characteristic of the pair. Indeed, bluebirds may be effectively responding to repeated social challenges from tree swallows via physiological mechanisms associated with social priming (reviewed in Rosvall & Peterson, 2014) or perhaps responding to cues from the nestlings. However, further experimentation is necessary to understand the proximate cause of greater parental coordination in the areas with greater densities of nest competitors. Also, only among those

bluebird pairs at the high competition nesting sites was partner alternation positively related to pair provisioning rates which indicates that coordination may improve productivity of pair provisioning efforts, and perhaps this is only evident when pairs are under increased environmental pressure. When the need for nest vigilance (territorial defense aggression) increases, pair coordination may therefore be selected for and promote matching of one's partner investment. Thus, equity in work rate of partners; increasing cooperation rather than intensifying sexual conflict (see Mariette & Griffith, 2015), may be a coping mechanism in response to harassment from tree swallows. This further supports the hypothesis that pairs respond to myriad environmental cues, such as increased brood size (Mariette & Griffith, 2015) offspring competition (Shen et al., 2010), or risk of nest predation (Raihani et al., 2010; Bebbington & Hatchwell, 2016), and can increase their nest visit coordination to reduce conflict and increase reproductive success.

Other coordinated parental care behaviors in this population of bluebirds appear to help partners improve reproductive success in areas of high tree swallow density. Similarity of partner territorial aggression (as measured by controlled simulated territorial intrusions) leads to higher nestling growth rates when bluebirds breed in high competition zones but the effect is not significant when they breed in areas of low tree swallow density (Harris & Siefferman, 2014). Thus, together, these studies suggest coordination of both territory defense and provisioning young benefits reproductive success, but the effects may only become apparent when tree swallows are present in high numbers. It is possible that assortatively mated birds are more likely to coordinate provisioning efforts with their partners and that the effects of the resolution of sexual conflict only becomes evident under the stress of interspecific competition.

Here, I show some of the first evidence that environmental conditions influence the degree to which a mated pair's coordinated parental provisioning can affect offspring fitness. Although partners in this bluebird population alternate offspring provisioning rates more than is expected by chance, only in the face of high nest competition is there evidence that alternation is associated with parental feeding rates and that alternation improves offspring growth. The study therefore provides an important new perspective on the resolution of negotiations between breeding partners. Biparental care is a widespread mating system and thus my data are relevant for understanding how environmental variation influences parental investment strategies in a wide variety of animals.

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TABLES

Table 1 Results of Linear Mixed Models using provisioning rate (feeds/hour) as dependent variable. Due to an interaction between categorical interspecific competition level and pair alternation, behavioral data were split and interpreted separately. There was a significant increase of provisioning rate with increased brood size. In low competition areas, there was no relationship between alternation and provisioning rate. Though the model did not converge, there appears to be a significant positive relationship between alternation and provisioning rate in high competition areas.

<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Brood Size</i>	0.83 ± 0.38	7.132	92	0.009
Low Competition				
<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Alternation</i>	-2.54 ± 1.92	1.746	79.5	0.19
High Competition				
<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Alternation</i>	3.67 ± 1.50	5.968	41	0.019

Table 2 Results of Linear Mixed Models using nestling growth (mass in g/age) as dependent variable. Behavioral data were split by categorical competition level due to an interaction between average pair provisioning and competition level. There was a significant negative effect of brood size on nestling growth rate. Average pair provisioning rate had no significant effect on nestling growth in areas of low competition; there was, however, a significant positive relationship between provisioning rate and nestling growth in high competition. Alternation had a significant positive effect in both low and high competition, though the effect is stronger in nestlings experiencing a high competition environment.

