

## Article

# Identifying Offspring Sex Ratio Skews in Zoological Facilities Using Large Historical Datasets

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**Abstract:** The Fisher principle states that species should produce offspring at a ratio of 1:1 unless there are sex-specific differences in rearing costs. Research conducted across taxa has found that animals will vary the sex ratio of their offspring so as to maximize personal fitness in response to various ecological and biological variables. This phenomenon has been especially well studied within the Avian class. Professionally managed populations provide a useful framework within which to study the impacts of numerous variables on sex allocation strategies. Zoological facilities may be especially motivated to investigate this phenomenon due to corresponding conservation and welfare implications. We analyzed a large dataset containing the demographic data of over 1 million zoo-housed birds for species-specific offspring sex ratio biases. The offspring sex ratios of 19,867 zoo-hatched dams were calculated, and the median offspring sex ratio of 277 species from 25 orders was calculated across two 20-year time periods. We used a Wilcoxon signed rank tests with a Holm Bonferroni alpha criterion in order to determine if species medians differed from parity. Only one species in one time period displayed a significant species median offspring sex ratio. The limits of our dataset are discussed. We propose that future research should further explore the determinants of sex allocation strategies for species held within zoological facilities.

**Keywords:** avian; sex bias; sex allocation; zoo science



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## 1. Introduction

The Fisher principle posits that populations without external interference will produce progeny, with a sex ratio of 1:1 [1]. In addition, it theorizes that differing parental investment between offspring of different sexes should facilitate an advantage to individuals that mediate offspring sex [1,2]. Decades of research have supported this theory, and evidence for selective sex allocation has been found in numerous species of plants and animals [3–5].

Biased offspring sex ratios are produced when individuals selectively distribute resources to offspring of the more advantageous sex. The adjustment of offspring sex ratios away from parity occurs on two levels: the primary level and the secondary level. The primary level occurs before fertilization, when the sex of the offspring has not yet been determined. The secondary level occurs after fertilization and results in the loss of the offspring. This loss may occur any time after fertilization, including before parturition or hatching [4]. Dedicated research has uncovered numerous biological and environmental factors which determine the presence and direction of offspring sex ratio biases. These variables often rely heavily on sex-specific biology, such as the direction of sexual dimorphism [6], sex-biased dispersal [7–9], mortality [10], and social behavior [9,11]. Nevertheless, factors which differ between individuals can also be determinate of offspring sex ratio biases. For example, maternal age [12–14] and condition [15–18] have been connected with offspring sex ratio biases in numerous taxa. Maternal rank is also predictive of offspring sex ratio biases in at least two species of ungulate: mountain goats (*Oreamnos americanus*) [14] and red deer

(*Cervus elaphus*) [19]. Finally, numerous environmental variables are predictive of offspring sex ratio biases. One such variable is season, which predicts offspring sex ratios in several species of bird [20–23], the aphid parasitic wasp (*Aphidius ervi*) [24], and the big brown bat (*Eptesicus fuscus*) [25]. Another is territory quality; Seychelles warbler (*Acrocephalus sechellensis*) females on high-quality breeding territories over-produce daughters, while those on low-quality breeding territories under-produce the same sex [9]. As dozens of variables have been identified with connections to offspring sex ratios, further research is needed to tease apart the effects of one factor from another.

A considerable amount of research into offspring sex ratio biases has focused on the class Aves. In birds, females are the heterogametic sex, and thus oocytes rather than spermatozoa determine the sex of resulting offspring [26–28]. While genetic factors may be at play [29,30], the hormonal profiles of mother birds have been identified as a prime candidate for the biological mechanisms underlying offspring sex ratio biases [26,28,31]. In particular, experimental evidence indicates that the hormones corticosterone [31–35] and testosterone [36,37] are key players in this phenomenon, with the exact direction of the sex ratio bias often relying on timing of the exposure [4,35]. The connections between biased sex ratios and the hormone corticosterone are of particular note and may indicate a connection between generalized activation of the hypothalamic–pituitary axis (HPA) and biased offspring sex ratios. Indeed, the connections between glucocorticoids, maternal stress, and female-biased offspring sex ratios have been well documented in humans [38]. Evidence for this association also exists in non-human mammals, with socially stressful conditions resulting in female-biased offspring in house mice (*Mus musculus domesticus*) [39] and male-biased offspring in bridled nail-tailed wallabies (*Onychogalea fraenata*). In giant pandas (*Ailuropoda melanoleuca*), females who displayed more stereotypic behaviors were more likely to produce female offspring, while males who displayed more stereotypic behaviors were more likely to produce male offspring [40]. In birds, seemingly stressful situations such as poor-quality diets [41,42] and mates [43,44] have been linked to offspring sex ratios. However, this relationship may not be straightforward, as the impacts of stress may be modulated by body maternal condition [15,16], and differing results have been produced in the same species [32,36,41,42,45]. As a result, more evidence is desperately needed to better understand how offspring sex ratio is impacted by the HPA axis.

