Maiersperger, B. D., J. D. Maddox, and C. J. Kellner. 2026. Sex ratio and plumage characteristics of juvenile American Robins (*Turdus migratorius*) in suburban areas of the Arkansas River valley. Journal of Field Ornithology 97(1):4. https://doi.org/10.5751/JFO-00758-970104

Avian Behavior, Ecology, and Evolution

Sex ratio and plumage characteristics of juvenile American Robins (*Turdus migratorius*) in suburban areas of the Arkansas River valley

Proporción sexual y características del plumaje de juveniles de Mirlo Americano (*Turdus migratorius*) en áreas suburbanas del valle del río Arkansas

Brandon D. Maiersperger [1], *J. Dylan Maddox* [2] and *Chris J. Kellner* [1]

ABSTRACT. Bird species that exhibit male-biased sexual size dimorphism (SSD) often demonstrate a female-biased fledging sex ratio (FSR). One hypothesis for this relationship is that male nestlings are more costly to raise and therefore at greater risk of mortality. However, not all male-biased size dimorphic species have been found to have a female-biased FSR, and many species have not been studied to better establish the relationship between SSD and FSR. We sought to determine the FSR of the American Robin (*Turdus migratorius*) and evaluate the relationship of SSD in the nestling stage to the FSR of the species. We also used qualitative and quantitative assessments of juvenile plumage to gauge the feasibility of sex determination through plumage. Male and female nestlings had substantial overlap in plumage characteristics, and we could not reliably distinguish between the sexes. Plumage differences between the sexes of juvenile robins may be insufficient to accurately determine sex in the field. The FSR was significantly skewed toward females; 63% of 59 nestlings were female. Size differences between male and female nestlings were minimal. Our findings do not provide strong support for the hypothesis that SSD leads to differential mortality of nestlings that skews fledging sex ratios toward the smaller sex. Other factors probably have a greater influence on the FSR of the species. More research is necessary to determine the primary drivers of skewed sex ratios in American Robins and other bird species.

RESUMEN. Las especies de aves que presentan dimorfismo sexual en tamaño (SSD por sus siglas en inglés) sesgado hacia los machos suelen mostrar una proporción sexual de polluelos o volantones (FSR) sesgada hacia las hembras. Una hipótesis para esta relación es que los polluelos o volantones machos son más costosos de criar y, por lo tanto, tienen mayor riesgo de mortalidad. Sin embargo, no todas las especies con dimorfismo sexual en tamaño sesgado hacia los machos presentan una FSR sesgada hacia las hembras, y muchas especies no han sido estudiadas para establecer mejor la relación entre SSD y FSR. Nuestro objetivo fue determinar la FSR del Mirlo Americano (*Turdus migratorius*) y evaluar la relación entre el SSD en la etapa de polluelo o volantón y la FSR de la especie. También utilizamos evaluaciones cualitativas y cuantitativas del plumaje juvenil para estimar la viabilidad de la determinación del sexo mediante el plumaje. Los polluelos machos y hembras mostraron una superposición sustancial en las características del plumaje, y no pudimos distinguir de manera confiable entre los sexos. Las diferencias de plumaje entre los sexos de los mirlos juveniles pueden ser insuficientes para determinar el sexo con precisión en campo. La FSR estuvo significativamente sesgada hacia las hembras; el 63% de 59 polluelos fueron hembras. Las diferencias de tamaño entre machos y hembras fueron mínimas. Nuestros hallazgos no respaldan de manera sólida la hipótesis de que el SSD conduce a una mortalidad diferencial de los polluelos que sesga la proporción sexual de polluelos o volantones hacia el sexo más pequeño. Otros factores probablemente tienen una mayor influencia en la FSR de la especie. Se necesita más investigación para determinar los factores principales que impulsan las proporciones sexuales sesgadas en el Mirlo Americano y otras especies de aves.