<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Brood Size</i>	-0.44 ± 0.15	8.357	164	0.004
Low Competition				
<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Average Pair Provisioning Rate</i>	0.11 ± 0.09	1.324	109.6	0.252
<i>Average Alternation</i>	2.74 ± 1.18	5.431	101	0.022
High Competition				
<i>Fixed Effect</i>	<i>Effect Size ± SE</i>	<i>F</i>	<i>df</i>	<i>p</i>
<i>Average Pair Provisioning Rate</i>	0.52 ± 0.17	9.443	72.9	0.003
<i>Average Alternation</i>	4.29 ± 1.45	8.686	75.4	0.004

FIGURES

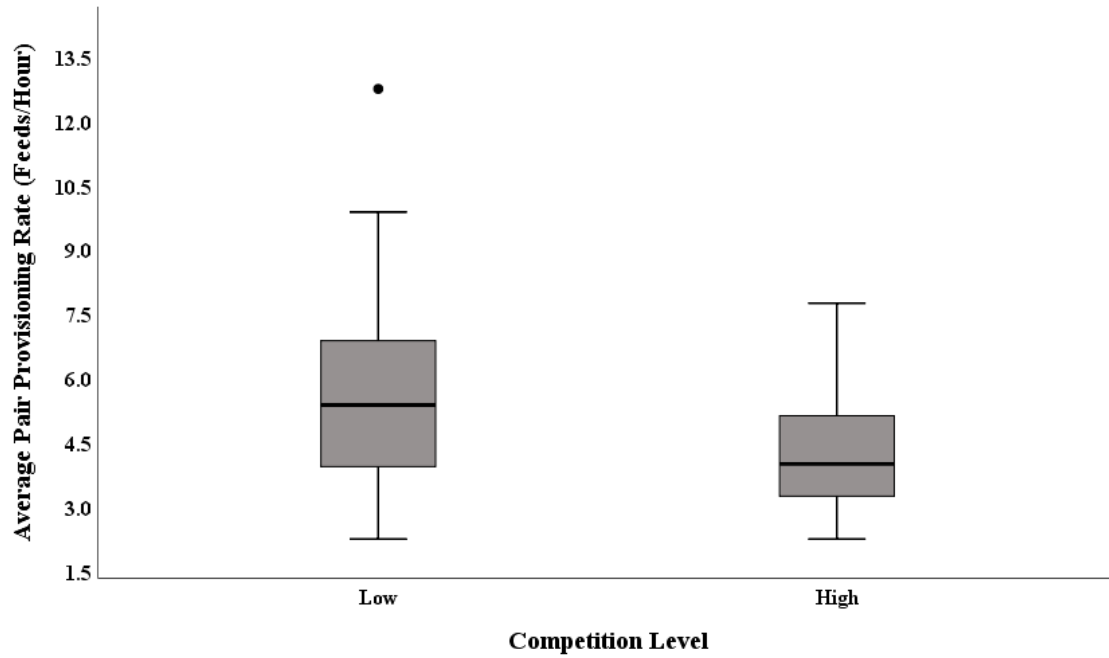


Figure 1. The effect of interspecific competition level with average pair provisioning (feeds/hour). There was a biologically relevant decrease in average pair provisioning ($t=1.921$, $df=43$, $p=0.061$).

