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- Title: Large female song repertoires and within-pair song type sharing in a temperate breeding
 songbird
- 3 Running Title: Song sharing in large female repertoires
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- 17 Abstract:

18 Female song has been significantly understudied in songbirds. While male song has been studied for centuries, female song has only begun to be explored in the last few decades. This is 19 especially true in relation to understanding repertoire size and function. In male songbirds, song 20 repertoires are thought to function primarily in mate attraction and territory defense. Only a few 21 studies to date have explored repertoire size in female songbirds, and many of those focused on 22 tropical duetting species. We quantified the size and explored the function of song repertoires in 23 a temperate breeding songbird, the eastern bluebird. Female song in eastern bluebirds functions 24 primarily in communication with a social mate in order to maintain long term pair-bonds. 25 Previous work in this species also documented that males have large repertoires serving a variety 26 27 of purposes. We found that female bluebirds have similar song repertoire sizes to males. Also, females share their repertoires and song types more closely with their mate than shared with non-28 mates. This is one of the first studies to document large female repertoires in a non-duetting 29 30 temperate species. Our findings indicate that large female repertoires and song type sharing in this species is integral to communication between social mates. Additionally, the large effect size 31 of song type sharing with newly formed mates suggests open ended learning may be present in 32 this songbird, a previously under documented phenomenon in females. This study provides the 33 34 groundwork to explore the ontogeny and evolution of song repertoire size in female songbirds and to expand our understanding of song repertoires beyond their functions in males as an 35 indicator of male fitness. 36

- 37 Keywords: Eastern Bluebirds, female song, repertoire, mate communication, long-term pair-
- 38 bond, open-ended learning

40 GRAPHICAL ABSTRACT



42 Female song repertoires are understudied and not well understood. We found that female eastern

43 bluebirds have large repertoire sizes similar to male repertoires in this species. Additionally, we

44 found significant song type sharing between mates suggesting that female repertoires function

45 for within-pair communication.

46 **INTRODUCTION**

Traditionally, the field of ornithology has viewed birdsong as a primarily male behavior 47 used for mate attraction and territory defense (Catchpole & Slater, 2008; Rose et al., 2019). 48 49 However, recent work has demonstrated that female song is both widespread and ancestral in 50 songbirds, and that song may have additional or different functions in females (Odom et al., 2014; Odom & Benedict, 2018). Despite these recent discoveries, there remains much to be 51 learned about female song. The degree of difference in male and female song varies between 52 species. In tropical regions, females are more likely to sing and sing at higher rates (Slater & 53 Mann, 2004; Illes & Yunes-Jimenez, 2008; Price et al., 2008). Conversely, in temperate species, 54 song is more likely to be produced exclusively or primarily by males (Morton, 1996; Slater & 55 Mann, 2004). However, in some temperate species, female song is comparable or more frequent 56 and more elaborate than male song (e.g. streak-backed oriole (partially temperate), Hall et al., 57 2010; house wrens, Krieg & Getty, 2016; eastern bluebirds, Rose et al., 2018). 58

Species differences also exist in female song function. Across species, male song is 59 60 thought to function primarily for mate attraction and territory defense (Catchpole & Slater, 2008; Rose et al., 2019). However, female song only shares these functions in some species 61 (Langmore, 2000; Illes, 2015). In other species, the function of female song is variable, from 62 resource defense in the superb fairy-wren (Malurus cyaneus) (Cooney & Cockburn, 1995; 63 Langmore, 2000), to aggressive same-sex interactions in stripe-headed sparrows (Peucaea r. 64 65 ruficauda) (Illes, 2015), and pursuit-deterrence in skylarks (Alauda arvensis) (Cresswell, 1994). Male and female song may also differ in acoustic structure, with some studies showing female 66 song to be shorter (Odom et al., 2016), quieter (Rose et al., 2018), less frequent and less complex 67 (Beletsky, 1982; Arcese et al., 1988; Price et al., 2009), or more frequent (Illes, 2015; Price et al., 68 69 2008) than male song. Conversely, males and females of some species sing structurally similar songs (Arcese et al., 1988; Campbell et al., 2016; Rose et al., 2018). Considering this variation in 70 the functional and structural similarities of male and female song, alongside the 71 underrepresentation of female song in the current literature, we still know relatively little about 72 73 female song (Odom et al., 2016). One aspect of female song that remains particularly understudied is that of female song repertoire size. 74