Key Words: *American Robin; avian sex ratio; fledging sex ratio; juvenile bird plumage; sexual size dimorphism; Turdus migratorius*

INTRODUCTION

Avian sex ratios at hatching are often assumed to be 1:1 (Clutton-Brock 1986, Slagsvold et al. 1986). However, by the time of fledging, sex ratios of species exhibiting sexual size dimorphism (SSD) typically deviate from unity (Weatherhead and Teather 1991, Gowaty 1993, Benito and González-Solís 2007). For species that exhibit male-biased SSD the fledging sex ratio (FSR) is often skewed toward females (Weatherhead and Teather 1991, Gowaty 1993, Benito and González-Solís 2007). One hypothesis for this is that the increased cost of raising males results in greater male mortality and leads to a post-hatching adjustment in sex ratio (Weatherhead and Teather 1991, Gowaty 1993, Benito and González-Solís 2007). Nestlings of the larger sex require more energy to raise (Slagsvold et al. 1986, Anderson et al. 1993). Therefore, the larger sex may experience increased mortality during the nestling stage when food resources are limited (Slagsvold et al. 1986, Teather and Weatherhead 1989, Nager et al. 2000). However, a statistically significant female-biased FSR has not been identified in many species that have male-biased SSD (Richter 1983, Koenig and Dickinson 1996, Koenig et al. 2001, Westneat et al. 2002, Ágh et al. 2020, Banach et al. 2024), and in some cases the FSR is skewed toward males (Koenig and Dickinson 1996, Koenig et al. 2001, Westneat et al. 2002).

Other factors may affect FSRs, which may explain the inconsistency in support of SSD as the primary driver of skewed sex ratios (Cockburn et al. 2002). Brood sex composition (Dijkstra et al. 1998, Nager et al. 2000), parental condition (Korpimäki et al. 2000, Nager et al. 2000), and hatching order (Teather and Weatherhead 1989, Badyaev et al. 2002, Maddox and

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[1] Arkansas Tech University, Biology Department, Russellville, AR, [2] Field Museum of Natural History, Pritzker Lab, Chicago, IL

Weatherhead 2008) may influence mortality during the nestling stage. Sex ratios may be biased at hatching, with differential mortality during the nestling stage only accounting for a small post-hatching adjustment (Benito and González-Solís 2007). Local resource competition (Clark 1978, Gowaty 1993) and habitat quality (Suorsa et al. 2003, Bell et al. 2014, Bouvier et al. 2016) are other possible explanations for skewed avian sex ratios. We chose to focus on how SSD may affect FSRs by contributing to greater mortality of the larger sex during the nestling stage, but acknowledge that there are many factors that may affect the FSR of birds (Cockburn et al. 2002). Our goal was to establish the FSR of a species not studied previously in this context, the American Robin (*Turdus migratorius*), and determine the relationship between FSR and SSD in the species.

Male American Robins are typically larger than females. Males are larger in terms of wing and tail length but are similar to females in mass and tarsus length. Male robins on average have 5.6% longer wings and 3.3% longer tails than females (Aldrich and James 1991). Mass differences between the sexes may change by season, with males (86.2 g, n = 26) weighing about 3% more than females (83.6 g, n = 18) during the winter and females (80.6 g, n = 6) weighing about 4% more than males (77.4 g, n = 21) during the breeding season (Wheelwright 1986). This magnitude of SSD places American Robins toward the center of the avian SSD spectrum (Székely et al. 2007). Assuming that size dimorphism is present in juvenile robins, it should lead to a female-biased sex ratio at fledging if males as the larger sex face a greater risk of mortality. However, the FSR of American Robins has not been well documented because sexing juvenile robins cannot be done reliably in the field.

Accurately sexing nestlings is essential for evaluating the FSR of a species. Genetic samples (blood or feathers) are commonly used to sex birds, but many species can be sexed by using adult plumage characteristics (Pyle 2022). Some bird species have monochromatic plumage, whereas others are clearly dichromatic, and some lie somewhere in between (Owens and Hartley 1998). Juvenile birds often have more cryptic plumage than adults of the same species, probably to help avoid predation (Hawkins et al. 2011). Sexually dimorphic plumage is uncommon in juvenile birds, but some species like the Cape Vulture (*Gyps coprotheres*; Mabhikwa et al. 2017), House Sparrow (*Passer domesticus*; Johnston 1967), Crossbills (*Loxia scotica* and *L. curvirostra curvirostra*; Edelaar et al. 2005), and Eastern Bluebird (*Sialia sialis*; Pinkowski 1974) can be sexed by plumage as juveniles. Sex-based differences in juvenile plumage have not been studied for many species. The ability to determine the sex of juvenile birds by using plumage characteristics could enhance demographic studies and allow researchers to more easily assess avian sex ratios and factors that affect them. In addition to evaluating the FSR of American Robins we sought to determine if sexing nestlings by plumage was possible.