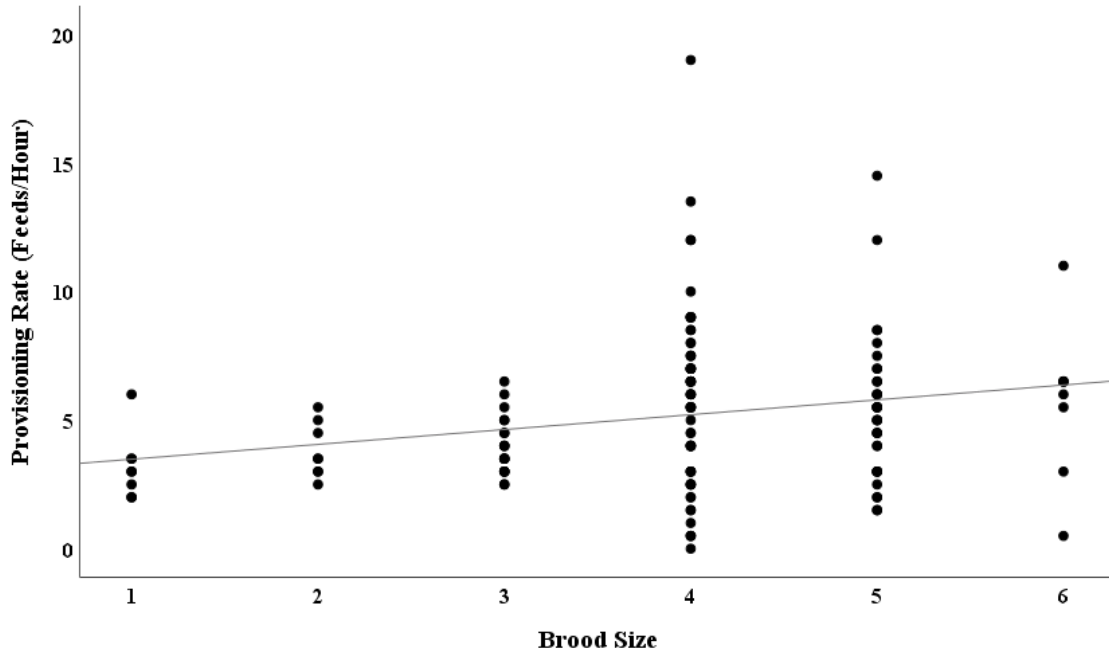


Figure 2. The effect of brood size on individual parent provisioning rate. Parents increase their provisioning efforts in response to larger broods (See Table 1).