Song repertoire is defined as the number of unique songs sung by an individual 75 (Robinson & Creanza, 2019). Song repertoire sizes can differ greatly between species, ranging 76 77 anywhere from a few songs to thousands of songs (Vargas-Castro et al., 2012). It has been suggested that song repertoire size functions in both male-male competition and female mate 78 choice, however it is not clear whether or not song repertoire size influences female mate choice 79 80 early in the season or if it is primarily used to attract extra-pair mates (Reid et al., 2004). Additionally, song repertoire size in males has been correlated with male quality (Catchpole 81 1996; Nowicki et al., 1998; Kipper et al., 2006), plumage color (Lampe & Espmark, 1994), body 82 condition (Lampe & Espmark, 1994), age (Howard, 1974; Catchpole & Slater, 1995), neural 83 vocal region volume (Devoogd et al., 1993; Székely et al., 1996), male parental effort (Buchanan 84 & Catchpole, 2000), breeding experience (Lampe & Espmark, 1994), lifetime reproductive 85 success (Hiebert et al., 1989), advantages in territory and mate acquisition (Howard, 1974), 86 territory quality (Lampe & Espmark, 1994), duration of territory possession (Hiebert et al., 87 88 1989), and parasitic infection (Buchanan et al., 1999). However, some of these correlations have been questioned (e.g., Searcy, 1992; Beecher et al., 2000; Gil & Slater, 2000; Gahr, 2000). 89

90 Despite extensive research on male song repertoire size, its functions, and correlations 91 with life and natural history traits, we still know very little about repertoire size in females. To date, relatively few studies have investigated female song repertoire size, specifically in 92 comparison to male song repertoire size (Brenowitz & Arnold, 1986; Brown & Farabaugh, 1991; 93 Gahr et al., 1998; Rogers, 2005; Hall, 2006; Vondrasek, 2006; Brunton & Li, 2006; Illes, 2015). 94 95 Two of these studies identified species in which females possess larger individual repertoires than males (Illes, 2015) or larger group chorus song repertoires than males (Brown & Farabaugh, 96 1991). However, the remainder of these studies primarily found that females possess smaller 97 repertoires than males (Brenowitz & Arnold, 1986; Rogers, 2005; Brunton & Li, 2006), except in 98 some duetting species in which females possess similar repertoires to males (Brenowitz & 99 Arnold, 1986; Gahr et al., 1998; Hall, 2006). 100

Whereas the size of song repertoires often differs between males and females, the use of
song repertoires is similar in many species. Females use their song repertoires for duetting,
territory acquisition, joint territory defense, and intra-sexual contest (Hall, 2000; Hall, 2004;
Slater & Mann, 2004; Rogers, 2005). In addition, female song repertoire size has been correlated

with the volume of song control regions in the brain (Brenowitz & Arnold, 1986; Ball, 2016),
however, this correlation has not been found in all species (Gahr et al., 1998; Lobato et al.,
2015). The comparative lack of research on female song repertoire size suggests that there is
much left to learn by continuing to study this aspect of vocal complexity.

109 In this study we compare song repertoire size in male and female eastern bluebirds, a 110 species known to have female song with equivalent acoustic structure to male song (Rose et al., 2018). Previous work by Ritchison and Huntsman (2003) found that male eastern bluebirds 111 112 demonstrated song repertoire sizes between 40 and 81 songs. However, a similar analysis of female eastern bluebird song repertoire sizes has yet to be performed. The large song repertoires 113 114 of male eastern bluebirds function in mate attraction (Gowaty & Plissner, 1998), territory defense (Gowaty & Plissner, 1998), and intersexual communication, including mate 115 116 communication and coordination of feeding activities (Huntsman & Ritchison, 2002). Female 117 song in eastern bluebirds also functions in mate communication and pair-bond maintenance 118 (Rose et al., 2019). However, the function and extent of song repertoires in female eastern bluebirds remains largely unknown. 119