We analyzed DNA extracted from blood samples to determine nestling sex and evaluate the FSR of American Robins, as well as examine the relevance of SSD to the FSR of the species. We also conducted visual and photographic assessments and took measurements of plumage characteristics in juvenile robins to ascertain the feasibility of sex determination through plumage. As male robins are typically larger than females, we expected to find a FSR that was skewed toward females. But, because the degree of skew in sex ratio may depend on the magnitude of sexual size dimorphism (Weatherhead and Teather 1991, Benito and González-Solís 2007), we predicted the sex ratio would only be slightly skewed toward females. Previous evaluations of juvenile American Robin plumage have stated that males may average darker crowns and darker and larger spots on the breast than females (Pyle 2022). Therefore, we anticipated that males would be darker on average than females. We aimed to contribute to a better understanding of skewed FSRs and identify sex-based plumage characteristics in juvenile robins that could benefit future evaluations of sex ratio, improve demographic studies, and provide a basis for similar assessments of juvenile plumage in other species.

METHODS

Study area

Our study was conducted between March and August in 2022 and 2023 at seven sites, six in Russellville, Arkansas (35.2781° N, 93.1337° W) and one in Dardanelle, Arkansas (35.2234° N, 93.1565° W), USA. The sites included public parks and the Arkansas Tech University campus, which was the largest site. Sites contained a matrix of short grass lawns, trees and shrubs, buildings, and impervious surface.

Nest monitoring and banding

We searched for robin nests by scanning suitable nest trees and shrubs and observing the behavior of adult robins (Reale and Blair 2005, Becker and Weisberg 2015, Malpass et al. 2018). To limit our impact on nests we followed the monitoring protocol outlined by Martin and Geupel (1993). We located 91 of 107 (85%) nests before hatching. An average nest produced 2.83 eggs ±1.10 SD and 2.67 nestlings ±0.87 SD. We banded nestlings on day 12 of the nestling stage, as robins typically fledge on day 13 of the nestling stage (Howell 1942), and we wanted to ensure we could band birds before they fledged. American Robin nestlings are fully feathered and typically near their maximum pre-fledging mass by day 12 (Howell 1942). We aged nestlings based on observations before hatching and by comparing nestling appearance to reference images (Vetspace 2nd Chance 2022, https://vetspace.2ndchance.info/american-robin-chicks-daily-photos-from-hatching-until-they-leave-their-nest/). When possible, we returned nestlings to the nest after processing them. In some cases the nest was too high off the ground for nestlings to be placed back in the nest, so we put them in short vegetation (shrub or small tree) near the nest. This meant that some nestlings were force-fledged shortly before their expected fledging date. Blood samples, photographs of plumage, and morphometrics of nestlings were obtained during banding.

Blood sampling and sexing

We collected blood samples from the brachial vein from all nestlings in a nest using a sterilized 27-gauge needle and microhematocrit capillary tubes. Samples consisted of less than 1% of each bird's body mass. The 1% cutoff is commonly accepted as within safe limits for wild birds based on guidelines from the Ornithological Council (Fair et al. 2023). We stored samples on Whatman Indicating FTA Classic Cards for preservation.

Robin nestlings were sexed via capillary electrophoresis (i.e., fragment analysis) by amplifying a portion of the CHD gene following the methods of Lee et al. (2010) with minor modifications. Polymerase chain reactions were performed in 10 µ l reactions with 1x PCR buffer (10 mM Tris-HCl, 50 mM KCl, pH 8.3), 1.5 mM MgCl2, 10 µg BSA, 200 µM of each dNTP, 1.0 µM of the 6-FAM labeled forward primer CHD1, 1.0 µM of the reverse primer CHD2, and 1 U Taq polymerase. Reactions were amplified with the following thermal conditions: 94 ºC for 3 mins, followed by 30 cycles of 94 ºC for 30 s, 59 ºC for 90 s, 72 ºC for 60 s and a final extension at 72 ºC for 10 mins. Polymerase chain reaction products (1 µl) were then combined with 8 µl of HiDi formamide and 1 µl of a custom internal ladder ALEXA-725 (Maddox and Feldheim 2014) and run on an ABI 3730xl DNA Analyzer (Thermo Fisher Scientific). Sex-specific products were visualized by using the Microsatellite Plugin v1.4.7 in Geneious Prime 2023.2.1 (Kearse et al. 2012) with females having two peaks, one at 344 bp from the W chromosome and another at 540 bp from the Z chromosome, whereas males had a single peak at 540 bp from the two Z chromosomes.