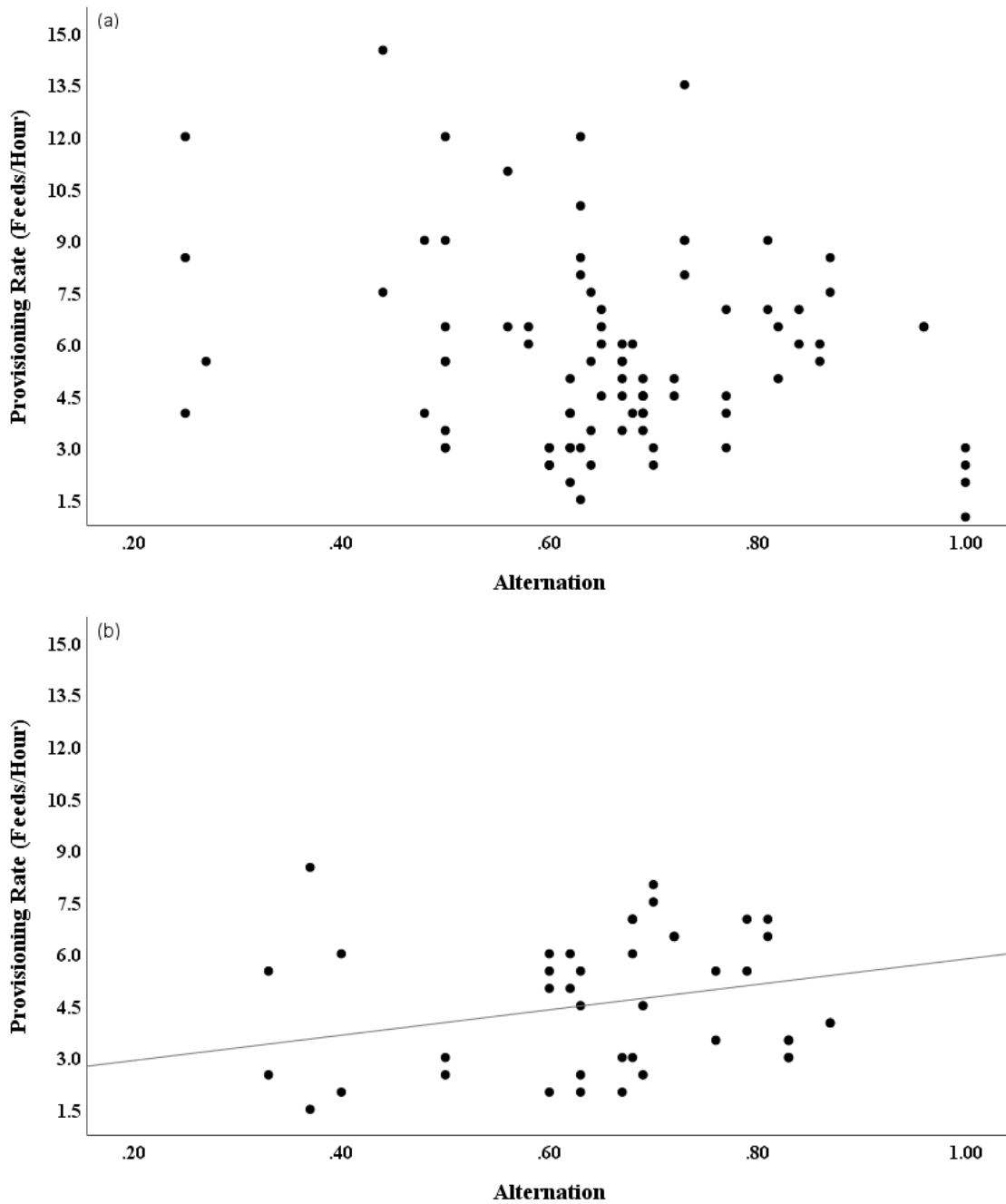


Figure 3. Relationship between individual provisioning rate (feeds/hour) and alternation, as affected by interspecific competition. There was no relationship between provisioning rate and alternation in areas of low competition (a), but there appears to be a relationship when pairs are pressured by high competition environments (b) (See Table 1).

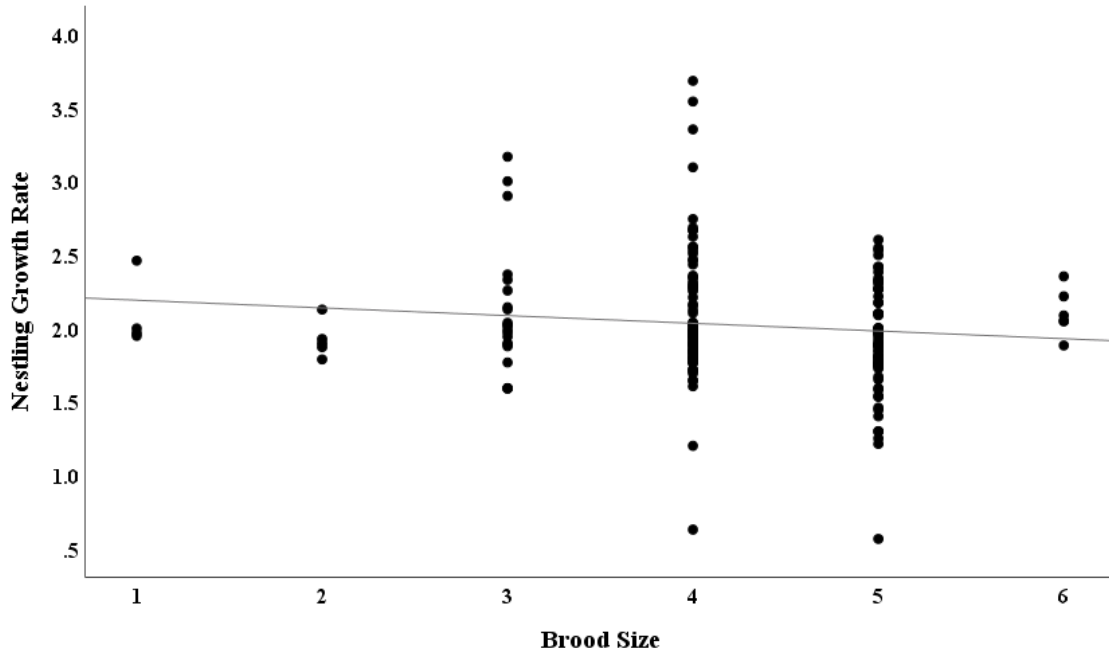


Figure 4. Effect of brood size on nestling growth rate. Growth rate significantly decreased in nestlings raised in larger broods (See Table 2).

