A TEST OF PARENTAL PREFERENCES FOR OFFSPRING SEX AND
ORNAMENTATION IN EASTERN BLUEBIRDS (*SIALIA SIALIS*)

A Thesis
by
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ABSTRACT

A TEST OF PARENTAL PREFERENCES FOR OFFSPRING SEX AND
ORNAMENTATION IN EASTERN BLUEBIRDS (*SIALIA SIALIS*). (May 2011)

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In addition to provisioning young, avian parents protect their fledglings from
potential predators. However, because parents have limited resources, they face trade-offs in
time and energy when simultaneously rearing multiple offspring. Thus parents may be
expected to favor particularly valuable offspring. Offspring characteristics like sex and
ornamentation influence their future reproductive value and thus may influence parental
favoritism. Because sons exhibit greater variability in reproductive potential than daughters,
parents in high-quality nest environments should preferentially defend sons. Eastern
Bluebirds (*Sialia sialis*) exhibit bright blue plumage and brighter individuals gain higher
reproductive success as adults, thus in this species, parents should favor the more-
ornamented sons. I tested parental favoritism for fledgling-aged offspring by simultaneously
threatening two offspring with mock predators and recording parental defense behaviors.
When given the choice of protecting sons versus daughters, fathers protected sons when
mated to high quality-mates, but protected daughters when prior parental investment was
high. When given the choice of protecting more versus less colorful sons, fathers favored
brighter over duller sons. Mothers did not discriminate between sons and daughters or
between brighter and duller sons. These differences in parental responses to offspring

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characteristics may occur because, in bluebirds, fathers assume the primary responsibility for

fledgling care and because plumage coloration in adults may mediate male-male interactions.

Further, these data suggest that ornamental plumage coloration in juvenile bluebirds

functions as an honest signal of offspring quality and serves to elicit greater parental care.

DEDICATION

I would like to dedicate this thesis to my family: My fiancé, Stephen Miller, my parents, Santiago and Debbie Barrios, and my brother, Jason Barrios.

ACKNOWLEDGEMENTS

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INTRODUCTION

A basic assumption of life-history theory is that organisms in pursuit of high

reproductive success have limited resources and face trade-offs in time and energy when

investing in multiple offspring (Williams 1966). Therefore, parents that rear multiple

offspring simultaneously may be expected to show favoritism (Trivers 1972). Within each

brood, variation in offspring morphology and behavior exists, thus parents can use nestling

characteristics to make strategic decisions about how to invest their resources in offspring.

When partitioning limited resources among the nestlings within a brood, parents have been

argued to preferentially invest in offspring following two strategies. First, parents may

preferentially invest in the offspring that are the neediest, thus equalizing the quality of their

offspring and giving each an equal chance at survival (Onnebrink & Curio 1991). For

example, female blue tits (*Cyanistes caeruleus*) preferentially feed their smallest nestlings,

even when all offspring in the brood are equally hungry (Dickens & Hartley 2007). Secondly,

evolutionary theory suggests that parents should preferentially invest in the highest-quality

offspring. By investing in the offspring that demonstrate the greatest likelihood of future

reproductive success, parents are expected to pass on the most genes to future generations

(Onnebrink & Curio 1991; Trivers 1972). For example, male green-backed tits (*Parus*

monticolus), but not females, preferentially feed their largest nestlings, even when all

offspring in the brood are equally hungry (Shiao et al. 2009). The second hypothesis has had

more support from the literature (Price & Ydenburg 1995; Krebs & Putland 2004; Dugas

2009; Shiao et al. 2009; Ligon & Hill 2010).

If parents use offspring characteristics to differentiate between offspring, and selection acts to encourage offspring to signal their need or quality to parents, parent-offspring conflict is expected (Trivers 1974). Nestlings use behavioral signals, such as begging, to elicit care from parents; nestlings that beg more frequently or more intensely often receive their parents' attention (yellow-headed blackbird, *Xanthocephalus xanthocephalus*: Price & Ydenburg 1995; tree swallows, *Tachycineta bicolor*: Leonard & Horn 1996). Begging behaviors, however, may not be entirely honest signals of nestling quality (Kilner & Johnstone 1997). Therefore, parents should benefit from making decisions about allocating limited resources by using honest and reliable indicators of offspring need or quality like sex, age, and morphology.

Because asynchrony in hatching time within broods is common in some species of birds, research on parental favoritism has focused on offspring age (Jeon 2008). In accordance with evolutionary theory, older offspring are more valuable because they have a higher chance of surviving to reproductive age than younger offspring (Redondo 1989). Additionally, signals of nestling condition may influence how parents invest their resources. Because they are more likely to survive to adulthood, larger offspring typically get fed more often than smaller offspring (yellow-headed blackbird: Price & Ydenburg 1995; green-backed tits: Shiao et al. 2009). Further, nestling ornamentation could also influence parental favoritism. For example, American coot (*Fulica americana*) parents often cannot successfully rear all the offspring in their broods. Coot parents preferentially feed nestlings with ornamental plumes over nestlings that have had their plumes dulled (Lyon et al. 1994). Subsequently, multiple studies have demonstrated nestling ornamentation to influence parental care decisions (Götmark & Ahlström 1997; Johnsen et al. 2003; Krebs & Putland

2004; de Ayala et al. 2007; Fargallo et al. 2007; Dugas 2009; Ligon & Hill 2010).

Parents should gain greater residual reproductive success, however, only if they are able to discriminate high- from low-quality offspring. Thus selection should act such that parents respond to honest signals of offspring quality. The condition dependence of ornamental traits in nestlings has rarely been studied. An observational study of barn swallows (*Hirundo rustica*), showed that nestlings with redder palates and brighter flanges had larger tarsi, greater body mass, and grew feathers faster than offspring with duller mouths (de Ayala et al. 2007). Experimentally manipulated natal environments reveal honest signaling of plumage coloration of nestling both blue tits (Jacot & Kempenaers 2007) and eastern bluebirds (*Sialia sialis*; Siefferman & Hill 2007). Thus, in these species, parents could use variation in plumage coloration to discern the quality of offspring and discriminate amongst them.

Predicting how offspring sex may influence parental favoritism is more complex. Because males can potentially inseminate many females while females can increase their reproductive success mainly by influencing offspring quality, differences in individual quality can have greater impacts on male than female reproductive success (Trivers & Willard 1973). Thus, high-quality sons should be more valuable than high-quality daughters. Likewise, average-quality or low-quality daughters should be more valuable than average-quality or low-quality sons. Moreover, because the quality of the natal territory often influences offspring quality (Hochachka & Smith 1991), habitat quality may influence the residual reproductive value of male versus female offspring. In high-quality nest environments, parents should preferentially invest in sons whereas, when the quality of nest environment is poor, parents should prefer daughters (Trivers & Willard 1973). In addition to

habitat quality, the quality of the nest site can be influenced by the quality of the parents. Thus one parent may perceive the nest site as higher quality when paired with a high-quality mate and thus may invest more in their offspring (Burley 1977).

Although there have been relatively few studies to test parental favoritism towards males versus daughters (Mock & Forbes 1995), more commonly researchers have demonstrated that mothers manipulate the sex ratio of broods in response to her perception of the nest environment. For example, when territory quality is experimentally increased, female bluebirds produce male-biased broods (Ligon et al. *in press*). Moreover, blue tit mothers that are paired with highly-ornamented mates tend to produce male bias broods (Sheldon, et al. 1999; Delhey et al. 2007).However, to my knowledge, no study has demonstrated an effect of nest environment on parental favoritism for offspring sex.