Plumage pictures and image analysis

We used a Canon EOS Rebel T3i camera with an EFS 18-55 mm lens to photograph all the nestlings we banded in 2023. To allow for unbiased comparison of the photographs, we used a constant ISO of 400 and a custom white balance in all images. RAW images were taken to preserve visual detail and offer flexibility for image analysis. We adjusted aperture and shutter speed on a per bird basis to prevent over or underexposing images. The crown and breast of each bird were photographed and we used an X-Rite ColorChecker Passport included in each image to compare plumage color to colored squares of known reflectance values (Figure 1). For each bird we visually assessed crown color as light or dark, and assumed that the sexes would be distinct.

We used the program ImageJ (https://imagej.net) with the Multispectral Image Analysis and Calibration (MICA) Toolbox (Troscianko and Stevens 2015) as a plugin to quantitatively assess plumage characteristics of nestlings. All plumage pictures were first normalized by using the MICAToolbox function “Generate Multispectral Image” and the ColorChecker. The ColorChecker contains a standard section that consists of 24 colored squares/standards, including a row of grayscale squares. We used the black and white standards at the extremes of the grayscale row to normalize images with the MICAToolbox by scaling image pixel reflectance values relative to the standards. Normalizing the images controls for differences in lighting intensity, color, and image exposure between images (MICAToolbox User Guide). After normalization, we used the freehand selection tool to select the full area of the crown from head images and the full area of the breast from chest images. We measured the mean pixel reflectance value for each selection and exported measurements for analysis. We also measured breast spots on each normalized chest image to determine if there were differences in the color and size of spots between sexes. Ten random points were generated within each breast selection by using a custom random point macro in ImageJ. We manually traced spots closest to the random points with the freehand selection tool and extracted the area in square millimeters and mean pixel reflectance values for each spot. Visual assessments of the shape of spots (circular, streaks, splotches) and the percentage of the chest covered by spots (<=25%, 25%–<50%, 50%–<75%, or 75%–100%) were also included to determine if they were useful visual indicators of nestling sex. Our goal was to assess plumage differences between the sexes from a human vision perspective, with the hope that any observed patterns could be used to help determine the sex of nestlings in the field. We did not explore plumage differences from the perspective of the avian sensory system, which may be more apparent as birds can perceive UV wavelengths (Eaton 2005).

Fig. 1. Example of plumage pictures taken to examine the coloration of the crown and breast of nestling American Robins. The top two pictures are of a female and the bottom two pictures are of different males.

Plumage and sex ratio data analyses

We used R version 4.2.1 (R Core Team 2022) to evaluate differences in plumage. We used the random forest procedure (package and function “randomForest”; Liaw and Wiener 2002) to find the most important variables for determining nestling sex (“VarImpPlot” function in the randomForest package). We included mean crown color, mean breast spot color, mean breast color, breast spot shape, breast spot coverage, and our in-field evaluation of sex as variables in the random forest model. We then used a binomial generalized additive model (GAM) to classify sex by using the two best predictor variables selected by the random forest procedure. Only two variables were included in the GAM because we wanted to keep plumage classification simple and avoid multicollinearity, and we found that additional variables did not improve model performance. We used the function “gam” in the “mgcv” package to produce our GAMs (Wood 2011). Random forest models (Cutler et al. 2007) and GAMs (Pedersen et al. 2019) are widely used in ecological research and can perform classification routines without adhering to specific data distributions. We used a binomial GAM instead of a logistic regression because the GAM was better at classifying sex for the given data and is well suited to model non-linear effects of covariates on a response variable. Additionally, the probability distribution of the data was not monotonic, which makes a logistic curve poor for modeling probability. We used confusion matrices to evaluate the performance of classification methods.