By comparing the song repertoires of male and female eastern bluebirds, we aimed to 120 answer three questions: 1) Do male and female eastern bluebirds have similar song repertoire 121 sizes? 2) Is sex or mate identity a better predictor of individual repertoire size? 3) Do mates share 122 123 more song types than non-mates? Because females share some song functions with males and 124 have otherwise complex songs, we propose that they may also have similar song repertoire sizes. Additionally, because a major function of song in eastern bluebirds is to communicate with 125 mates, the benefit of increasing information shared between mates might select for vocal learning 126 of songs from a social mate and partially drive the evolution of repertoire size in this species. 127 128 Mates may benefit in increased breeding success and pair bond maintenance from additional 129 information such as individual identity, location on the territory, nestling feeding status, nest relief. Access to these kinds of information could make nestling feeding and joint territory 130 131 defense more efficient, could reduce unnecessary aggression between mates from mistaken territory defense, and could increase future coordination and breeding success. 132

133

134 **METHODS**

135 Study Site and Subjects

136 Eastern Bluebirds (Sialia sialis) are a sexually dimorphic socially monogamous thrush 137 (Turdidae) that sustain long-term pair bonds (Coss et al., 2019). Breeding pairs maintain a territory throughout the breeding season, and may have up to two or three broods per summer 138 (Gowaty & Plissner, 2015). We recorded five breeding pairs of eastern bluebirds at our long term 139 140 field site at West Friendship Park in Howard County, Maryland, U.S.A. This 151-hectare farm 141 contains a trail of 25 nest boxes approximately 20-60 m apart from one another. Breeding pairs of eastern bluebirds were color banded according to the methods in Rose et al (2018, 2019). All 142 field methods and protocols were approved by the University of Maryland, Baltimore County 143 Institutional Animal Care and Use Committee (IACUC, approval KO01741417). Briefly, each 144 individual received a unique combination of color bands, along with an aluminum U.S. 145 Geological Survey (USGS) band in order to properly identify individuals while recording. Of the 146 five breeding pairs observed in this study, all birds had been banded and observed at the field site 147 in a previous year. Banded individuals were observed throughout the 2019 breeding season, 148 which runs from mid-April to August for eastern bluebirds in this region of the United States. 149

150 Field Methods and Data Collection

We recorded birds three days a week from May to July 2019, between the hours of 6AM 151 152 and 10AM. All recordings were taken with a Marantz PMD 661 recorder and a Sennheiser ME67 shotgun microphone with K6 powering module. The nesting stage of each of the five breeding 153 154 pairs was checked and recorded once per week. Individuals were only recorded during egg laying (pre-incubation) or when nestlings were present, as female song rates are low during 155 incubation, and birds are not present centrally in their territory between nesting attempts (pers. 156 obs. Rose). On each day of recording, individual breeding pairs were recorded once for 15 to 60 157 minutes. If neither individual was present or singing within the first 15 minutes of recording, we 158 deleted the recording and moved to the next breeding pair with eggs or nestlings. Additionally, if 159 there was any 15-minute interval without song during the entire 60 min window, we ended the 160 recording early and moved to the next breeding pair with eggs or nestlings. Due to the low 161 amplitude at which male and female eastern bluebirds sing outside of the morning chorus, we 162

made our recordings from a distance of approximately 10-20 meters from the birds to maximizeour signal to noise ratio.

Field recordings were annotated and individual songs were identified using the program Syrinx PC (J. Burt, Seattle, WA, U.S.A., www.Syrinx-PC.com). We only included songs where the individual's sex and identity had been visually verified in the field. We then clipped and pasted these songs into separate image files for each bird. For birds with more than 100 songs recorded, we used the first 50 and the last 50 songs recorded chronologically. For birds with fewer than 100 songs recorded, we used all songs recorded. These image files were used by our independent observers in order to categorize songs for each individual.

Three independent observers assessed novel song types and song type matches while 172 blind to bird sex and individual ID. All three observers were experienced at interpreting 173 spectrograms and practiced together on a sample set of 10 eastern bluebird spectrograms from 174 175 www.xeno-canto.org to increase inter-observer accuracy. Differences in song type were primarily determined by the type and order of syllables in a song (e.g., Fig. 1). All values were 176 averaged between the counts and measurements of the three observers. Variance between 177 observer counts (average 8.4 song types) was lower than variation between individual birds 178 (average 9.2 song types). We calculated inter-observer reliability using the "icc" command in the 179 R package "irr" which ranges from low to high consistence 0 - 1 (ICC = 0.7). The measurements 180 181 of variance and inter-observer reliability were calculated from the averaged full data set used in 182 this paper. For each individual bird, observers placed songs into categories based on the 183 spectrograms. After song type categories were established for each bird, all birds were compared pair-wise to establish shared song types between individuals. 184