Mothers and fathers, however, may not be equally likely to discriminate amongst offspring. In species that exhibit bi-parental care of offspring, parental role specialization can occur (Wesolowski 1994). Female birds typically invest more heavily in producing eggs and incubating young while male birds typically invest more energy in defending the territory or nest from competitors and predators (Wesolowski 1994). Moreover in species that produce multiple broods during the breeding season, males are more frequently responsible for the care of fledglings while females prepare to lay the second clutch (Verhulst & Hut 1996). Thus, as male and female parents may experience different demands on their time and energy, the sexes may make different decisions when favoring young or may vary in how responsive they are to offspring signals (Markman et al. 1995; Verhulst & Hut 1996; Schuster & Sealy 1997; Wheelwright et al. 2003). For example, male meadow pipits (*Anthus pratensis*) increase the intensity of mobbing towards mock predators as the age of their

offspring increase while females defend the nest with a consistent intensity as nestlings age (Pavel & Bures 2001). Moreover, male eastern bluebirds provision the brightest offspring more often, while the conditions under which mothers discriminate amongst offspring is much more subtle and complex (Ligon and Hill 2010).

Objectives

My study had two primary goals. First, I investigated whether eastern bluebird parents exhibit favoritism when defending their fledgling-aged offspring from potential predators. I designed experiments such that parents could only defend one of two offspring at a time, and parents were given 1) offspring of different sexes, and 2) male offspring that differed in plumage coloration. Brighter male fledglings tend to be in better body condition than duller fledglings, and therefore have the potential to provide the parents with greater reproductive fitness. Thus, I predicted that parents should favor brighter sons. When discriminating between offspring of opposite sex, however, I predicted that favoritism should be influenced by the parents' perception of the nest environment. In higher-quality nest environments parents should favor sons to daughters and the opposite in low-quality nest environments. Secondly, I tested whether the male and female parents exhibited favoritism independently from one another. Because males provide most of the care to fledgling-aged young, I predicted that males would be more likely to discriminate amongst fledglings based on plumage coloration or sex.

METHODS

Study Species

Eastern bluebirds are socially monogamous passerines that nest in open grasslands or mixed grassland-woodlands. They are insectivorous obligate cavity nesters that readily breed in nestboxes (Gowaty & Plissner 1998). In the mountains of North Carolina, their reproductive season lasts from April to early August, and parents can produce one or two successful broods (~4 nestlings per brood) per season (Gowaty & Plissner 1998).

Eastern bluebird males share the responsibility of nest defense and provisioning offspring with their mates (Pinkowski 1978). Although females can achieve some reproductive success without the aid of a mate, when males are present their reproductive success is higher (Gowaty 1983). Thus, males and females demonstrate differences in the allocation of their resources. Females spend more energy on their offspring in the form of egg-laying, incubation, and nestling care (Pinkowski 1977). As female eastern bluebirds prepare for and initiate a second brood, post-fledgling care of the first brood falls on the male (Gowaty & Plissner 1998), thus males allocate more resources to the fledglings. In addition to bi-parental feeding of young, eastern bluebirds actively defend their territories from conspecifics and defend offspring from potential predators. Male and female eastern bluebirds engage in aggressive behaviors with same-sex conspecifics but males exhibit more aggressive behaviors than females (Gowaty & Wagner 1988). Further, bluebirds exhibit a range of behaviors when defending their young, from retreating from a potential nest predator to diving at and attacking the threat (Gowaty & Plissner 1998).

Eastern bluebirds exhibit sexually dichromatic structural plumage coloration as both adults and juveniles. Males are bright blue on their heads, rumps, tails, and wings, and also have a rusty color on their breasts. Females follow the same color patterns as males, but are duller overall. In both males and females, plumage coloration is correlated to mate quality, brighter more UV chromatic males and females feed offspring more often and achieve higher reproductive success (Siefferman and Hill 2003, Siefferman and Hill 2005a). Like other obligate cavity nesters, bluebirds compete with conspecifics when nest sites are limited (Gowaty & Plissner 1998). Male coloration also likely signals resource holding potential as brighter males are more likely to obtain high-quality nest sites compared to duller males (Siefferman & Hill 2005b).

By the age of 13 days post hatch, juveniles display blue coloration on their wings and tails. First-year bluebirds only undergo a partial molt during their first fall, thus second-year birds display the wing and tail coloration that they acquired as nestlings (Gowaty & Plissner 1998; Siefferman & Hill 2007). Because fledglings are dichromatic, parents should be able to recognize the sex of offspring. Moreover, in this species, the blue coloration is condition-dependent in both adults (Siefferman & Hill 2005a) and nestlings (Siefferman & Hill 2007), suggesting that parents can predict nestling condition by assessing plumage coloration. Indeed, a recent study indicates that parents feed brighter male offspring more often than duller male offspring (Ligon & Hill 2010).

Study Sites, Nest Monitoring, Measurements, and Identification

From April to August 2010, I studied a population of breeding eastern bluebirds in rural Watauga County, NC (latitude 36.3, longitude 81.676). I monitored 180 nestboxes and identified those that were obtained as territories by eastern bluebirds. I then continued to

observe the nestboxes for the presence of completed nests, eggs, and nestlings.

Once the offspring started to hatch (first nestling hatches = day 1), each nestling was uniquely identified with colored markers (Sharpie™ marker) so they could be distinguished from siblings. I returned to the nests every three days to measure nestling body mass and the length of tarsi and wings on days 2, 5, 8, 11, and 14 post-hatching. When the nestlings were eight days old, I placed a United State Fish & Wildlife Service (USFWS) aluminum band on the nestlings for further identification. Once the nestlings had reached fledging age (approximately 15-18 days post hatch), I collected the left and right fifth primary feathers from each nestling to be used for spectrophotometric analysis in the lab. Additionally, during my visits, I captured and banded the parents of each brood with both color bands and USFWS bands. To assess parental ornamentation, I collected eight feathers from the rump of each adult for spectrophotometric analysis.

Habitat Quality Survey

I assessed the availability of suitable prey (i.e., insects) by sweep net sampling a 200 m transect at each nestbox occupied by eastern bluebirds. Sweep net sampling was done once during the study at each nestbox from June 8th to July 29th regardless of the time when nestlings and parents occupied the territory. The samples were then frozen and stored in the laboratory until they could be processed.

Once processing began, I separated arthropods from plant and soil debris manually and categorized them by taxonomic categories of order if they were insecta, by class arachnida if they belonged to orders opiliones (Harvestmen) or araneae (Spiders), and by order isopoda (Wood lice). Opiliones were then included with araneae due to a limited number of harvestmen that I collected in samples. I discarded any insects that were smaller

than approximately 2.5 mm from the samples because of the minute size; however, I included all size classes of arachnids and crustaceans in the samples. Following categorization and count of the arthropods, samples were dehydrated in a drying rack for 24 hours and mass was measured. I only included arthropod taxa that were determined to be crucial to nestling diet (Pinkowski 1978) in the tally of total arthropod abundance at territory for data analysis. These included insect orders orthoptera, lepidoptera, and the chelicerate class of arachnida. However, all arthropod taxa in the sample were included in the calculation of dry mass.