The “binom.test” function in R was used to determine whether the observed female:male FSR differed from an equal sex ratio. We specified an alternative hypothesis that the sex ratio would be skewed toward females. Binomial tests use a binomial distribution that models the probability of two outcomes to determine if the recorded values of the two outcomes are different from a specified proportion, often 0.50 (Abdi 2007). We ran a binomial test on a dataset containing all sexed nestlings from 2022 and 2023, and on separate datasets for each year. An alpha value of 0.05 was used to determine the significance of all statistical tests.

RESULTS

Fledging sex ratio and morphometrics

We determined the sex of 59 robin nestlings by using capillary electrophoresis, 22 in 2022 and 37 in 2023. In 2022 the female to male sex ratio was 15:7, or about 68% females. In 2023 the sex ratio was 22:15, or about 59% females. The overall sex ratio was 37:22, or about 63% females. The binomial test on the sex ratio of the combined dataset differed from 1:1 ($p = 0.033$), indicating that the overall FSR was significantly skewed toward females. For each year separately, binomial tests (2022: $p = 0.067$, 2023: $p = 0.162$) were not statistically significant. The average nest did not have a significantly skewed FSR ($V = 167.5$, $p = 0.171$).

We measured morphometrics for 57 robin nestlings. Males weighed 53.13 g ±4.62 SD (range 46.3–62.2) and females weighed 52.63 g ±4.82 SD (range 37.8–60.0). There was not a statistically significant difference in mass between the sexes ($W = 397.5$, $p = 0.987$). Male tarsus length was 37.7 mm ±0.87 SD (range 36.2–39.5) and female tarsus length was 37.3 mm ±1.46 SD (range 34.6–43.2). The difference in tarsus length between the sexes was statistically significant ($W = 267$, $p = 0.039$).

Plumage characteristics

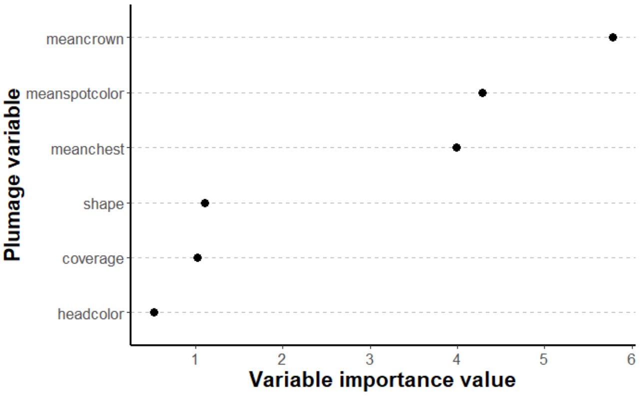
An in-field visual assessment of the crown color of nestlings (light or dark) was not useful for distinguishing the sexes (Table 1). The random forest procedure identified mean crown color and mean breast spot color as the best plumage variables for classifying sex of the 37 nestlings we banded in 2023. Mean breast color was the next best variable, and the qualitative assessments of shape, coverage, and in-field crown color were poor for distinguishing the sexes (Figure 2). We decided not to include breast spot size in the random forest procedure. The 10 random points we generated were not sufficient to represent spot size on a nestling, and delineating spot borders often felt subjective because the margins of the spots gradually fade into the surrounding plumage. Mean breast spot color and mean breast color were highly correlated ($r = 0.634$, $p < 0.001$) so we decided to use only the two best variables, mean crown color and mean breast spot color, in the binomial GAM. Those variables were weakly correlated ($r = 0.156$, $p = 0.356$).

The binomial GAM was better at classifying female nestlings than males (Table 2). On the full dataset the GAM classified 20 of 22 (90.9%) females correctly and 11 of 15 (73.3%) males correctly. The spline for mean crown color was fit with more effective degrees of freedom (6.061) than the spline for mean breast spot color (1.000), indicating that crown color had a more complicated, non-linear relationship with sex. The deviance explained of the full dataset GAM was 42.4%. To further evaluate the performance of the GAM the dataset was split into training and test datasets consisting of 70% ($n = 25$) and 30% ($n = 12$) of the data respectively. We produced a model on the training dataset and then tested it on the test dataset. The GAM performed well on the training dataset but struggled to correctly classify males on the test data. Just 1 of 5 (20%) males were classified correctly compared to 6 of 7 (85.7%) females (Table 2).