185 Statistical Methods

We used simple enumeration of novel song types, with up to a 100 song subset, to compare repertoire size between five males and five females. Bluebird repertoires are highly variable, mostly made up of rare (only appearing once) song types. We documented the number of rare and common (occurs at least ten times) song types in each bird's repertoire. Additionally, not all song types had equal probability of occurrence and bluebird song patterns did not correspond well to the traditional categories of immediate variety versus eventual variety (Molles Wehrencamp, 1999). Therefore, common types of repertoire estimation (e.g., coupon collector,
exponential curve fitting, and Wildenthal curve fitting) are not appropriate (Kershenbaum et al.,
2015; Luttrell et al., 2016). In light of this, we focused on comparing male and female repertoires
over the first 100 songs rather than predicting total repertoire.

Not all birds sang 100 songs during the recording periods. Therefore, to ensure that all repertoire counts were comparable, we adjusted the repertoire count for each bird to account for the total number of songs measured with the following equation: adjusted count = (actual count/No. songs measured) * 100. We used Microsoft Excel to calculate unpaired two-sample ttests and reported effect size (Cohen's D) using adjusted counts to compare male and female repertoire sizes. We also compared the similarity in mate repertoire size to the similarity of repertoire sizes within each sex using unpaired two-sample t-tests.

To quantify song sharing between individuals we calculated the number of song types each individual shared with their mate and compared it to the average number of song types each individual shared with all other birds of both sexes. We then used a two-sample paired t-test to compare each individual's song type sharing. Finally, we compared song type sharing between reunited mates and new mates (reunited mates from last year vs. newly formed pair-bonds) using a two-sample t-test.

209

210 **RESULTS**

211 Repertoire Size

Female and male eastern bluebirds did not sing significantly different numbers of novel 212 song types over the course of 100 songs analyzed (p = 0.55, Cohen's D = 0.44, N = 5, Fig. 2). 213 Over 100 songs, females sang an average of 38.2 song types (range 22.0 - 47.4 song types) and 214 males sang an average of 34.7 song types (range 24.3 - 43.0 song types). Accumulation curves 215 for both male and female eastern bluebirds did not approach an asymptote (Fig. 2B). 216 Additionally, the proportion of rare (occurs once) and common (occurs at least ten times) song 217 types did not differ between males and females (respectively p = 0.79, Cohen's D = 0.2; p =218 219 0.16, Cohen's D = 1.09; Fig. 3).

Mate repertoire size, rather than sex, was a better predictor of individual repertoire size 220 (Fig. 4). On average mates differed less in repertoire size than members of the same sex (p =221 222 0.036, N = 5, mates differ: 5.2 ± 3.7 song types, same sex differ: 9.5 ± 6.6 song types). This difference seems to be driven by female repertoire size. The significant difference between mate 223 similarity versus same sex similarity disappeared for males when the two sexes were analyzed 224 225 separately. In females, mate repertoire size, rather than sex, was still a better predictor of individual repertoire size (p = 0.031, N = 5, mates differ: 5.2 ± 3.7 song types, females differ: 226 12.6 ± 8.1 song types). However, in males, mate repertoire size was not a significantly better 227 predictor of individual repertoire size (p = 0.19, N = 5, mates differ: 5.2 ± 3.7 song types, males 228 differ: 8.4 ± 5.2 song types). 229

230 Song Type Sharing

Mates shared more song types than non-mates of both sexes (p < 0.01, N = 10, Fig. 5). On average mates shared 5.7 song types (range: 4.7 - 7. 3), while non-mates only shared 2.6 song types on average (range: 2.0 - 3.2). Two out of the five breeding pairs were also mated to each other in the previous year. Long-term mates (N=2) shared an average of 4.7 ± 0 song types while new mates (N=3) shared an average of 6.4 ± 1.3 song types.

236

237 **DISCUSSION**

We compared male and female repertoire sizes in eastern bluebirds via simple enumeration across 100 songs. Female bluebirds had comparable repertoire sizes to male bluebirds. We did not find any significant differences despite a medium effect size (p = 0.55, Cohen's D = 0.44). Additionally, males and females had similar proportions of rare and common song types suggesting that their repertoires likely accumulate novel song types at a similar rate beyond the first 100 songs.