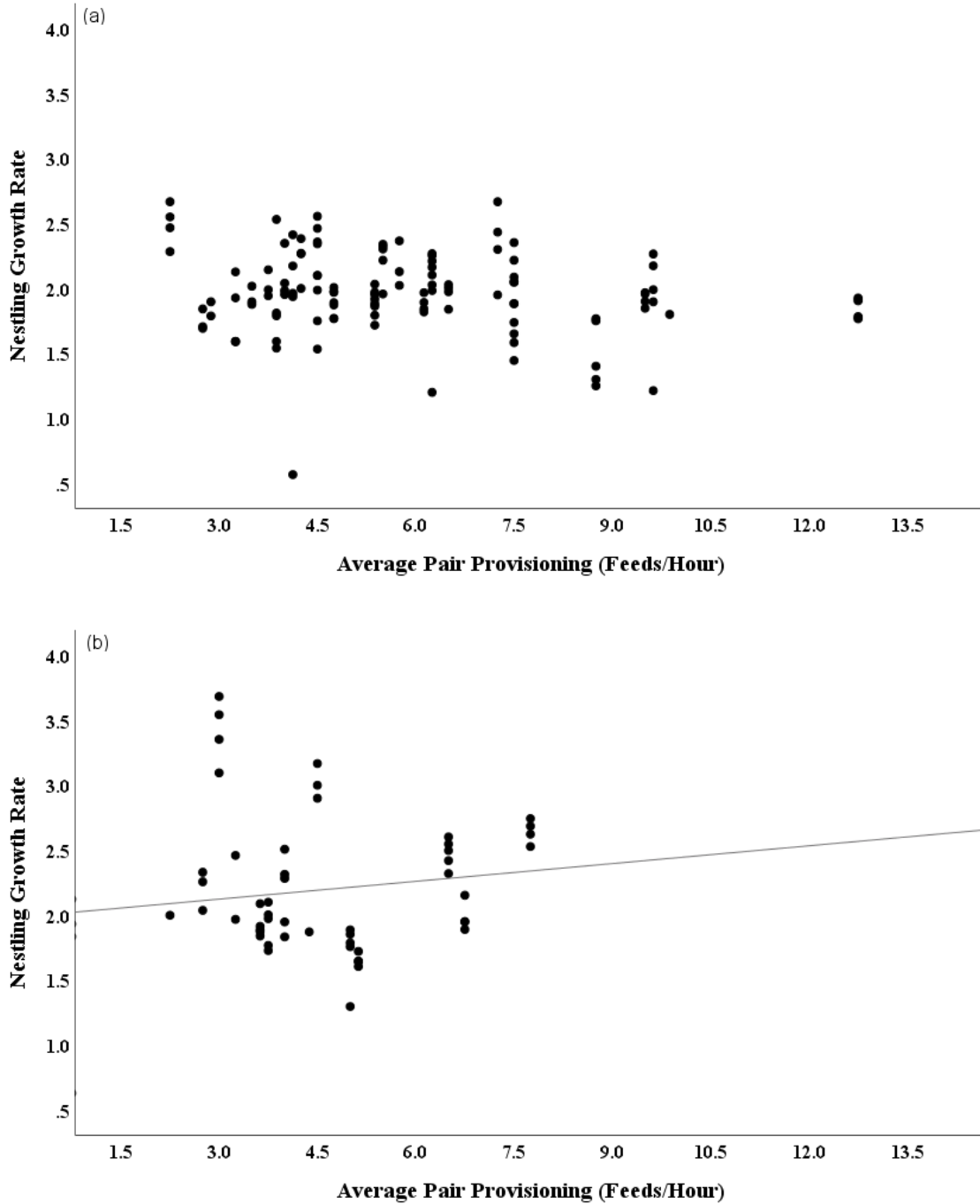


Figure 5. Effect of average provisioning rate of the pair (feeds/hour) on nestling growth rate.

There was no significant relationship found in low competition areas (a), but a significant positive relationship between average pair provisioning and nestling growth in high competition nests (b) (See Table 2).