Table 1. Comparison of in-field visual assessment of American Robin nestling crown color to verified nestling sexes. N = 51 birds banded in 2022 and 2023.

Sex	Crown color	
	Dark	Light
Female	16	15
Male	12	8

Fig. 2. Random forest model variable importance plot ranking of plumage measurements in classifying American Robin nestling sex. A higher variable importance value means the variable is more useful for distinguishing the two sexes. The two variables with the highest variable importance values were selected for the binomial GAM.



Nestlings with low and high values of mean crown color were more likely to be identified as males (Figure 3A). Most females had moderate crown color measurements, although two females had the lightest and darkest values. Mean breast spot color had a weaker relationship with sex. A nestling was slightly more likely to be classified as male if they had lighter breast spots, but we found considerable overlap between the mean breast spot color measurements of the two sexes (Figure 3B).

DISCUSSION

Fledging sex ratio

We found that the FSR of American Robins is significantly skewed toward females, but our results do not provide strong support for the hypothesis that SSD leads to a skew in FSR because of greater mortality of the larger sex (Weatherhead and Teather 1991, Benito and González-Solís 2007). Size differences between the sexes of American Robin nestlings in our study were minimal. Male nestlings had a significantly longer average tarsus length (but the difference between the raw measurements was small) and were not significantly heavier than females. The small size difference would probably not solely explain the sex ratio we observed at fledging. Other factors are likely to affect the FSR of the species. Small sample size and year-to-year variation in FSR (Koenig and Dickinson 1996, Westneat et al. 2002) also weaken our support for SSD as the main driver of a skewed FSR in

Table 2. Summary of binomial generalized additive model (GAM) confusion matrices for full (n = 37), training (n = 25), and test (n = 12) datasets used to classify nestling American Robin sex based on plumage measurements. GAMs were run with mean crown color and mean breast spot color as the two predictor variables for all datasets.

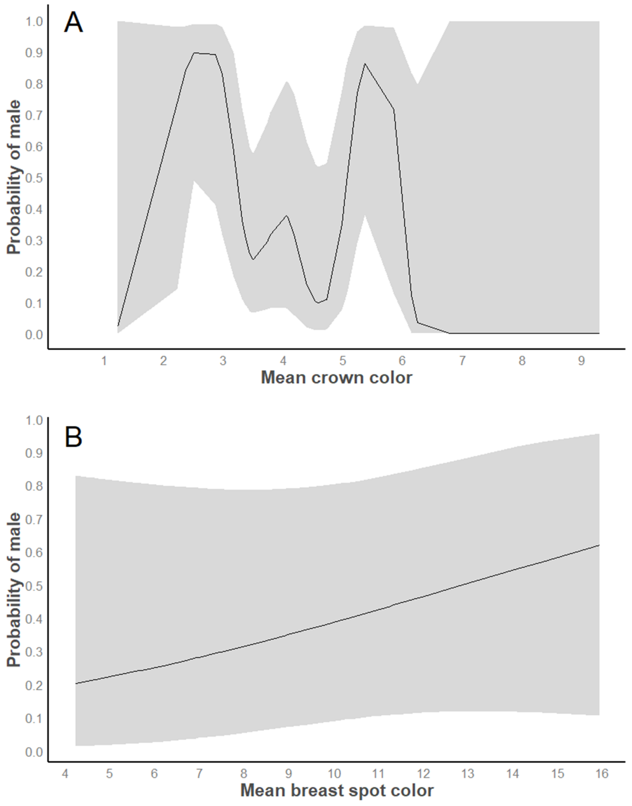
Dataset	Female correct/ total	Male correct/ total	Error rate female (%)	Error rate male (%)
Full	20/22	11/15	9.1%	26.7%
Training	14/15	9/10	6.7%	10.0%
Test	6/7	1/5	14.3%	80.0%

American Robins. We studied one population over two breeding seasons and determined sex for a small number of nestlings. Without a larger sample, it is unclear if a skewed FSR and weak SSD at fledging are typical for the species. Studies that have examined the FSR of several other species that exhibit male-biased SSD have not found evidence of a significantly female-biased FSR (Richter 1983, Koenig and Dickinson 1996, Westneat et al. 2002, Ágh et al. 2020, Banach et al. 2024). More study is needed to determine if the FSR of American Robins is consistently skewed toward females, and if other species with weak SSD also demonstrate FSRs that are skewed toward the smaller sex.

