

Abstract

Sex ratio theory states that there should be a 1:1 ratio of males to females providing that the investment to produce each sex is equal. Research in avian populations shows that sex ratio often deviate from the expected 1:1 ratio and it was predicted that this investigation would also find this trend. Sex ratio was calculated for 23 species of passerines from data on captured birds collected from the Monitoring Avian Productivity and Survivorship (MAPS) through the Institute of Bird Populations for the states of Indiana, Kentucky, Missouri, and Virginia for the years between 1992 and 2003. Birds were captured through standardized mist netting during the months from May to August of these years. A chi square test was used to determine if the ratios deviated significantly from the .50 males predicted. There were 10 species of passerines that had significantly skewed ratios, seven with male-biased ratios and three with female-biased. Life history traits and morphological measurements of the biased and balanced species were also analyzed. Clutch size was the only trait that differed significantly. Mating system, extra pair copulations, sexual dimorphism, and resources availability are other proposed mechanisms for controlling sex ratio.

Introduction

Sex ratio theory is concerned with the study of the ratio of males to females in a population. It is interesting to study this theory in order to understand the selective pressures that have effects on sex ratio. Sex ratio is defined as the proportion of males in the population and can be measured as primary sex ratio (the ratio at conception), secondary (the ratio at birth), or tertiary (the ratio at reproductive age). Most populations show a balanced sex ratio because as males become rare in the population they would become a resource and sons would be produced. As females become rare in a population more daughters are produced because they become a resource (Fisher 1958). Fisher was the first to offer this frequency-dependent selection theoretical explanation of why equal numbers of sons and daughters is an evolutionarily stable strategy (Ellegren et al. 1996). His principle states that as long as the investment involved in the production of either of the two sexes is equal, both will be produced in equal numbers (Beimborn 1976). The actual mechanisms controlling sex ratio are not completely understood, but the Mendelian explanation for sex ratio states that it results from sex-determining chromosomes. The heterogametic sex produces two kinds of gametes in equal numbers thus resulting in a balanced ratio (Symington 1987). In populations that deviate from the evolutionary expected 1:1 ratio of the sexes, genetic and environmental factors, such as unequal investment required for each sex, can result in sex ratio biases in many species. Unequal investment can result in differential costs of producing each sex, such as one sex with a larger body size requiring additional food. This bias can occur at any level- primary, secondary, or tertiary- and it can be difficult to determine the level at which the bias occurs. Different factors can affect each primary, secondary, and tertiary sex ratio and a biased primary ratio could lead to a bias in secondary ratio.

Parental fitness is the main cause of a sex ratio bias and quality, quantity, and the sex of an individual's offspring can have effects on fitness. The ratio of sons to daughters is the

outcome between genetic interests and potential environment effects with the ratio varying due to specific fitness benefits of sons and daughters. These effects can cause to the individual to vary the sex ratio of offspring as has been observed in several species of birds. Male-biased sex ratios are a result of males in polygynous species having a greater variance in reproductive success than females. However, males also have skewed reproductive success in socially monogamous species, which varies more than previously thought. Paternity analyses show many offspring in these species are sired by a nonmate male as a result of extra pair fertilizations (Moller and Birkhead 1994). In some species a male biased brood is produced when the female deems her mate to be attractive and her sons can inherit this attractive trait, which will greatly influence their reproductive success. In a population of wild birds studied, female collared flycatchers are able to adjust the primary sex ratio of their eggs in response to the attractiveness of their mate's phenotype, although the mechanism is unknown (Ellegren et al. 1996). In a captive population of zebra finches, females manipulated sex ratio by withholding resources from hatched offspring depending on the attractiveness of the color of a leg band placed on her mate. If her mate was attractive male offspring had greater value and more resources were allocated to these hatchlings (Burley 1986). These examples demonstrate the role of genetic factors in causing a sex ratio bias.

