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Sex-Specific Movements in Postfledging Juvenile Ovenbirds (*Seiurus aurocapilla)*

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ABSTRACT.—Understanding sex-specific differences in behavior and survival is essential for informative population modeling and evolutionary biology in animal populations. Uneven sex ratios are common in many migrant passerine species; however, the underlying mechanisms remain unclear. We used molecular sex determination, nest monitoring, and radio telemetry of fledgling Ovenbirds (*Seiurus aurocapilla*), to determine if sex-specific patterns of production, survival or behavior were present prior to the first migration. We tested whether: 1) sex ratios were skewed towards males at fledging; 2) postfledging survival of males was higher than females; 3) distances moved over time were equal between sexes; and 4) if observed parental care was equal between sexes over time. We determined the sex of 33 hatch-year Ovenbirds in central Missouri in 2015 and followed 19 individuals using radio telemetry. We found no difference in sex ratios within broods, overall numbers of male ($n = 18$) and female ($n = 15$) nestlings, or in the survival of male ($n = 8$) and female ($n = 11$) fledglings followed with radio telemetry. However, we did find that sex affected the relationship between age and distance moved from the nest, suggesting females moved further from the natal site after independence from adults. These results provide a better understanding of postfledging ecology and support the common assumption that annual production of females is half of total productivity, a fundamental premise in most population growth models. *Received 6 February 2017. Accepted 22 August 2017.*

Key words: movements, postfledging, *Seiurus aurocapilla*, sex ratio, survival, radio-telemetry.

Knowledge of sexual variation in ecology and behavior is essential for understanding the evolutionary biology and demography of animals. A sex ratio of 1:1 is generally expected in wildlife populations (Fisher 1930). However, in wild populations, this concept is not always true. Sex ratios of breeding adults can vary widely across species and have been shown to influence species behavior, ecology, and life histories (Székely et al. 2014). In many avian populations, adult sex ratios tend to be male-skewed (Mayr 1939, Donald 2007). Potential mechanisms underlying skewed sex ratios in a population include: initial sex bias at hatching (Fisher 1930), parental manipulation of sex ratio in young (Donald 2007), and variation in sex-specific survival at different life stages (Stienen et al. 2008, Leshyk et al. 2012).

Knowledge of possible sexual variation in survival rates is needed throughout the annual cycle for migratory birds because female survival is often assumed to limit population growth in migratory songbirds (Rushing et al. 2016). Sexual variation in mortality during the postfledging juvenile period is of particular interest due to high mortality rates in songbirds shortly after fledging (Cox et al. 2014). However, postfledging ecology has not been well studied because birds become quiet and secretive during this period, and often move to areas with dense cover where they are more difficult to find (Cox et al. 2014). Only with the development of lightweight radio transmitters in the last 20 years have we been able to follow small migratory birds during this important period.

Sex-specific differences in parental investment or movement may lead to disparate survival rates in the postfledging period. A parent providing sex-skewed protection or resources to nestlings or postfledging juveniles has the potential to lower fitness for the neglected sex (Donald 2007, Székely et al. 2014). Differential movements of male and female fledglings may present a mechanism for increased mortality rates in the farther ranging sex, due to increased opportunities for predator interactions, or signal potential competitive exclusion from local habitats. Female biased natal dispersal (movement from natal area to first breeding territory) and breeding dispersal (adult movement from a prior breeding territory) is widespread in philopatric birds (Greenwood and

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Harvey 1982). Sexual variation in choice of wintering habitat has also been observed for adult Neotropical migrant populations (Faaborg et al. 2010), thus sex-specific behavior patterns may also occur post-fledging before migration.

Ovenbirds (*Seiurus aurocapilla*), a monomorphic interior forest nesting Neotropical migrant, have strongly skewed sex ratios in favor of males on the breeding grounds, especially in fragmented forests (Van Horn et al. 1995). There is also evidence that Ovenbirds migrate to different regions of the Neotropics, with the females migrating further south than males, a process known as latitudinal segregation (Komar et al. 2005). They show slightly female-dominated populations (>60%) at some Puerto Rico wintering sites, where other species (American Redstart [*Setophaga ruticilla*] and Black-and-white Warbler [*Mniotilta varia*]) have populations where females exceed 90% (Faaborg et al. 2013). In this study, we used radio telemetry and molecular sex determination to investigate potential sex-specific differences in production, survival, and behavior of nestling and fledgling Ovenbirds during the 2015 breeding season in central Missouri. We conducted an exploratory analysis to test whether sex ratios were skewed prior to the first migration. We tested four hypothesis: 1) sex ratios were skewed towards males at fledging; 2) postfledging survival of males was higher than females; 3) distances moved over time were equal between sexes; and 4) observed parental care was equal between sexes over time.