There are several alternative explanations to SSD for a skewed FSR. Sex ratios that are skewed at fledging may be skewed at hatching (Benito and González-Solís 2007). We found 85% of nests during the egg stage, but unfortunately did not assess the hatching sex ratio. The female-biased FSR we detected may have been present at hatching instead of resulting from differential mortality during the nestling stage. Evidence of skewed hatching sex ratios has been found for some species and may arise from adaptive sex allocation (Ellegren et al. 1996, Ewen et al. 2001, Badyaev et al. 2002, Rutkowska and Badyaev 2008), although the prevalence of this phenomenon in birds remains inconclusive (Maddox and Weatherhead 2009). Adjusting the sex ratio as early as possible would be the most efficient way for mothers to control how many male and female offspring they produce (Benito and González-Solís 2007). Assessing the sex ratio at different developmental stages and at fledging may help us understand how skewed sex ratios develop in American Robins and other bird species (Banach et al. 2024).

Habitat quality may affect FSRs. Several passerine species produce more females in poor quality habitat (Suorsa et al. 2003, Bell et al. 2014, Bouvier et al. 2016). Our study areas were suburban and included public parks and the Arkansas Tech University campus. Abundance of many bird species is lower in urbanized areas (Chace and Walsh 2006), indicating poor quality habitat. However, American Robins typically thrive in developed environments (Mills et al. 1989, Marzluff 1997, Bock et al. 2001). Habitat quality is unlikely to be a major factor contributing to the skewed FSR of American Robins but may be relevant to the FSR of other bird species. Habitat quality may be related to the local resource competition (LRC) hypothesis, another potential explanation for skewed FSRs.

Fig. 3. Relationship between mean crown color (A) and mean breast spot color (B) and the probability of a nestling American Robin being classified as male from the binomial GAM run on the full dataset (n = 37) with mean crown color and mean breast spot color as classifying variables. Binomial GAM results: deviance explained = 42.4%, edf = 6.061 (mean crown color) and 1.000 (mean breast spot color). Larger mean crown color and mean breast spot color values represent lighter colored plumage. The shaded area represents a 95% confidence interval.



The LRC hypothesis posits that the sex that disperses farther competes less with closely related individuals for resources (Clark 1978). Therefore, adults would be expected to produce more of the sex that disperses farther to limit competition in the natal area. Originally an explanation for skewed sex ratios in mammals, Gowaty (1993) has suggested that this hypothesis may be applicable to birds. Females are typically the farther dispersing sex in passerines (Greenwood 1980). Passerines may produce more females on average to reduce future conflict with offspring for resources (Gowaty 1993). Reducing conflict for resources in the natal area would be especially important in low-quality habitat where resources are even more limited. The LRC hypothesis may be relevant to American Robins, especially if the effect of SSD on FSR is weak (Gowaty 1993). However, sex did not have a significant effect on the movement of juvenile American Robins during the post-fledging period (B. D.

Maiersperger, unpublished data), suggesting that the sexes may not be significantly different in their post-fledging dispersal behavior.

Brood sex composition, parental condition, and hatching order may influence sex-specific mortality during the nestling stage. If broods have a greater proportion of the larger sex, they could have increased food demand that would contribute to increased mortality of the larger sex (Dijkstra et al. 1998). The combination of a male-biased brood sex composition and poor parental condition may lead to a female-biased sex ratio at fledging in Lesser Black-backed Gulls (*Larus fuscus*), a species that also exhibits male-biased SSD (Nager et al. 2000). Parents in poorer condition are less equipped to provision offspring, and depressed parental condition may have a biased effect on the survival of the larger sex (Korpimäki et al. 2000, Nager et al. 2000). However, parental condition may not have a significant effect on the sex ratio of some bird species (Westneat et al. 2002, Ding et al. 2017).