Environmental conditions and the higher cost of producing offspring of the larger, more expensive sex contributes to the sex ratio biases found in birds. Behavioral or physiological differences between male and female offspring can leave one sex more susceptible to environmental stress, such as food shortages. When unfavorable environmental conditions exist the more demanding sex will have a lower rate of survival and the sex that requires less investment will be produced (Cichon et al. 2005). Maternal body condition is one such

environmental factor that can lead to a sex ratio bias when sons are more costly to produce. Mothers in good condition produce high quality sons to achieve greater fitness because these females are better able to gather food for their offspring. Mothers in poor condition gain more by producing daughters, a less risky fitness return, rather than sons in poor condition. Female body condition correlated with brood sex ratio has been observed in house wrens (Whittingham et al. 2002). This relationship has also been observed in lesser black-backed gulls, where females in poor condition produce female-biased broods because they are unable to produce heavier eggs (Nager et al. 1999). Male-biased broods were produced by female tree swallows in better body condition and with lower parasite loads (Whittingham and Dunn 2000). Available resources in the environment are another factor affecting sex ratio. Common grackles adjust the sex ratio of their broods, producing females, the cheaper sex, when environmental conditions are unfavorable and males at times when resources are more abundant (Howe 1977). All of these species show the impact of environmental conditions, such as available resources or the presence of parasites, on sex ratio of offspring in a brood. These biased primary and secondary sex ratios at the individual nest level can influence tertiary sex ratios and can lead to a sex ratio bias of the entire population.

Monitoring Avian Productivity and Survivorship (MAPS) was created in 1989 by the Institute for Bird Populations as a cooperative effort to collect long term data on populations of over 100 land bird species across the continent. MAPS provides annual indices of adult population size and post fledging productivity, which is calculated from data on the numbers of young and adult birds captured. Additionally, this program provides annual estimates of adult survivorship and population size, along with the population growth rate from mark-recapture data. The program aims to identify and describe temporal and spatial patterns in demographic

indices and estimates. To accomplish these goals, data for each bird that is captured is collected, including species, band number, age and how aged, sex and how sexed, date, capture time, and other measurements such as wing chord and body mass. Data for the program is gathered through the use of standardized mist netting and banding during the breeding season, extending from May to August, across North America (DeSante et al. 2007). The aim of this study is to investigate sex ratio and look for any significant deviations for the 1:1 to ratio of males to females expected evolutionarily. It is expected that most species in the MAPS data will not have sex ratios significantly different from 1:1, however some species will deviate from this ratio for reasons such as sexual dimorphism. Patterns among the species with biased sex ratios will be examined to determine the possible causes for either male or female biases in these species. Additionally, differences between the unbiased and biased populations will be analyzed to understand why some species have the expected balanced sex ratio and others deviate. The expansive network of MAPS stations, long term length of station operation, and the standardized capturing procedures make this data set a valuable resource in investigating sex ratio in a number of species in a particular region.

Materials and Methods

The existing data set was acquired through the Institute for Bird Populations MAPS program for the species captured in the states of Indiana, Kentucky, Missouri, and Virginia. The birds in Indiana, Kentucky, and Missouri were captured in 24 stations operating in the years from 1994 to 2002; data from Virginia were gathered between 1992 to 2003 from 47 operating stations. The numbers of birds captured in both of these databases for each species were combined by species for analysis in this study. Birds were caught during the breeding season by mist netting at each station once approximately every ten days. Netting began at local sunrise

time and, if possible, nets were closed six hours after sunrise time. Nets were checked every 15 to 20 minutes. Number of birds of each species captured every year and sex of each captured bird were recorded. The number of birds for which sex was unknown was also recorded. This data set did not contain age or any morphological measurements for any of the captured birds.

Many species were eliminated from the original MAPS data set. Only species that had a minimum of 50 individuals captured were considered a large enough sample size to analyze for a sex ratio bias. This was to eliminate possibility that the bias in sex ratio was only observed because the small sample size was an inadequate representation of the population. Of these species any in which unknowns were 50 percent or greater of the captured birds were eliminated. Species with a greater percentage of unknowns would not have been useful to analyze because it is unknown whether the bias is only observed due to difficulties in accurately sexing the birds. In these remaining species the proportion of the captured birds that were male and female was then determined. This data set provides information on tertiary sex ratio in these populations. A chi-square test was used to analyze the significance of any deviations from a 1:1 sex ratio in these species. Statistical tests were done using SPSS. Additionally, life history and morphological information was gathered on each species (Gray 1996; Read and Weary 1900; Robbins et al. 1966). Significance in differences, using a t-test, in these characteristics was analyzed to determine if they were possible reasons for the biased or balanced sex ratios found in the species.