In males, song repertoires are thought to be primarily used to attract mates and to defend territories (Searcy & Andersson, 1986; Searcy, 1992; Beecher et al., 1996). In mate attraction it is thought that the songs of a male's repertoire are interchangeable and serve only to increase the diversity, and thereby the complexity, of the signal (Krebs & Kroodsma, 1980; Catchpole, 1987;

Beecher et al., 1996). However, studies of male repertoire size, as it concerns territory defense, 248 have theorized that repertoires are used through song matching and song type switching (Morton 249 250 & Young, 1986; Beecher et al., 1996; Searcy & Beecher, 2009). In these cases, the content of the repertoire matters. Neighboring males who are able to match a song type to their neighbor's in 251 quick succession or demonstrate large repertoire through constant type switching have an 252 increased ability to defend their territory (Searcy & Beecher, 2009). While these are the two 253 most commonly cited functions for repertoires in males, other studies have begun to 254 acknowledge additional functions of male song and uses for their repertoires (e.g., Johnson, 255 1983; Ritchison, 1991). For example, Huntsman and Ritchison (2002) found that, aside from the 256 major functions of large male eastern bluebird repertoires in territory defense and mate 257 attraction, male song repertoire has minor applications in coordinating feeding activities and 258 communicating distress. Therefore, it is likely that additional functions, like within-pair 259 communication, exist for male song repertoires. 260

261 Male repertoire size has been the focus of inquiry for decades, whereas only a few studies have documented female repertoire size and function in songbirds. Of these studies, a handful 262 263 focused on tropical duetting species and reported similar male and female repertoire sizes (Brenowitz et al., 1985; Illes, 2015; Beck, 2019; Moser-Purdy et al., 2019). To our knowledge, 264 265 only a few studies have examined female repertoire size in temperate non-duetting songbirds. Female European starlings (Sturnus vulgaris) have considerably lower repertoire sizes than 266 males (Pavlova et al., 2005). A preliminary examination of female bellbirds reported a large 267 disparity between male and female repertoires (Brunton & Li, 2006). Females sang only a few 268 269 song types compared to the extensive repertoire of males (Brunton & Li, 2006). However, in northern cardinals, males and females have similar and small repertoires (Vondrasek, 2006). All 270 these previous studies focused on species with relatively small repertoire sizes (8 - 23 song 271 types). Another study, in the European robin (Erithacus rubecula), showed that two females 272 seemed to have smaller repertoires than male robins (Hoelzel, 1986). Our study is one of the first 273 to: 1) document female repertoire size in a north temperate songbird species, 2) focus on a non-274 duetting species, and 3) document large female repertoires (38+ song types). However, as is the 275 case for tropical duetting species, male and female eastern bluebirds share similar repertoire 276 277 sizes.

There are a variety of reasons that male and female eastern bluebirds might possess 278 similar repertoires. The first option, given that song likely evolved simultaneously in male and 279 280 female songbirds (Odom et al., 2014), is that their repertoires have evolved over the same length of time under independent selective pressures of similar strength and direction. For example, 281 large repertoires in females might be favored for attracting extra pair mates, acting as a tutor to 282 offspring, conveying complex information such as individual identity, or alerting offspring to 283 specific threats. However, none of these options reflect the major functions of female song in 284 eastern bluebirds. Given that female song in this species functions primarily in mate 285 communication and pair bond maintenance (Rose et al., 2019), it is far more likely that a second 286 explanation is in order. A second possible explanation for similar male and female repertoire 287 sizes is that these repertoires evolved together in response to a joint evolutionary pressure. For 288 289 example, this could include joint territory defense, mutual mate attraction, or intra-pair communication. 290

291 Additional Implications of Repertoire Size: Song Learning

292 In this study, we found that not only do male and female eastern bluebirds share similar repertoire sizes over a 100-song sample, but that mate identity was a better predictor of an 293 294 individual's repertoire size than sex. This trend seems to be primarily driven by female repertoire size. In other words, each individual had a repertoire estimate closer to their mate's than to 295 296 members of their same sex. Additionally, mates, even in their first year mated, shared 297 significantly more song types with each other than with other birds. This might imply several not 298 mutually exclusive mechanisms: 1) that eastern bluebirds may practice assortative mating by 299 shared song type, 2) that eastern bluebirds practice selective attrition, and/or 3) that eastern bluebirds are open ended learners and that the birds are learning songs from their mates. 300