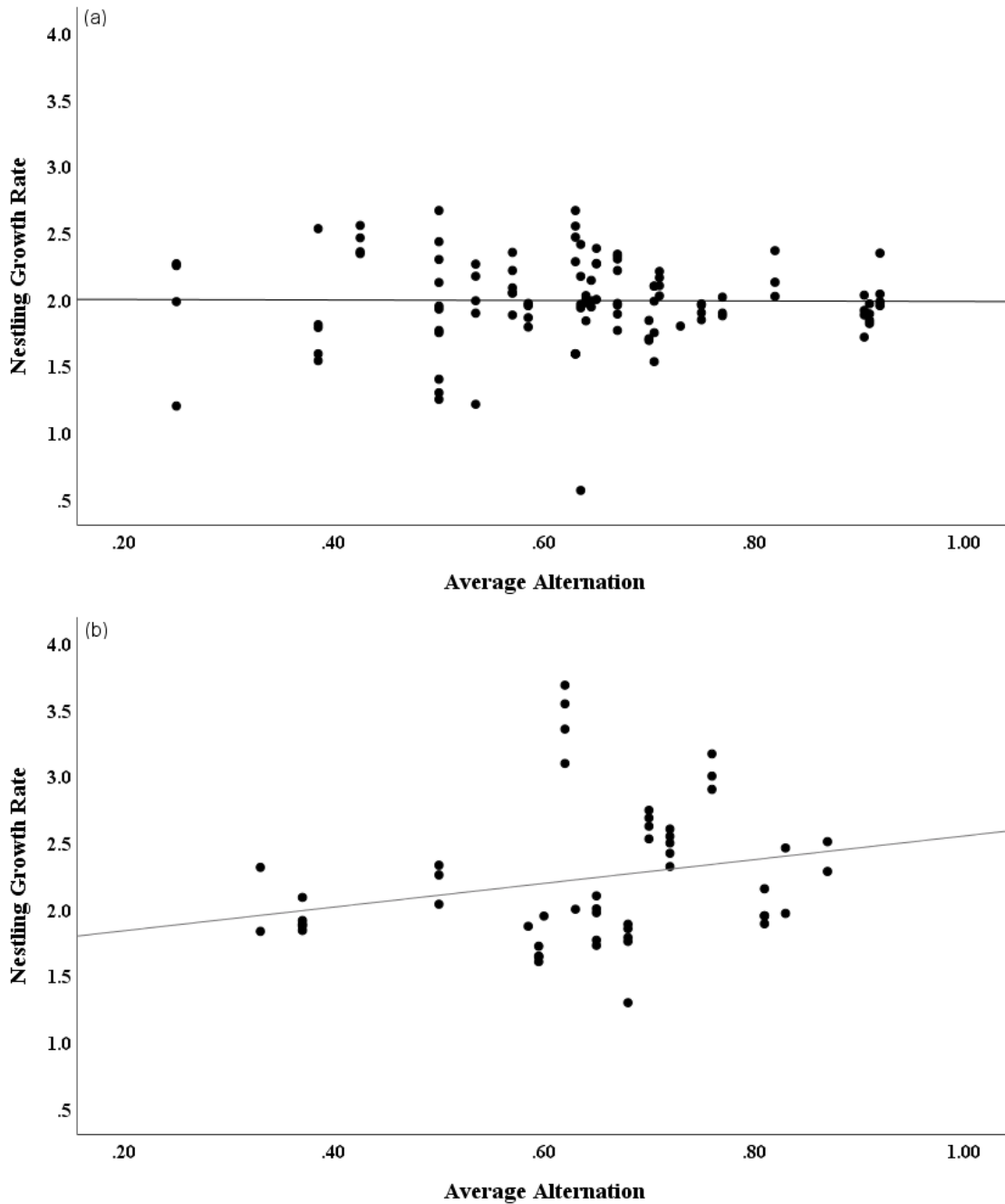


Figure 6. The effects of average alternation values of both provisioning observations on nestling growth rate. There was a significant positive relationship between alternation and nestling growth found in both low (a) and high (b) competition environments, though a slightly stronger effect of alternation can be seen in nestlings raised in high competition environments (See Table 2).

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