Results

There were 26 species that remained from the original MAPS data set for analysis after the elimination of species based on the criteria of having a large enough sample size and less than 50 percent unknowns left (Table 1). Analysis with the goodness of fitness test ($\chi^2=3.841$,

df= 1, $p < .05$) revealed significant sex ratio biases in 11 of these 26 species (Figure 1). There were eight species with a male biased sex ratio and three species with a female biased sex ratio at the tertiary or reproductive stage (Table 2a and 2b).

Information on breeding habitat, nest type, clutch size, length of incubation, days to fledging, and diet were obtained for 23 species, 10 with a biased sex ratio and 13 with a balanced sex ratio (Table 4). Each characteristic was analyzed to determine significant difference between species with biased sex ratios and unbiased ratios. Only clutch size was significantly different between biased and balanced species ($p < .05$). Dichromatism measurements were also obtained for 16 of the species, 9 with skewed sex ratios and 7 with unbiased sex ratios (Table 5). Although analysis showed that this relationship was not statistically significant ($p = .147$), there was a general trend of species with biased ratios having higher dichromatic measurements. Differences between male and female-biased populations were not analyzed due to small sample sizes.

Discussion

Of the eleven species with significantly biased sex ratios, ten were of the order Passeriformes and one, the red-bellied woodpecker, was of the order Piciformes. Only the sex ratios of the passerines will be discussed because only three Piciformes were included in the 26 species. This small sample size does not allow for adequate analysis. Additionally, it is easier to compare life history and morphological traits among species in the same order. All but one of the passerines have socially monogamous mating systems. In many of these species extra pair copulations are observed, which can lead to extra pair fertilizations. Also, these species were similar in their life histories, breeding in the same areas, same nesting types, and similar diets. Thus mating system and life history are not the best possible explanations for the skewed sex ratios found in these passerines. Another consistent pattern found among these biased species is

sexual dimorphism, where the males are brightly colored and have distinct markings and the females are nondescript (Perrins 2003).

One possible explanation for the male biased sex ratios is the increased value of males in species with sexually dimorphic traits and observed extra pair copulations. In passerines, sexual dimorphism is usually observed in plumage coloration or ornamentation, not body size differences. Extra pair fertilizations result in males having a higher variances of reproductive success, such as in the hooded warbler where high over winter mortality means that birds only breed for one or two years (Stutchbury et al. 1997). Thus females will produce more male offspring, especially if her mate has a trait associated with attractiveness or overall health and her sons are therefore higher in value compared to daughters. Brighter plumage has been found to correlate with lower mite parasite prevalence on birds, showing that these traits are not only deemed attractive by female choice they also can indicate health of the birds (Figuerola 2000). Mating success, including increased numbers of extra pair young, is influenced by the size of black face mask in the common yellowthroat, the black hood of the hooded warbler, black head ornaments of the Kentucky warbler or the brighter plumage of the American goldfinch (Thusius et al. 2001; Parker et al. 2003; Petit 1991; Rosen and Tarvin 2006). These four sexually dimorphic species were found to be male-biased in this study. The increased reproductive fitness of males with these traits balances the cost of producing and rearing these offspring and the cost of the males maintaining these traits. These biases begin at the individual nest level and extend to the overall population. This explanation is supported by the trend that species with higher dichromatic measurements were more likely to have a biased ratio. However, this mechanism does not explain why some female-biased species exhibit similar sexual dimorphic traits or why some sexually dimorphic species maintain a balanced sex ratio.

Male attractiveness can also be used to explain female-biased sex ratios. Effectiveness of male guarding of his mate during her fertile period could have effects on the sex ratio of a population. Male guarding during the female's fertile period is a common behavior among passerines that has been found to correlate with lower rates of extra pair paternity of offspring (Chuang-Dobbs et al. 2001). Females seek extra pair copulations in socially monogamous species because not all females can form a pair bond with the most attractive males and seeking extra matings with an attractive male improves this situation (Hasselquist and Sherman 2001). If a low rate of polygyny is found to occur in a species it would be advantageous for females to produce more daughters since most females will not mate with the most attractive male (Carey and Nolan 1979). Females will have more daughters because their sons might not be attractive enough to obtain mates.