I collected Global Positioning System (GPS) coordinates for each nestbox on the field site. I used this information along with remote sensing technology from the NASA Landsat program to create maps designed to obtain Normalized Difference Vegetation Index (NDVI) readings of the study site at 30 m resolution. In grassland areas similar to the eastern bluebird habitat, NDVI correlates significantly positively with annual Net Primary Production (ANPP), such that areas of higher NDVI have higher ANPP (Paruelo et al. 1997). The NDVI is calculated by the reflectance of red and near infrared light off of the vegetation in the area being measured. For each eastern bluebird territory, the NDVI was determined using the average of five randomly selected points around the nestbox during the nestling period.

As a third measure of habitat quality, I examined parental provisioning rates at each territory. Birds in low-quality habitats must travel farther for food resources because they exhaust the resources close to their nestboxes quickly (Ligon, Siefferman & Hill, in press). Consequentially, they tend to feed offspring less often in a 2 hr period due to increased travel time (Tremblay et al. 2005). I set up video cameras outside each nestbox when the nestlings were eight days (± 1 day) old. I recorded the activity at the nestboxes for approximately 2 hrs. I then played back each video and recorded the time, duration, and type of activity of

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each parent. As it was often impossible to distinguish the sex of the parent from the videos,

parental provisioning rate was not quantified separately for each parent. I calculated parental

provisioning rate as the number of feeds divided by the total number of minutes that were

scored and then divided by the number of nestlings in each brood.

Field Experiment

For each pair of breeding bluebirds, I conducted two experiments of parental

favoritism on two consecutive days. On the first day, the trial tested parental preferences for

male versus female offspring. On the second day, the trial tested parental preferences for

duller versus brighter male offspring. I commenced the first trial when offspring were near

fledging age (between age 14 and 18 days); when primary wing feathers had emerged >2cm

from the feather sheath. In each trial, my goal was to mimic how offspring of fledgling age

might be dispersed in the natal territory. At this stage, fledglings can only fly short distances

(<2m), move primarily by hopping, cannot forage on their own, and are still under the care of

their parents (Gowaty & Plissner 1998).

For each trial, I set up two wire cages (71 cm x 46 cm x 11.5 cm) each at opposite

ends of a 5 m transect, equal distant from the nestbox. Adjacent to each cage, I erected a 50

cm perch for the parents. Above each cage, I hung a replica of an American crow (*Corvus

brachyrhynchos*) (©This Place is a Zoo, Snohomish, WA) as a "threat" to the offspring to

invoke parental defense behavior. I played an audio recording of the crow calls and the cries

of eastern bluebird nestlings. I used a video camera placed 10 m from each trial to record

parental behavior. Additionally, I watched each trial from a distance of 40 m and, using

binoculars and a voice recorder. I quantified the behavior of both parents separately (Fig. 1).

Following each trial, I returned all the nestlings to their nests.

For the first trial (N = 47), I chose two offspring of opposite sex but of similar size and randomly assigned them to a cage. I recorded the USFWS band number of each nestling and in which cage it was placed. In the second trial (N = 28), I chose two males and randomly assigned one male the dulled and one to the brightened treatment. Wing feathers were dulled using a black Sharpie™ marker and brightened using a violet mist Prismacolor™ marker. In both trials, if a nest did not have appropriate nestlings, I moved nestlings from another nest of similar age (± 1 day). During both experiments, the nestlings were chosen such that they were most similar in mass, tarsus length, and wing length to reduce the likelihood that other morphological characteristics would influence parental favoritism.

Using both digital videos and voice recordings, I quantified the behavior of the male and female parents separately. Each parent was given a numerical score of the most intense behavior it exhibited in defense of each nestling, such that more aggressive behaviors were scored higher than less aggressive ones: (1) absent, (2) present but ignoring trial, (3) watching silent, (4) chattering, (5) diving 1-2 times, (6) diving 3-5 times, (7) physically striking the predator, (8) diving > 5 times, (9) physically striking the predator > 1 time. Any trial in which the parent's score for both nestlings was the same was excluded. I also determined the percentage of time each parent spent on the side of each nestling by calculating the number of seconds spent with each nestling divided by the total number of seconds spent with any nestling multiplied by 100. If a parent spent >55% of the time near one offspring, I scored that nestling as the favorite. Any trial for which a nestling did not receive > 55% of the parental attention was excluded. Male and female parents were evaluated separately.

Plumage Coloration Analysis

I measured plumage coloration of the wing feathers of each male nestling used in the trials and of the rump coloration of all parents using an Ocean Optics S2000™ spectrometer (range 250-880 nm; Dunedin, FL) with a micron fiber-optic probe to record spectral data at a 90° angle to the feather surface. From these spectral curves, I determined brightness, UV chroma, and hue. Mean brightness was calculated as the average of the total reflectance from 300 to 700 nm. UV color was calculated as the average of the proportion of the total reflectance that is within the UV range ($\int$ 300-400 nm / $\int$ 300-700 nm). Hue was calculated as the wavelength with the highest reflectance. I only quantified brightness and UV chroma for nestlings because the reflectance curves are relatively flat making hue measures inaccurate. The wing feathers of the male offspring were collected prior to the color manipulation in the field. Thus, I measured both the original plumage coloration and manipulated plumage coloration.

Statistical Analysis

In all of the analyses, I only used first brood nests so that each parent would not be counted more than once. I used Wilcoxon signed rank tests to verify that nestlings that had been experimentally manipulated differed in plumage coloration (brightness and UV chroma). I used Chi-square tests to determine if parents more aggressively defended one sex of offspring over the other and if they more aggressively defended brighter or duller male offspring. I also used Chi-square tests to determine whether parents spent more time with male versus female offspring and to determine whether parents preferred brighter versus duller sons. I tested favoritism of mother and fathers separately. Because I expected that the nest environment would influence parental preferences for offspring sex, I used backward

stepwise logistic regressions to determine if habitat (insect abundance, insect mass, NDVI, and provisioning rates) or mate coloration (brightness, UV chroma, and hue) influenced parental favoritism. I used separate logistic models for male and female parents and for habitat quality and mate coloration. Next, to test whether parents exhibited preferences based on offspring size, I used Chi-square tests to determine whether parents preferred the heavier or lighter offspring. Sample sizes vary because some trials ended in a tie, some parents did not respond to the experiment, and I failed to collected habitat for all territories or I failed to collected plumage coloration data for all parents. Finally, I used Pearson's correlations to test whether the strength of parental preferences correlated to the differences between offspring characteristics.

RESULTS

Parental Favoritism for Male versus Female Offspring

Without considering the nest environment, eastern bluebird parents showed no significant favoritism for offspring sex by either defense behavior intensity or time. There were 34 trials of offspring sex conducted. For analysis of females, three were excluded due to the parent not responding to the trial. Using time as the proxy for favoritism, nine trials of female preferences were excluded because they ended in a tie. In 50% of the trials, females spent the majority of their time defending male offspring, and in 50% of the trials, they spent the majority of their time defending female offspring ($\chi^2_{1,21} < 0.01$, P = 1.00). Using intensity of defense behavior as the proxy of favoritism, 16 of the female trials were excluded from analyses because they ended in a tie. In 67% of the trials, females more intensely defended male offspring, while in 33% of the trials, they more intensely defended female offspring ($\chi^2_{1,14} = 1.67$, P = 0.20).