The eggs of most bird species hatch asynchronously, with the last laid egg hatching last (Badyaev et al. 2002). Several species have been found to have sex biases in hatching sequence (Bortolotti 1986, Teather and Weatherhead 1989, Bednarz and Hayden 1991, Torres and Drummond 1999, Badyaev et al. 2002). Certain positions in the hatching order may increase or decrease odds of survival (Badyaev et al. 2002). Nestlings that hatch later can experience slower growth, which results in increased mortality (Teather and Weatherhead 1989, Maddox and Weatherhead 2008). If individuals of one sex hatch later, they may be more vulnerable to starvation, resulting in a FSR bias toward the other sex. Hatching order of the sexes may be manipulated by females to reduce or encourage competition among offspring, affecting the subsequent FSR (Cockburn et al. 2002). American Robin nestlings compete for food by jockeying for position (McRae et al. 1993) and by begging (Smith and Montgomerie 1991). Differences in the competitive abilities of American Robin nestlings may offset the effect of hatching order and/or SSD on the species' FSR.

Several of these factors may have contributed to the female-biased FSR we observed in American Robins. We are unable to directly examine the relevance of these factors to the FSR because we were focused on the effect of SSD during the nestling period. As with other bird species, the fledging sex ratio of American Robins is probably dependent on a suite of influences. We hope that future research can build upon our initial assessment of the species' FSR by directly testing alternative hypotheses for skewed FSRs and conducting experimental manipulations to determine how and why more female American Robins may be produced than males.

Plumage characteristics

We found that plumage characteristics were not reliable for distinguishing sex in nestling American Robins. Crown and breast spot color were the best plumage measurements for sexing nestling robins, but substantial overlap in the measurements made them unreliable indicators of sex. Female nestlings generally had intermediate values of crown color compared to lighter or darker males, but the two lightest and darkest individual birds were females. These results partially support Pyle (2022) in that the darkest nestlings were typically male, but the prevalence of females with moderately dark crowns and males with light crowns contradicts the notion that male nestlings are darker on average, at least in terms of crown color. This makes visually sexing juvenile American Robins unreliable.

At the time of processing, we visually assigned the crown color of nestlings to two categories: light and dark. Our visual assessment was not an accurate indicator of nestling sex, which is supported by the results of the binomial GAM. Our visual assessments were inaccurate because we assumed males would be darker than females and that birds could be easily categorized as light or dark. In practice many birds were difficult to assign as light or dark. Because female nestlings typically had intermediate crown color values in our quantitative analysis, we may have been more successful at determining sex in the field if we had classified birds in an intermediate category. We did not visually reclassify sex by using the images we collected because our goal was for visual assessments to be a tool for sexing birds in the field, and the images were not a perfect rendering of a bird's appearance in the field.

Our results suggest that finding a quick and accurate method of visually sexing nestling American Robins may be impossible. Future research should increase the complexity of image analysis methods and determine if an intermediate crown color category can be used to help classify the sex of nestling robins in the field.

CONCLUSION

We found a significant female bias in the fledging sex ratio of American Robins but did not find compelling evidence that sexual size dimorphism is the primary driver of the skewed FSR. Additionally, our evaluation of nestling plumage indicates that sexing juvenile American Robins by plumage is unreliable due to substantial overlap in crown and breast coloration. Sex ratios should be reported even if evidence of a skewed ratio is not conclusive. Avian sex ratios are liable to publication bias, where sex ratios that are not statistically different from a 1:1 ratio are not published (Benito and González-Solís 2007, Donald 2007, Banach et al. 2024). A skewed ratio over multiple years would suggest selective pressure on the sex ratio of a species, even if results are not statistically significant (Gowaty 1993). We encourage researchers to publish sex ratio information even if results are not significant to develop a clearer picture of how SSD and other factors affect avian sex ratios.

Author Contributions:

Maiersperger led data collection and analysis, and wrote and edited the manuscript. Kellner assisted in data analysis and edited the manuscript. Maddox conducted lab analyses and edited the manuscript.

Acknowledgments:

This material is based upon work supported by the National Science Foundation under Award No. OIA-1946391. Funding for this research was also provided by the Arkansas Audubon Society Trust. We would like to thank Michael DeVito, who assisted with this research as a field technician in 2022 and 2023.

Data Availability:

The data/code that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.27115369 and https://doi.org/10.6084/m9.figshare.27115366.

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