Another possible mechanism is sex ratio is dependent on the resources available in the environment, where the more expensive sex is produced in higher numbers when resources are abundant and the other when resources are limited. Research has shown a link between acorn masting and veery population growth, but more studies are necessary to determine the correlation between males produced and acorn masting (Schmidt 2003). A study of the common grackle exhibited this same correlation of resource dependence across seasons. Earlier nesters had female-biased broods because insects, the primary food supply, are not abundant at this time of the year and female fledge at a significantly smaller size than males (Howe 1977).

Additional overall sex ratio patterns these species are dependence on higher male or female mortality rates. This difference can be present in adulthood, for example, females could have higher mortality due to the expenditure of energy necessary for egg laying, as seen in the brown-headed cowbird, and males with bright markings could be more susceptible to predators

(Darley 1971). Also, this difference in mortality rates could be present at the time of fledging as seen in the common grackle (Howe 1977).

Errors and incomplete information in the MAPS data set could also contribute to the observed sex ratios in these species. Since the birds are captured during the breeding season this could contribute to a skewed ratio, as more of one sex could be captured depending on which incubates the eggs. In the common yellowthroat, only the females incubate the eggs, which could contribute to the male-biased sex ratio (Stewart 1953). Also there could have been sexing errors in the captured birds and the large number of unknowns, although we attempted to limit this effect, could ultimately have a great effect on the actual sex ratio in the population. The lack of morphological data made it difficult to correlate body size or other measurements with sex ratio. Age data would have been helpful in ensuring that tertiary sex ratio was the stage studied in this investigation. Additionally, a larger number male-biased versus female-biased species would have allowed for better analysis for significant differences between these species.

Research on the life history, including mating systems and investment necessary for each sex, and morphological measurements is necessary to understand the reasons for the biased or balanced sex ratios found in each of these species. This will explain why there are differences in sex ratio in these populations, especially in species of that share characteristics. More research is also necessary to understand the complete effects of dichromatism, mating system, and clutch type on the sex ratio as these characteristics appear to have the greatest effect on determining sex ratio.

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Figure Legend

- Table 1. The 26 species that fit the criteria for study.
- Table 2. The eight species with male-biased sex ratios.
- Table 3. The three species with female-biased sex ratios.
- Table 4. Summary of life history traits for the 26 species.
- Table 5. Dichromatism measurements for 16 species.
- Figure 1. Graph showing the proportion of males and females in each species.

Table 1.

Species	Males	Females	Total	Proportion Male	Proportion Female	χ^2
American Goldfinch	244	195	439	0.56	0.44	5.469*
Black-throated Blue Warbler	25	57	82	0.30	0.70	12.488*
Blue-winged Warbler	289	273	562	0.51	0.49	0.456
Brown-headed Cowbird	23	149	172	0.13	0.87	92.302*
Canada Warbler	95	95	190	0.50	0.50	0.000
Chestnut-sided Warbler	44	35	79	0.56	0.44	1.025
Chipping Sparrow	33	27	60	0.55	0.45	0.600
Common Grackle	252	225	477	0.53	0.47	1.528
Common Yellowthroat	843	536	1379	0.61	0.39	68.346*
Downy Woodpecker	375	367	742	0.51	0.49	0.086
Eastern Towhee	377	333	710	0.53	0.47	2.727
Field Sparrow	231	208	439	0.53	0.47	1.205
Hairy Woodpecker	114	117	231	0.49	0.51	0.039
Hooded Warbler	682	451	1133	0.60	0.40	47.097*
Indigo Bunting	858	987	1845	0.47	0.53	9.020*
Kentucky Warbler	890	622	1512	0.59	0.41	47.503*
Northern Cardinal	1001	1071	2072	0.48	0.52	2.365
Northern Parula	82	90	172	0.48	0.52	0.372
Prairie Warbler	238	183	421	0.57	0.43	7.185*
Prothonotary Warbler	305	247	552	0.55	0.45	6.094*
Red-bellied Woodpecker	62	37	99	0.63	0.37	6.313*
Rose-breasted Grosbeak	53	51	104	0.51	0.49	0.038
Scarlet Tanager	232	249	481	0.48	0.52	0.601
Summer Tanager	85	87	172	0.49	0.51	0.023
Veery	365	271	636	0.57	0.43	13.893*
Yellow-breasted Chat	393	389	782	0.50	0.50	0.020

*indicates $\chi^2 \geq 3.841$, $p < .05$

Table 2.