For analysis of males, four trials were excluded due to the parent not responding to the trial. Using time as the proxy for favoritism, nine trials were excluded because they ended in a tie. In 62% of the trials, males spent the majority of their time defending male offspring, and in 38% of the trials, they spent the majority of their time defending female offspring ($\chi^2_{1,20} = 1.19$, P = 0.28). Using intensity of defense behavior as the proxy of favoritism, 23 trials were excluded because they resulted in a tie. In 67% of the trials, males more intensely defended male offspring, while in 33% of the trials, male more intensely defended female offspring ($\chi^2_{1,8} = 1.00$, P = 0.32).

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However, Chi-square analysis demonstrated that bluebird pairs were significantly likely to spend the majority of their defense time with the same offspring when both parents were present. In 70% of the trials, the parents preferred the same offspring, whereas they preferred opposite offspring in only 30% of trials ($\chi^2_{1,26} = 4.48$, P = 0.03). The analysis only included the 27 trials in which both parents were present, and neither parent's behavior resulted in a tie. In contrast, using defense behavior intensity, parents were not significantly likely to prefer the same offspring. In 67% of the trials, the parents preferred the same offspring, whereas they preferred opposite offspring in 33% of the trials ($\chi^2_{1,5} = 0.67$, P = 0.41). This analysis had limited power, however, as I only included the six trials in which both parents were present, and neither parent's behavior resulted in a tie.

Pearson's correlations showed no significant positive relationships between habitat variables and mate coloration variables (Table 1). Using time spent with each nestling as the proxy for favoritism, two female trials were excluded because of lack of habitat quality variables, and five were excluded due to the absence of mate coloration variables. Backward stepwise logistic regression revealed that habitat quality (insect abundance, insect mass, NDVI, and provisioning) did not influence female favoritism for offspring sex (Best Model: $\chi^2_{1,19} = 1.09$, $R^2 = 0.05$, P = 0.30) and that their preference was not influenced by their mate's coloration (Time: Best Model: $\chi^2_{1,16} = 0.45$, $R^2 = 0.00$, P = 0.50).

Using intensity of defense behavior as the proxy of favoritism, of the 15 trials in which females more aggressively defended one nestling sex over the other, three were excluded due to the absence of habitat quality variables, and six were excluded due to the absence of mate coloration variables. Backward stepwise logistic regression revealed that habitat quality (insect abundance, insect mass, NDVI, and provisioning) did not influence

female favoritism for offspring sex (Best Model: $\chi^2_{4,11} = 4.08$, $R^2 = 0.02$, $P = 0.40$). I was unable to generate a regression model for the effect of mate coloration on female preferences for offspring sex. Again, these analyses had limited power due to small sample sizes.

For males, using time spent with each nestling as the proxy for favoritism, of the 21 trials in which males they spent more than 55% of the time with one nestling, one was excluded due to the absence of habitat quality variables, and two were excluded due to the absence of mate coloration variables. Males, however, were more likely to spend a majority of their time defending female offspring when provisioning rates were high (Model: $\chi^2_{1,19} = 4.27$, $R^2 = 0.19$, $P = 0.04$; Feeding Rate Per Chick: Beta = 44.00, Wald = 3.23; Fig. 2a), and were more likely to favor male offspring when mated to highly-ornamented females (Model: $\chi^2_{1,18} = 7.26$, $R^2 = 0.32$, $P = 0.03$; Mate Rump Brightness: Beta = -29.24, Wald = 1.11; Mate Rump Hue: Beta = 0.16, Wald = 3.69; Fig. 2b).

Using intensity of defense behavior as the proxy of favoritism, of the nine trials in which males more aggressively defended one nestling sex over the other, two were excluded due to the absence of habitat quality variables. Habitat quality appeared not to influence males' preferences for offspring sex (Best Model: unable to generate model). Males were significantly more likely to favor sons over daughters when mated to females displaying low UV chroma and low hue, however, the models suggest the likelihood was very low (Best Model: $\chi^2_{2,8} = 11.46$, $R^2 = 0.72$, $P < 0.01$; Mate Rump Hue: Beta = -7666.40, Wald < 0.01; Mate Rump Hue: Beta = -9.05, Wald < 0.01). These analyses had small sample sizes and low statistical power.

After manipulation, experimentally brightened males were significantly brighter than their experimentally dulled brothers (Z_{21} = -4.11, P < 0.01; Fig 3), thus the manipulation succeeded in altering offspring plumage coloration. Nestling UV chroma, however, did not differ significantly between experimentally brightened and dulled brothers (Z_{21} = -1.19, P = 0.24).

I conducted 22 trials in which parents were given the option of defending experimentally brightened versus dulled offspring. For analysis of females, two were excluded due to the parent not responding to the trial. Using time spent with each nestling as the proxy for favoritism, four trials were excluded because they ended in a tie. Female eastern bluebirds did not favor brighter or duller male offspring. Females preferentially defended brightened offspring in 56% of the trials and dulled offspring in 44% of the trials ($\chi^2_{1,15}$ = 0.25, P = 0.62). Using intensity of defense behavior as the proxy of favoritism, 14 trials were excluded from analysis because they ended in a tie. Again, female eastern bluebirds did not favor brightened or dulled male offspring, however, this analysis had low statistical power. In 33% of the trials, females defended brightened male offspring more intensely, while in 67% of the trials, they defended dulled male offspring more intensely ($\chi^2_{1,5}$ = 0.67, P = 0.41).

For analysis of males, two trials were excluded due to the parent not responding. Using time spent with each nestling as the proxy for favoritism, six trials were excluded because the ended in a tie. Male eastern bluebirds significantly preferentially defended brightened offspring in 79% of the trials and males defended dulled offspring in 21% of the trials (Fig. 4). Using intensity of defense behavior as the proxy of favoritism, 14 trials were

excluded because they ended in a tie, thus this analysis had low statistical power. The coloration of sons did not influence favoritism by male parents; in 50% of the trials, males more intensely defended brightened offspring, and in 50% of the trials, males more intensely defended dulled offspring ($\chi^2_{1,5} < 0.01$, P = 1.00).

However, Chi-square analysis demonstrated that bluebird pairs were not significantly likely to spend the majority of their defense time with the same offspring when both parents were present ($\chi^2_{1,9} = 1.60$, P = 0.21); in 70% of pairs preferred the same offspring while 30% chose different offspring. The analysis only included the 10 trials in which both parents were present, and neither parent's behavior resulted in a tie. Similarly, using defense behavior intensity, parents were not significantly likely to prefer the same offspring. In 67% of the trials, the parents preferred the same offspring, whereas they preferred opposite offspring in 33% of the trials ($\chi^2_{1,2} = 0.33$, P = 0.56). The analysis had low statistical power; only included the three trials in which both parents were present, and neither parent's behavior resulted in a tie.

Using time spent with each nestling as the proxy for favoritism, Pearson's correlations determined that the strength of the parents' favoritism was not influenced by the difference in the plumage brightness of the experimentally brighter and duller male offspring (Female: N = 22, r = -0.07, P = 0.77; Male: N = 22, r = 0.30, P = 0.18).