Assortative mating in songbirds is often characterized by females choosing males with songs similar to their father's song (Miller, 1979; Grant & Grant, 2018). However, in cases where females sing, females might choose males with songs more similar to their own. Therefore, we would expect that if birds share a large number of song types with only a few males in a population, that birds would not re-mate within the population very often. Additionally, we might expect mates to share a large portion of their repertoire. However, only two of the five pairs in this study were mates in the previous years, and birds at our field site frequently switched mates after failed nests (Coss et al., 2019). Additionally, breeding pairs in
this study only shared 8% - 33% of their repertoires. We propose that given frequent mate
changes and given that some breeding pairs shared as little as 8% of their repertoire, that
assortative mating by song type is not a likely explanation for our results.

312 Mate switching within and between seasons also conflicts with the selective attrition 313 hypothesis. Selective attrition occurs when birds over-produce song types and then selectively retain the song types best matching their neighbors or mates (Nelson, 2000). Again, in the case 314 315 of selective attrition we would expect only rare mate-switching. However, while some birds maintained multi-year pair bonds, many birds in this population frequently switched mates mid-316 317 season after failed nests. This kind of mate switching would imply high levels of plasticity in remembering the full repertoire, retaining primarily relevant song types to a single mate and then 318 319 returning to that full repertoire again during mate switching. Therefore, selective attrition is also 320 an unlikely explanation for increased song sharing between mates.

The final possibility to explain song sharing between mates is open ended learning 321 (Beecher & Brenowitz, 2005). If eastern bluebirds are open ended learners, we would expect 322 them to acquire new song types throughout their lives, especially each spring and when acquiring 323 324 a new mate. We did not test for learning and changes in repertoire between years or mates. However, none of our findings directly contradict expectations for open-ended learning. 325 326 Therefore, we propose that eastern bluebirds may be open ended learners and that both males and 327 females are able to learn additional song types in adulthood through social interactions. This is 328 further supported by previous work showing that selection on traits like large repertoire support vocal plasticity and open-ended learning (Robinson et al., 2019). If female bluebirds are open-329 ended learners, able to learn new songs seasonally via social interaction throughout their lives, 330 331 this would be one of the first times open-ended learning has been demonstrated in a female 332 songbird (but see Pavlova et al., 2010; Walsh et al., 2019). It is imperative that we fully understand the implications of female repertoires if we are to understand the evolution and 333 334 ontogeny of complexity in animal communication.

Similar male and female repertoire sizes also suggests that song repertoires in eastern
 bluebirds are, at least in part, under similar or joint selective pressures. Furthermore, the content
 of these repertoires is relevant in an intra-pair communication context. Whereas male repertoires

clearly seem to function in mate attraction and territory defense (Pinkowski, 1971; Huntsman &

- Ritchison, 2002), they also seem to function in communicating with their mated female. These
- 340 large repertoires in female bluebirds may also have additional functions such as joint territory
- 341 defense (as is likely the case for all of the tropical duetting species discussed earlier; e.g.,
- Brenowitz et al., 1985; Illes, 2015; Beck, 2019; Moser-Purdy et al., 2019) or conveying
- information to their mate, such as individual identity (Rose et al., 2019).

344 Additional Implications of Repertoire Size: Song Function

Repertoire size has been used as a metric of fitness as well as social and cognitive ability 345 346 (Botero et al., 2008; Kershenbaum et al., 2015; but see: DuBois et al., 2018; MacKinlay & Shaw, 2019). Specifically, researchers have linked male repertoire size with overall male quality 347 (Catchpole, 1996; Nowicki et al., 1998). This quality may represent physical condition such as 348 parasite load (Buchanan et al., 1999), body condition (Lampe & Espmark, 1994), age (Catchpole 349 350 & Slater, 1995), and brain morphology (DeVoogd et al., 1993); or non-physical quality such as resource holding potential (Howard, 1974), lifetime reproductive success (Hiebert et al., 1989), 351 352 and parental provisioning (Buchanan & Catchpole, 2000). However, all these studies were based solely on male subjects. We posit that many of these trends will hold true for female repertoire 353 354 size, albeit with potential variation due to differences in song function.