METHODS

From May to August 2015, Ovenbird nests were located and monitored using song and site cues and systematic searching in 2 mature oak-hickory forest fragments in central Missouri, the Thomas Baskett Research and Education Area (890 ha reserve; 38° 45′ N, 92° 12′ W) and the Rudolf Bennitt Conservation Area (146 ha reserve; 39° 8′ N, 92° 15′ W). We captured all available nestlings 1 day prior to their projected fledge date and collected 2–3 body feathers from each juvenile for molecular testing. If birds fledged prior to our nest visit we captured fledglings opportunistically. All juveniles received unique leg-band combinations and 1 or 2 individuals from each brood were fitted with a 0.3g radio transmitter (model A2414, Advanced Telemetry Systems Inc., Isanti, MN, USA) attached with a figure-8 harness (Rappole and Tipton 1991). Transmitters weighed less than 3% of the birds' body weight in accordance with current regulations.

Tracked individuals were relocated daily or every other day by homing using handheld antennas. We recorded location coordinates, evidence of parental care, and survival status at each observation until radio failure, mortality, or loss of signal. Parental care was assigned as present if an observation included begging to or feeding by an adult. We recorded locations using handheld GPS units (GPS error < 10 m). We calculated 2 movement metrics for each location: 1) linear distance from the nest; and 2) daily movement rate based on the linear distance between subsequent locations divided by the elapsed time in days (m/day).

Molecular Sex Determination.—We extracted DNA from feather samples using InstaGene matrix (Bio-Rad Laboratories Inc., Hercules, CA, USA) and the protocol of Eggert et al. (2005), and amplified DNA via PCR-based methods. Originally, we amplified the ATP5A1 gene region, in which the W- and Z-specific fragments are often of different sizes in avian species, using the F2/R1 primer set (Bantock et al. 2008) and visualized the amplification products in a 4% agarose gel. However, due to a genetic polymorphism found in the ATP5A1 gene, the results were not clear (Toms et al. 2012). We received clear results (differentiation in W- and Z-specific fragment bands) when we amplified the CHD1 gene with primer set P2/P8 and visualized the results in a 3% agarose gel (Griffiths et al. 1998). We ran known-sex adult control samples with all juvenile samples for comparison as well as a negative (no DNA) control to detect possible contamination of the reagents.

Statistical Analysis.—We compared the proportions of males and females within broods, among all nestlings at fledging, and among all tracked birds at fledging using *t*-tests and chi-square tests. We report means and standard errors (±SE) for brood sizes and observation periods. Broods containing one ovenbird nestling per nest, usually due to Brown-headed Cowbird (*Molothrus ater*) parasitism, were excluded from within brood comparisons.

TABLE 1. Sex ratios were not skewed for Ovenbird nestlings or fledglings sampled in Boone County, Missouri in 2015. *P*-values from *t*-test or chi-square tests of samples given.

	Male	Female	*P*-value
Mean (±standard deviation) proportion within broods[a] ($n = 8$)	0.538 ± 0.25	0.463 ± 0.25	0.69
Proportion across nestlings ($n = 33$)	0.545	0.455	0.60
Proportion of radio marked fledglings ($n = 19$)	0.421	0.579	0.49
Proportion of surviving radio marked birds ($n = 12$)	0.417	0.583	0.56

[a] Only includes broods with >1 Ovenbird fledgling.

We used the logistic exposure method to test the effects of sex, age, their interaction, and site on daily survival of postfledging juveniles (PROC GENMOD, SAS Institute Inc., Cary, NC, USA; Shaffer 2004). Because we monitored 2 Ovenbird juveniles from the same brood for 2 nests, we adjusted standard errors for repeated measures using generalized estimating equations by identifying brood as the subject (SAS Institute Inc. 2011; Schreiber et al. 2016). We used generalized mixed linear models with a gamma distribution and log link to test for effects of sex on distance moved from nest and on daily movement rate (PROC GLIMMIX, SAS Institute Inc., Cary, NC, USA). We used logistic regression to determine whether observed parental care in the dependent period (1–23 days post-fledge; Jenkins et al. 2017) varied between sexes. Age, sex, and their interaction were used as fixed effects in movement models and in the parental care model. Age is a strong predictor of postfledging survival, behavior, and movements (Yackel Adams et al. 2001, White and Faaborg 2008, Vitz and Rodewald 2010). An additional variable, lag-distance, the prior distance from the nest, was used in the nest distance model to account for spatial autocorrelation. We included individual as a random effect to account for the non-independence of repeated observations of individuals in movement and parental care models; we did not consider a random effect of brood since early mortalities reduced our sample to one individual per brood. Data for the first movement away from the nest was censored from movement analysis to avoid bias from birds escaping researchers after capture and radio attachment. Observers limited disruption to family groups on subsequent observations. We considered regression coefficients significant if 95% percent coefficient confidence intervals (CI) did not contain zero.