Parental Favoritism for Nestling Size

Whether favoritism was measured as time spent with offspring or level of parental aggression, in the trials involving female versus male offspring, female adult eastern bluebirds did not prefer heavier or lighter offspring. Using time spent with each nestling as the proxy for favoritism, of the 22 trials that did not end in a tie, six were excluded due to an

absence of nestling mass. Females preferentially defended heavier offspring in 44% of the trials and lighter offspring in 56% of the trials ($\chi^2_{1,15} = 0.25$, P = 0.62). Using intensity of defense behavior as the proxy of favoritism, 15 trials did not end in a tie, however, three were excluded due to an absence of nestling mass. Females more aggressively defended heavier offspring in 58% of the trials and lighter offspring in 42% of the trials ($\chi^2_{1,11} = 0.33$, P = 0.56).

Whether favoritism was measured as time spent with offspring or level of parental aggression, in the trials involving female versus male offspring, male adult eastern bluebirds did not prefer heavier or lighter offspring. Using time spent with each nestling as the proxy for favoritism, of the 21 trials that did not end in a tie, three were excluded due to an absence of nestling mass. Males preferentially defended heavier offspring in 41% of the trials and lighter offspring in 59% of the trials ($\chi^2_{1,17} = 0.53$, P = 0.47). Using intensity of defense behavior as the proxy of favoritism, of the nine trials that did not end in a tie, two were excluded due to an absence of nestling mass. Males more aggressively defended heavier offspring in 14% of the remaining trials and lighter offspring in 86% of the remaining trials ($\chi^2_{1,6} = 3.57$, P = 0.06), however, this analysis suffered from low statistical power.

In tests of parental favoritism for male versus female offspring, Pearson's correlations revealed that the strength of the parental preferences was not correlated with the magnitude of the difference in offspring mass (Female: N = 28, r = 0.20, P = 0.31; Male: N = 28, r < -0.01, P = 0.99). Of these 34 trials, 6 were excluded due to the absence of nestling sex.

In tests of parental favoritism for brightened versus dulled male offspring, female parents did not show preferences based on offspring mass. Using time as a proxy for favoritism, of the 16 female trials that did not end in a tie, one was excluded due to the

absence of nestling mass. Females preferentially defended heavier offspring in 53% of trials and lighter offspring in 47% of trials ($\chi^2_{1,14} = 0.067$, P = 0.796). Using behavioral intensity as the proxy for favoritism, six trials did not end in a tie. Females more aggressively defended heavier offspring in 33% of trials and lighter offspring in 67% of trials ($\chi^2_{1,5} = 0.67$, P = 0.41), however, this analysis suffered from low statistical power.

In tests of parental favoritism for brightened versus dulled male offspring, male parents did not show preferences based on offspring mass. Using time as a proxy for favoritism, 14 trials did not end in a tie. Males preferentially defended heavier offspring in 57% of trials and lighter offspring in 43% of trials ($\chi^2_{1,13} = 0.29$, P = 0.60). Using behavioral intensity as the proxy for favoritism, six trials did not end in a tie. Males more aggressively defended heavier offspring in 33% of trials and lighter offspring in 67% of trials ($\chi^2_{1,5} = 0.67$, P = 0.41), however, this analysis suffered from low statistical power.

Of the 22 trials in which parents were to choose between brighter versus duller male offspring, one trial was excluded due to the absence of nestling mass. Pearson's correlations revealed no significant correlation between the strength of the parents' preference and the difference in the mass of the two offspring in the trial (Female: N = 21, r = -0.07, P = 0.77; Male: N = 21, r = 0.29, P = 0.21).

DISCUSSION

I found that male, but not female, eastern bluebirds exhibited parental favoritism when defending fledgling-aged offspring from a potential predator. Parents invest energy in their offspring in an effort to reach one goal: high reproductive success. Parents should perceive higher-quality offspring as more reproductively valuable (Trivers 1972). In accordance with idea that brighter sons are higher-quality offspring, I found that fathers were significantly more likely to act protectively toward brighter sons. Because the plumage coloration of offspring was experimentally manipulated, I am confident that fathers used feather coloration to discriminate between sons. Male eastern bluebirds also showed preferences for offspring sex that appeared to be influenced by habitat quality and parental provisioning rates. Consistent with the concept that highly-ornamented mates are high-quality mates, males mated to highly-ornamented females preferentially defended their male offspring. In pairs that displayed high parental provisioning rates toward eight-day old nestlings, males preferentially defended daughters over sons. This result was contrary to the expectation that parents in high-quality territories would significantly prefer sons to daughters. Aside from male eastern bluebirds being significantly more likely to display higher intensity defense behaviors towards their sons when their mates were highly ornamented, all other favoritism was displayed by a majority of time spent with one offspring over the other.

I used two proxies of favoritism: 1) the offspring for which each parent spend more time with (>55% of the time) and 2) the offspring toward which the parent showed a higher

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level of defensive aggression. Not surprisingly, I only found evidence of favoritism using

time spent with each offspring, but not with the intensity of the aggressive defense behaviors

that the parents. Sample sizes were very small when I used the intensity of aggression as a

proxy for favoritism which caused low statistical power. The number of trials that ended in a

tie was high because parents appeared to reach a peak level of aggression and remain at that

level when moving back and forth between the two offspring. It is likely that once a parent

had attained a level of excitement, it remained at that level for the 10 min trial period and

toward both model crows. In birds, aggression is correlated to the amount of circulating

hormones; higher levels of testosterone cause to higher levels of aggressive behavior

(Schlinger & Callard 1990). Once the hormone levels have elevated, they cannot be rapidly

changed (Schlinger & Callard 1990). It is likely that the aggressive defense behaviors

displayed by adult bluebirds during our experiments were hormone mediated.

Although protecting offspring from potential predators during the fledging stage is a

common avian behavior, to my knowledge this is the first study to test parental response to

variation in nestling plumage coloration within sons or test whether parents preferentially

defend sons versus daughters. To date, studies of how nestling characteristics can influence

parental provisioning are more common but most focus on the importance of mouth

coloration in signaling quality or need (i.e. de Ayala et al. 2007, Ewen et. al 2008). As

plumage ornamentation in juvenile birds is relatively rare, few studies have focused on how

variation in plumage coloration can signal offspring quality. Nestling blue tits that had the

yellow nape coloration experimentally dulled grew more slowly than control nestlings

suggesting that parents fed dulled nestlings less often (Galvan et al. 2008). Similarly, nestling

blue tits that had their chest and cheek feathers UV-blocked using lotion, were fed less often

by their female parents (Tanner & Richner 2008). Parental provisioning in eastern bluebirds is also influenced by a manipulation of nestling coloration (Ligon & Hill 2010).

My goal was to simulate conditions that parents experience just after their offspring have left the nest, thus I conducted the experiment when nestlings were within days of fledging. In the trials, the offspring were separated by 5m because, just after fledging, they are unable to fly well, are dispersed in the parents' territory, and beg to their parents for food (Gowaty & Plissner 1998). Bluebirds, like many passerine species, exhibit bi-parental care; both males and females share in the responsibility of investing resources in the offspring. However, because bluebirds produce more than one brood during the breeding season; as the female prepares to produce the next brood, males assume primary care of the fledglings (Gowaty 1983). Therefore, males invest more time and energy in offspring protective behaviors during the fledgling stage. This division of labor may explain why I found that male, but not female, parents exhibited favoritism towards particular offspring. However, it is possible that fathers are simply more inclined to play favorites amongst their offspring because males are more likely to cue in on differences in plumage coloration. Past research with adult bluebirds has shown that, although male coloration is indicative of male quality (Siefferman & Hill 2003, Mercandante 2010) females do not chose mates based on plumage coloration (Liu et al. 2007). Males, however, likely use plumage coloration to assess male quality and to make decisions about whether to challenge another male for a territory (Siefferman & Hill 2005c; Mercandante 2010).