It is likely that traits such as resource holding potential are also correlated with female 355 repertoire size. However, the resources may differ between males and females. Male repertoires 356 are used to defend nesting territories, feeding areas, and mating opportunities (Howard, 1974; 357 Searcy & Andersson, 1986; Catchpole, 1987). Female repertoires may play a different role in 358 359 these same processes. In the case of eastern bluebirds, this resource may be a long-term pair-360 bond (Rose et al., 2019), selected for by increased reproductive success with long-term partners (Coss et al., 2019), rather than an increased number of mates. In tropical duetting species, female 361 repertoires may function more similarly to male repertoires in acquisition and maintenance of a 362 nesting territory with food resources (Hall, 2000; Hall, 2004; Slater & Mann, 2004). Through 363 these mechanisms, female repertoire size is also likely correlated with lifetime reproductive 364 365 success.

366 Future Directions

In this study we compared male and female repertoire size in eastern bluebirds and found
that breeding pairs shared similar repertoire sizes and shared more song types than non-mates.
This study is one of the first to report a large repertoire size for females in a temperate species.
The function and control of female song repertoires is largely unknown. Therefore, many
questions remain unanswered.

372 Bluebirds provide a unique system for further investigation of these topics. Given that female bluebirds are temperate breeders, yet sing complex songs (Rose et al., 2018) and maintain 373 long-term pair bonds (Coss et al., 2019), they provide an interesting comparison to tropical 374 duetting birds. Additionally, female bluebirds have large repertoires with a known song function 375 376 (Rose et al., 2019). However, there is still a lot to be learned about this system. One goal of future studies should be to increase sample size and further evaluate the patterns documented 377 378 here. We would then need to determine if eastern bluebirds are indeed open-ended learners and to what extent the neurological structure differs between males and females. Then we will be 379 380 able to pursue questions of repertoire ontogeny. Do eastern bluebird repertoires increase with age? Does song sharing between mates increase with the length of a pair bond? 381

Additionally, one of the major reasons bird song has been such a valuable model for 382 studying vocal learning and the neural control of complex vocalizations is the existence of 383 discrete neural regions that control vocal learning, memory, and production. Interestingly, male 384 385 repertoire size has been closely linked with the size of various neural regions in the brain, 386 especially the HVC (the acronym is the name) (Nottebohm et al., 1981; Canady et al., 1984; DeVoogd et al., 1993; Garamszege & Eens, 2004; but see: Kirn et al., 1989; Bernard et al, 1996). 387 However, neural volumes have not been explored extensively in conjunction with female 388 repertoire size (but see Brenowitz et al., 1985). Neural volumes are generally smaller in female 389 390 songbirds, even in species in which females sing at similar or greater rates and at similar complexity to males (e.g., streak-backed orioles; Icterus pustulatus) (Price et al., 2008; Hall et 391 al., 2010; Ball, 2016). This sexual disparity in the volume of neural regions is puzzling, but more 392 393 answers may be found through additional examination of sex differences in song learning and its neuroendocrine control. 394

This study provides the groundwork for pursuing deeper questions of the evolution, ontogeny, and mechanisms controlling female repertoires that are integral for our broader understanding of vocal communication and complexity.

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618	FIGURE LEGENDS
619	Figure 1. Examples of three song types from a single female bluebird. Two examples are given
620	of each song type to show the variability within the song categories. 1A/B) Song type 1. 2A/B)
621	Song type 2. 3A/B) Song type 3.
622	
623	Figure 2. A) The accumulation curve for each individual's song repertoire. B) The average
624	accumulation curve for male and female eastern bluebirds. (Note: The jump in average repertoire
625	size for males just after 90 songs is a statistical result of two of the five males having less than
626	100 songs.)
627	
628	Figure 3. Male and female bluebirds have similar numbers of rare (occurs only once, $p = 0.79$)
629	and common (occurs more than 10 times, $p = 0.16$) songs in their repertoires.
630	



Figure 4. Average \pm SE difference between individual repertoire size and the repertoire size of their mate / individuals of the same sex. * p < 0.05

Figure 5. Average \pm SD number of shared song types between mates versus non-mates. * p <

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0.05

644 Figure 1.