Species	Common Name	Total	Proportion Male
<i>Carduelis tristis</i>	American Goldfinch	439	0.56
<i>Geothlypis trichas</i>	Common Yellowthroat	1379	0.61
<i>Wilsonia citrina</i>	Hooded Warbler	1133	0.60
<i>Oporornis formosus</i>	Kentucky Warbler	1512	0.59
<i>Dendroica discolor</i>	Prairie Warbler	421	0.57
<i>Protonotaria citrea</i>	Prothonotary Warbler	552	0.55
<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	99	0.63
<i>Catharus fuscescens</i>	Veery	636	0.57

Table 3.

Species	Common Name	Total	Proportion Male
<i>Dendroica caerulescens</i>	Black-throated Blue Warbler	82	0.30
<i>Molothrus ater</i>	Brown-headed Cowbird	172	0.13
<i>Passerina cyanea</i>	Indigo Bunting	1845	0.47

Table 4.

Species	Breeding Habitat	Nest type	Clutch Size	Incubation length (days)	Days to fledge	Diet
American Goldfinch*	Successional-scrub	Open-cup	5	11	14	seeds
Black-throated Blue Warbler**	Woodland	Open-cup	4	12.5	11.5	insects
Blue-winged Warbler	Successional-scrub	Open-cup	3.5	10.5	9	insects
Brown-headed Cowbird**				11.5	10.5	seeds
Canada Warbler	Woodland	Open-cup	4			insects
Chestnut-sided Warbler	Successional-scrub	Open-cup	4	12.5	11	insects
Chipping Sparrow	Urban	Open-cup	4	12.5	10	seeds
Common Grackle	Urban	Open-cup	4.5	13.5	18	seeds
Common Yellowthroat*	Successional-scrub	Open-cup	4	12	10	insects
Eastern Towhee	Successional-scrub	Open-cup	4	12.5	11	seeds/fruits
Field Sparrow	Successional-scrub	Open-cup	4	12	7.5	seeds
Hooded Warbler*	Woodland	Open-cup	3.5	12	8.5	insects
Indigo Bunting**	Successional-scrub	Open-cup	4	12.5	9.5	insects
Kentucky Warbler*	Woodland	Open-cup	4.5	12.5	9	insects
Northern Cardinal	Successional-scrub	Open-cup	3.5	12.5	9.5	seeds/fruits
Northern Parula	Woodland	Open-cup	5	13		insects
Prairie Warbler*	Successional-scrub	Open-cup	4	12	9.5	insects
Prothonotary Warbler*	Woodland	Cavity	5.5	13	11	insects
Rose-breasted Grosbeak	Woodland	Open-cup	4.5	13.5	10.5	insects
Scarlet Tanager	Woodland	Open-cup	4	13.5	10	insects
Summer Tanager	Woodland	Open-cup	3.5	12		insects
Veery*	Woodland	Open-cup	4	11	10	insects
Yellow-breasted Chat	Successional-scrub	Open-cup	4.5	11	8	insects
*male biased, **female biased						

Table 5.

Species	Dichromatism
American Goldfinch*	8
Black-throated Blue Warbler**	3.91
Chestnut-sided Warbler	3
Chipping Sparrow	0
Common Yellowthroat*	2.8
Field Sparrow	1
Indigo Bunting**	9.8
Northern Cardinal	8
Northern Parula	2
Prairie Warbler*	3
Prothonotary Warbler*	4.87
Rose-breasted Grosbeak	8.75
Scarlet Tanager	10
Summer Tanager	11
Veery*	0
Yellow-breasted Chat	3.54
*male-biased, **female-biased	

Figure 1.