I found that fathers preferentially protected brighter sons over duller sons. In this species, feather brightness is an honest indicator of nestling condition. Nestling bluebirds reared in crowded conditions are fed less often and grow duller blue plumage than nestlings

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reared in smaller broods (Siefferman & Hill 2007). Thus, my results are in accordance with the prediction that parents should perceive the more-ornamented fledglings as having greater reproductive potential than their duller brothers. While eastern bluebirds are socially monogamous (Gowaty & Plissner 1998), extra-pair paternity occurs (Gowaty & Karlin 1984). Thus high-quality males could father offspring in the nests of many neighboring females thus experience very high reproductive success. Indeed in the sister species, mountain bluebirds (*Sialia currucoides*), more colorful males sire more offspring both in their mate's brood and sire more offspring with extra-pair mates (Balenger et al. 2009).

When mated to highly-ornamented females, fathers exhibited favoritism towards sons. Male bluebirds should perceive highly-ornamented females as better mates; those females provision offspring more often, produce larger fledglings, and experience higher reproductive success (Siefferman & Hill 2005a). Moreover, a quantitative genetic study found that the blue coloration of eastern bluebirds is a heritable trait (Siefferman, unpublished data), thus a more-ornamented mother should produce more-ornamented sons. According to the "sexy son" hypothesis (Weatherhead & Raleigh 1979), sons of attractive males will inherit their father's ornamentation, be more likely to achieve greater reproductive success, and thus are more valuable to their mothers. Likewise, the sons of highly-ornamented females should be more reproductively valuable to their fathers. Male bluebirds mated to highly-ornamented females may perceive the nest bout as higher-than-average quality and this should increase the likelihood that they favor sons over daughters.

Fathers also preferentially protected female offspring when parental provisioning rates were high. This result contradicted my original expectation that fathers should favor sons in high-quality habitats. This expectation was based on the assumption that high

provisioning indicates high insect abundance, yet the data revealed no positive correlations between provisioning rates and either insect abundance or NDVI. However, I did not quantify parental effort (Tremblay et al. 2005) and high provisioning rates could have been the result of parents that worked harder rather than a simple reflection of habitat quality. Neither insect mass, insect abundance, nor NDVI - more direct measures of habitat quality - predicted parental favoritism. It is possible that habitat did not vary greatly enough to influence favoritism decisions. If the study site had included a greater variety of habitat, parental favoritism towards males in higher-quality habitats and females in lower-quality habitats may have been revealed. In a similar study of parental favoritism in which the researchers used provisioning rates to measure favoritism, Ligon and Hill (2010) found that mothers fed brightened sons more often when fathers had provided a lower proportion of the overall nestling provisioning. The authors interpret these results as mothers making strategic parental care decisions when her workload is heavier, i.e. when her energy is more limited. Unfortunately, because I was unable to quantify the proportion of provisioning provided by males and females, I cannot test how mate investment influences favoritism in my study.

While only fathers demonstrated preferences based on offspring sex, mothers and fathers were significantly more likely to choose the same offspring than would be expected from chance. These results suggest that the behavior of one parent may influence the other. I was unable to determine which sex of adult was copying the other. However, three lines of evidence suggest that females may copy males. First, males showed favoritism in both experiments, while females did not. Second, male bluebirds are more aggressive than females and spend more time defending the territory than do females (Gowaty & Plissner 1998). Third, fathers are the primary care givers for fledgling-aged birds. If, indeed, mothers copied

the behavior of fathers, this may explain why I was unable to detect a clear effect of offspring sex or color on mothers' preferences.

I have shown that eastern bluebird fathers preferentially defend their higher-quality sons during the fledgling period. While male bluebirds are more colorful than females, female coloration is an honest indicator of body condition and reproductive potential. Thus future studies should manipulate the plumage coloration of juvenile females to determine whether parents preferentially defend brighter (higher-quality) daughters. Likewise, it would be beneficial to conduct a similar experiment under broader habitat variation to resolve whether habitat quality influences parental preferences for offspring sex.

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TABLES AND FIGURES

TABLES

Table 1. Pearson's correlations comparing the four habitat quality variables that were measured for each pair of eastern bluebirds: provisioning rates (feedings/min/chick), total insect abundance, insect dry mass, and NDVI; and the six coloration variables: female rump brightness, female rump UV chroma, female rump hue, male rump brightness, male rump UV chroma, and male rump hue.