RESULTS

We monitored 29 Ovenbird nests in 2015 and sampled 13 broods before fledgling (31 nestlings) and an additional 4 opportunistically captured fledglings (less than 2 days postfledging). We successfully determined the sex for 33 birds, including 19 (1–2 per brood) that were fitted with a radio transmitter. Fifty-four percent of nests ($n = 7$) were parasitized by Brown-headed Cowbirds with 2.0 ± 0.14 (range 2–5) cowbird nestlings. There were 2.4 ± 0.81 (range 1–5) Ovenbird fledglings per nest. Differences in proportions of males and females within broods that had more than one fledgling ovenbird, across all nestlings, or across radioed birds were not significant (all $P > 0.1$, Table 1).

There was no difference in the number of monitoring days for females (13.0 days ± 0.95; 1–43) and males (12.7 ± 1.06; 1–32). We observed 7 mortalities and had an effective sample size of 309 days for daily survival models. There were no significant effects of sex ($CI_{sex} = –2.50, 1.47$) or sex × age interaction ($CI_{sex\_age} = –0.14, 0.43$) on daily survival. Adult care was observed in 55 of 147 observations of 14 dependent fledglings. There was no significant effect of sex ($CI_{sex} = –1.45, 1.60$) or sex × age interaction ($CI_{sex\_age} = –0.07, 0.16$) on observed parental care. Sample sizes of both movement models were reduced due to mortalities that occurred prior to the second relocation. We used 175 daily movements from 14 fledglings from 14 broods for the model of movement rate. There were no significant effects of sex ($CI_{sex} = –0.35, 0.31$) or sex × age interaction ($CI_{sex\_age} = –0.21, 0.27$) on movement

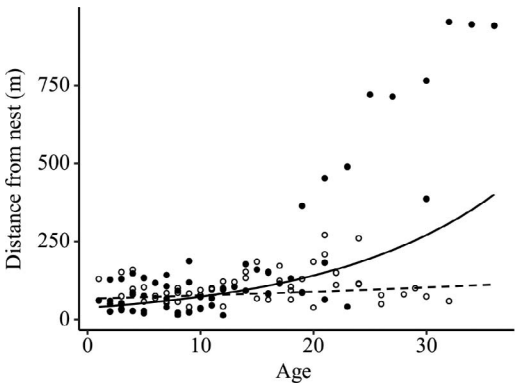

FIG. 1. Distance moved from the nest over time for fledgling female (black points) and male (open circles) Ovenbirds in Missouri in 2015. Trend lines from mixed logistic regression were estimated by holding other covariates at their means for females (solid line) and males (dashed line).

rate. We used 118 observations from 10 fledglings in our regression of distance moved from the nest. Data from 4 fledglings initially captured away from their nests were censored from the nest distance analysis. There was no significant effect of sex ($CI_{sex} = -0.39, 0.57$) on distance from nest, but there was a significant sex × age interaction effect ($\beta_{sex\_age} = 0.43$, $CI_{sex\_age} = 0.23, 0.63$), suggesting that females had a higher propensity to move away from their natal site as they aged (Fig. 1).

DISCUSSION

We found no evidence for a biased nestling sex-ratio or sex-specific postfledging mortality. This aligns with other bodies of work supporting non-skewed offspring sex ratios at the population level (Donald 2007). We cannot rule out sexual bias in juvenile mortality during the first migration or on the wintering grounds, however, our finding that sex ratios and survival were equal prior to migration supports the common assumption that annual production of females is half of total productivity, which is a fundamental premise in most population growth models (Etterson et al. 2011).

Results from juvenile movement away from the nest suggest that females may move farther from the natal site than males after independence from adults. Fledgling Ovenbirds in our study area became independent from adults around day 23 post-fledging (Jenkins et al. 2017). We observed female juveniles moving 350 to 750 meters further from the nest in comparison with male juveniles after 20 days post-fledging (Fig. 1). Prior to day 20, male and female movement was similar. While it is important to note the small sample size for juvenile movements from nest after day 20 ($n = 6$, 3 females), this result opens several potential avenues for future research, especially for those interested in natal dispersal, the distance moved between the natal territory and the first breeding territory, or those interested in initiation dates and survival during the first migration.

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Natal Philopatry and Juvenile Survival in Swainson's Warblers (*Limnothlypis swainsonii*)

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ABSTRACT.—Understanding natal dispersal and rates of philopatry can help provide minimum estimates of juvenile survival, a vital demographic parameter for which little information is available. However, despite the large number of hatch-year migratory birds banded every year at their natal sites, few are resighted or recaptured. Here, we report on the return of 22 Swainson's Warblers

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