| Variables	Variables	N	r	P
Provisioning rate	Total Insect Abundance	30	0.20	0.28
Provisioning rate	Insect Dry Mass	32	-0.04	0.82
Provisioning rate	NDVI	33	-0.01	0.96
Provisioning rate	Female Rump Brightness	30	-0.13	0.48
Provisioning rate	Female Rump Hue	30	-0.10	0.61
Provisioning rate	Female Rump UV	30	0.04	0.82
Provisioning rate	Male Rump Brightness	25	0.05	0.83
Provisioning rate	Male Rump Hue	25	-0.08	0.69
Provisioning rate	Male Rump UV	25	0.23	0.26
Total Insect Abundance	Insect Dry Mass	31	0.24	0.19
Total Insect Abundance	NDVI	31	0.09	0.63
Total Insect Abundance	Female Rump Brightness	29	-0.10	0.59
Total Insect Abundance	Female Rump Hue	29	-0.12	0.53
Total Insect Abundance	Female Rump UV	29	-0.01	0.95
Total Insect Abundance	Male Rump Brightness	22	0.21	0.36
Total Insect Abundance	Male Rump Hue	22	0.25	0.27
Total Insect Abundance	Male Rump UV	22	0.09	0.71
Insect Dry Mass	NDVI	33	0.16	0.38
Insect Dry Mass	Female Rump Brightness	30	< 0.01	0.99
Insect Dry Mass	Female Rump Hue	30	-0.22	0.24
Insect Dry Mass	Female Rump UV	30	0.10	0.62
Insect Dry Mass	Male Rump Brightness	24	-0.02	0.92
Insect Dry Mass	Male Rump Hue	24	0.15	0.50
Insect Dry Mass	Male Rump UV	24	0.19	0.37
NDVI	Female Rump Brightness	31	-0.12	0.54
NDVI	Female Rump Hue	31	0.09	0.62
NDVI	Female Rump UV	31	0.03	0.88
NDVI	Male Rump Brightness	25	-0.12	0.58
NDVI	Male Rump Hue	25	-0.09	0.66
NDVI	Male Rump UV	25	0.17	0.41
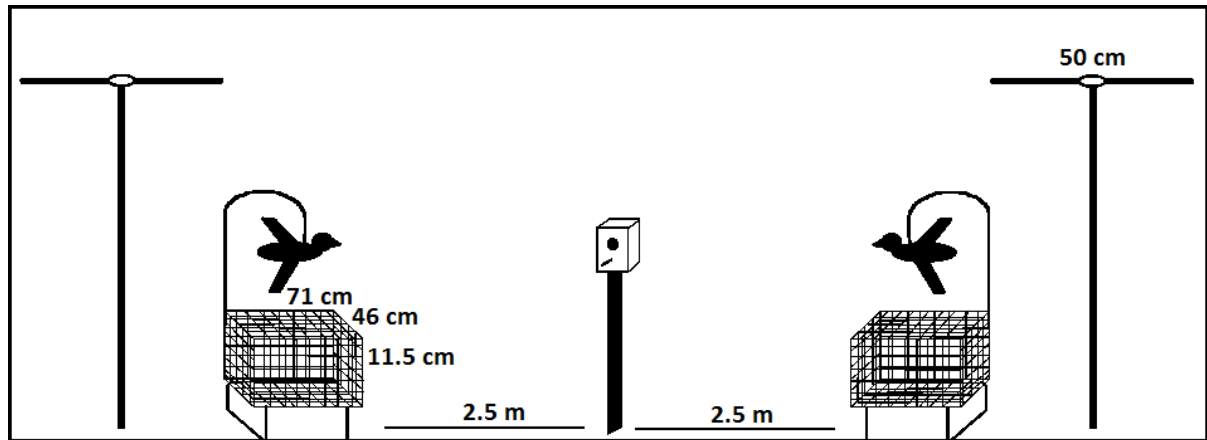
Figure 1. Nestling bluebirds were placed in two wire cages; each cage had a replica American crow hanging above. Cages were placed at the ends of a 5 m transect with the nestbox located in the center. Adjacent to each cage, I placed 50 cm perches for parents. Experimental trial set up was similar when parents chose between offspring of different sex and when parents chose between experimentally brighten and dulled male offspring.
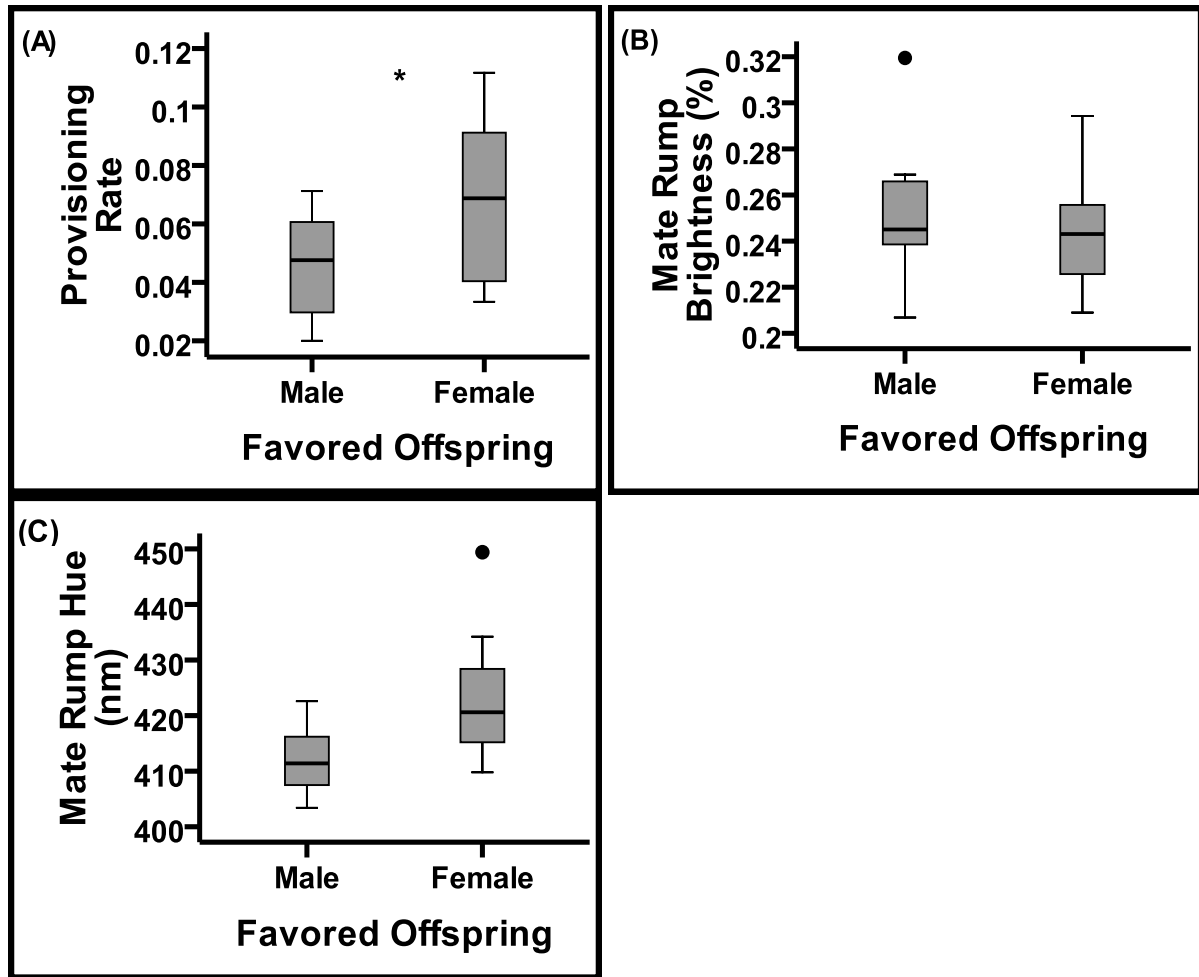
Figure 2. (A) Provisioning rate of (feedings per min per nestling) of male parents that preferentially defended male and female nestlings. Male eastern bluebirds were significantly more likely to defend female offspring when parental provisioning rate was high (Model: χ^2 = 4.267, R^2 = 0.192, P = 0.039; Feeding Rate Per Chick: Beta = 44.00, Wald = 3.23). (B-C) Male bluebirds mated to more-highly ornamented females were significantly more likely to defend male offspring (Model: χ^2 = 7.259, R^2 = 0.318, P = 0.027; Mate Rump Brightness: Beta = -29.24, Wald = 1.11; Mate Rump Hue: Beta = 0.16, Wald = 3.69). The line within each box represents the median; the upper and lower borders of each box represent the 25 and 75% percentiles; the lower and upper bars are the 10 and 90% percentiles. One asterisk represents P < 0.05, two asterisks represent P < 0.001.
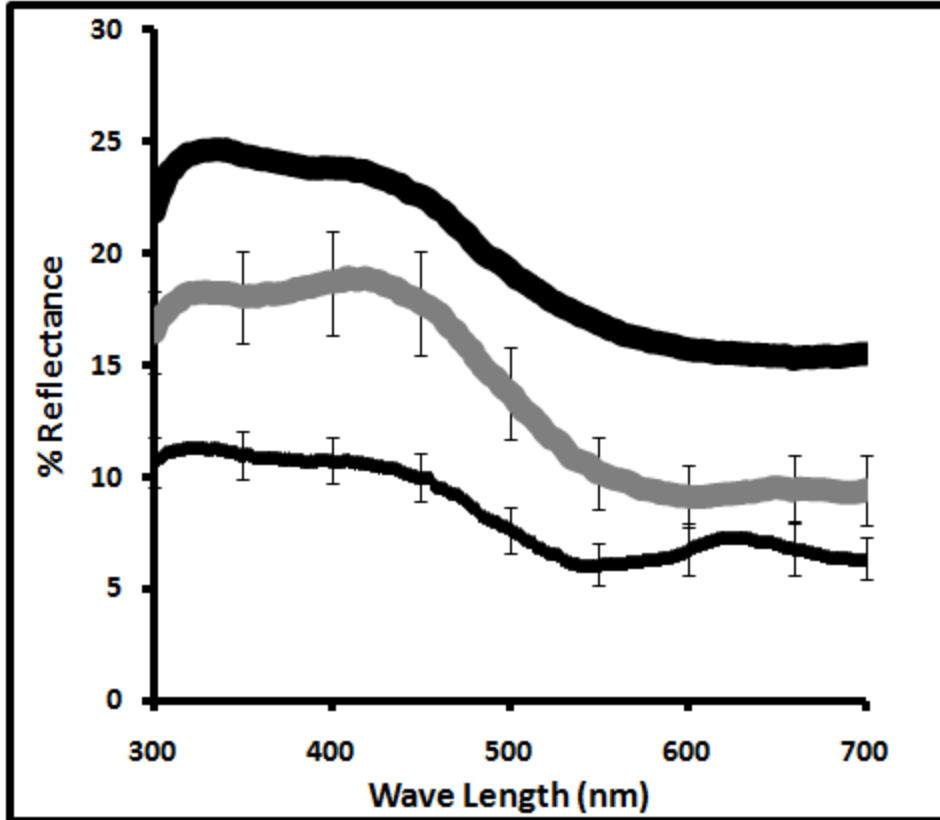
Figure 3. Reflectance curves of male offspring that had wing plumage 1) experimentally brightened using Prismacolor™ violet mist markers, 2) experimentally dulled with black Sharpie™ markers, and 3) males prior to experimental manipulation. Brightened males were significantly brighter than their dulled siblings (Z_{21} = -4.107, P < 0.001). The *thick black line* is the spectrum before any manipulation. The *thick gray line* represents the mean spectrum after manipulation to be experimentally brighter, with SD error bars at every 50 nm interval. The *thin black line* represents the mean spectrum after manipulation to be experimentally duller, with SD error bars ate every 50 nm interval.
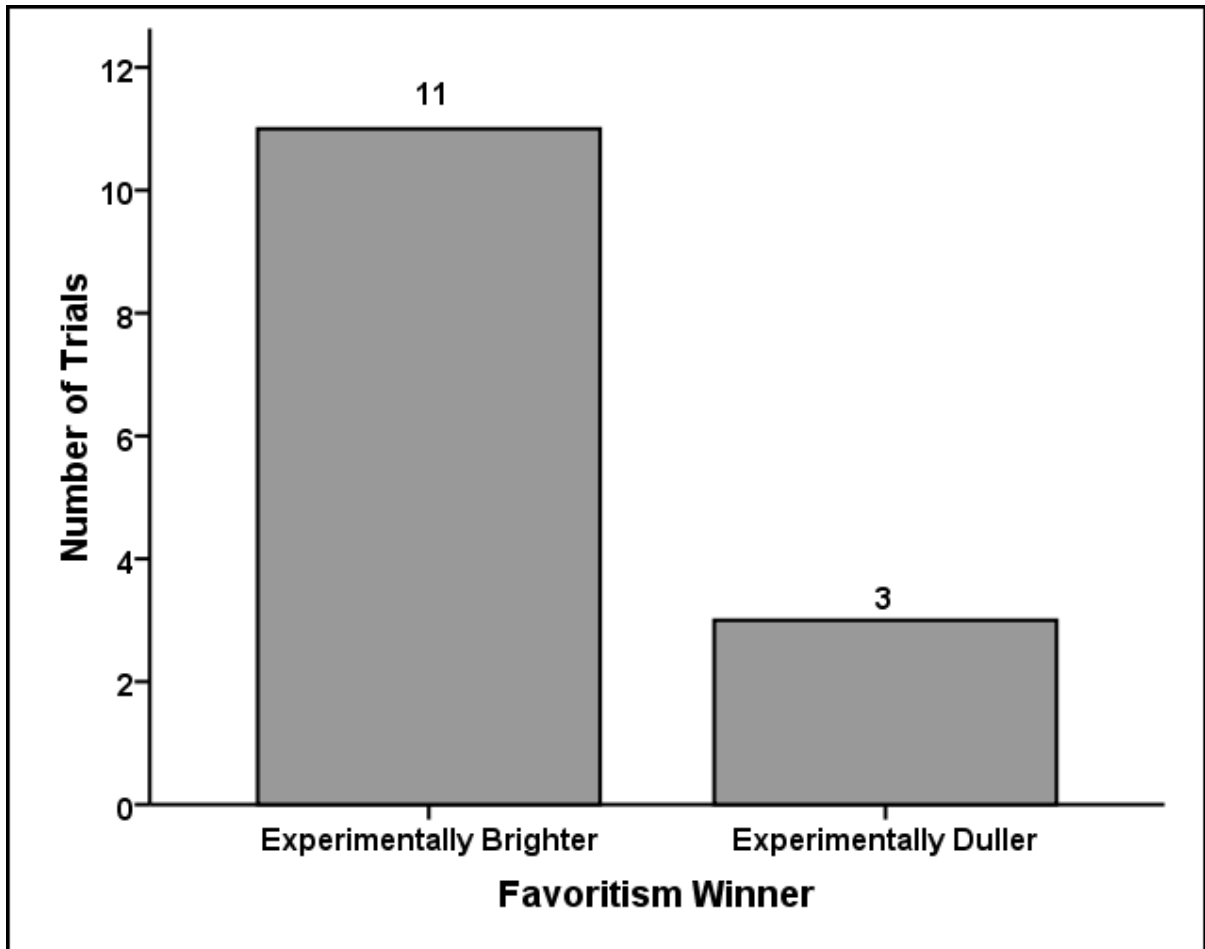
Figure 4. Number of male adult bluebirds that spent the majority of their time during the trials defending their experimentally brightened male offspring and their experimentally dulled male offspring. Males were significantly more likely to favor brightened sons ($\chi^2_{1,13} = 4.57$, $P = 0.03$).

BIOGRAPHICAL INFORMATION

Nicole Laura Barrios was born Manhasset, New York, on June 16, 1986. She attended elementary and half of junior high school in Queens, New York. In December of 1999, her family relocated to Charlotte, North Carolina, where Ms. Barrios finished middle school and attended high school. She graduated from Providence Senior High School in June 2004. In August 2004, Ms. Barrios enrolled in Wingate University, a private liberal arts university in Wingate, North Carolina, to study biology. She was awarded a Bachelor's of Science degree in May 2008. Following a year off of school, Ms. Barrios accepted a graduate assistantship in the Siefferman laboratory at Appalachian State University in August of 2009 and was awarded a Master's of Science degree in biology in May 2011.

While at Appalachian State University, Ms. Barrios was one of only twenty students to receive a Graduate Research Assistant Mentor Fellowship to fund her for two years of research. Her parents are Debbie Joy and Santiago Barrios and her younger brother is Jason Santiago Barrios. She is currently engaged to Stephen Robert Miller and will become Mrs. Nicole Laura Miller on August 6, 2011.