Professionally managed populations may be a useful and underrepresented sample with which to study sex allocation as we can control certain factors known to influence offspring sex ratios and facilitate the study of others. For example, diet quality and maternal condition is often standardized across human care, allowing for variations in stress, mate quality, and maternal age to be examined strategically. The zoo environment is characterized by the presence of guests, restricted space, and the management of important variables such as group composition and feeding routines [46]. Consequently, dedicated investigation is required to tease out how sex allocation strategies function in this unique setting. Furthermore, zoological facilities have a vested interest in maintaining self-sustaining and genetically diverse populations to preserve professionally managed breeding programs [47,48]. Additionally, healthy ex situ populations are vital to reintroduction and genetic supplementation programs of endangered or extinct fauna, programs which are often considered central to the zoological mission [47–49]. As biased offspring sex ratios can have detrimental impacts on long-term feasibility, zoos may be especially concerned about biases in populations [50]. Finally, zoological facilities are increasingly dedicating resources towards the investigation of animal welfare [51]. As such, the connections between the HPA axis and biased offspring sex ratios offer a promising avenue for identifying species which may be at risk of poor welfare outcomes. All together, these factors suggest that zoological facilities should be especially motivated to identify and investigate sex ratio biases in their collections.

The goal of this project was to chart the offspring sex ratios of a large taxonomic group held within zoological facilities. We chose to investigate the class Aves due to the wealth of published work on sex ratio biases in wild bird populations. We wanted to identify

if stable-specific offspring sex ratio biases could be identified across time using a large historical dataset. We believe that this project represents the first step to identifying and investigating factors which contribute to sex ratio biases in zoological populations.

## 2. Materials and Methods

We submitted a data application request to Species360, the organization which coordinates the Zoological Information Management System (ZIMS). The ZIMS represents the world's largest database of ex situ wildlife populations [52]. Our request was approved by several departments within Species 360, including the Research Council, the Science departments, the Product Development department, and the Board of Trustees. We then received two large ZIMS datasets. The first dataset was composed of 1,570,825 first acquisition entries and represented the entirety of avian entry events within the Species360 records. This dataset contained information on the sex of the hatchling, hatch-date, certainty of hatch-date, hatch location (wild or within a zoological facility), and acquisition date. This allowed us to identify 1,141,196 hatching events in human care. Other acquisition events, namely transfers, were excluded from analysis. The second database contained parentage data for 2,876,296 parent-offspring dyads and included information on the origin of the parent (ZIMS or non-ZIMS), parent type (sire or dam), and the probability of parentage. Using this database, we identified 1,018,723 dam-offspring dyads. By cross-referencing the anonymous individual IDs between these two databases, we formed a single database containing the species, sex, parentage, and hatch date of 829,009 zoo-hatched birds representing 1672 species.

Several species names within the ZIMS database were deemed out-of-date or synonymous with more common scientific names. Animals were thus organized at the species level using the International Ornithologist Congress (IOC) World Bird List (11.2), which was cross-referenced with a list of alternative scientific names collected from the literature (Supplementary Table S1). This resulted in a database containing demographic information on 1582 species.

In order to account for the impact of evolving husbandry on the health and welfare of zoo-housed animals [49–51], birds which were listed as hatching before 1980 were removed from analysis ( $n = 20,095$ ). Our database was further divided into birds which hatched from 1980 to 1999 (Time Period 1) and 2000 to 2019 (Time Period 2).

Within our database, we considered dams to be birds who were sexed as female, who had 2 or more sexed offspring, and whose parentage over said offspring was considered certain. All other animals were removed from the analysis. Offspring sex ratios were calculated per dam as male offspring/male offspring + female offspring [52]. Species median offspring sex ratios, interquartile ranges, minimum, and maximum offspring sex ratios were calculated for species which had 20 or more dams who fit our criteria. Medians were chosen over means as our data were non-normally distributed within species (Supplementary Figure S1).

One-sample two-tailed Wilcoxon signed rank tests were then run to ascertain if species median offspring sex ratios differed significantly from the expected 50:50. Due to the high number of statistical tests run in each time period, a standard alpha criterion of less than 0.05 could be expected to result in as many as 5 false positives in Time Period 1 and 13 in Time Period 2. Holm's Bonferroni corrections were calculated for each statistical test run in order to reduce the possibility of a Type 1 error [53], and significance was determined using these corrected  $\alpha$  criteria.

## 3. Results

### 3.1. Descriptive Statistics

Our final dataset contained 5029 dams representing 21 orders, 39 families, and 120 species in Time Period 1. In Time Period 2, our final dataset contained 14,838 dams representing 28 orders, 66 families, and 266 species. One hundred and nine species were present in both time periods. In both time periods, the orders Anseriformes and Psittaci-

formes were particularly prevalent (Figure 1A,B). Anseriformes represented 26% of the dataset in Time Period 1 (31 species) and 16% in Time Period 2 (44 species). The vast majority of this representation was due to a single a family, *Anatidae*, which contained 30 species in Time Period 1 and 43 species in Time Period 2. Psittaciformes represented 14% of the database in Time Period 1 (17 species) and 16% in Time Period 2 (43 species). Family representation throughout the order was more widespread than for Anseriformes; however, the family *Psittacidae* was best represented in both Time Period 1 (10 species) and Time Period 2 (21 species).

Certain orders appeared to display a larger percentage of species with female- or male-biased skews than others (Figure 2A,B). For example, in Time Period 1, 52.94% of the Psittaciformes species and 100% of the Columbiformes species analyzed had a male-biased skew, which was any sex ratio higher than 0.50. However, by Time Period 2, both orders appeared more balanced, with 27.91% of Pscittaciformes species and 42% of Columbiformes species displaying a male bias.

(A)

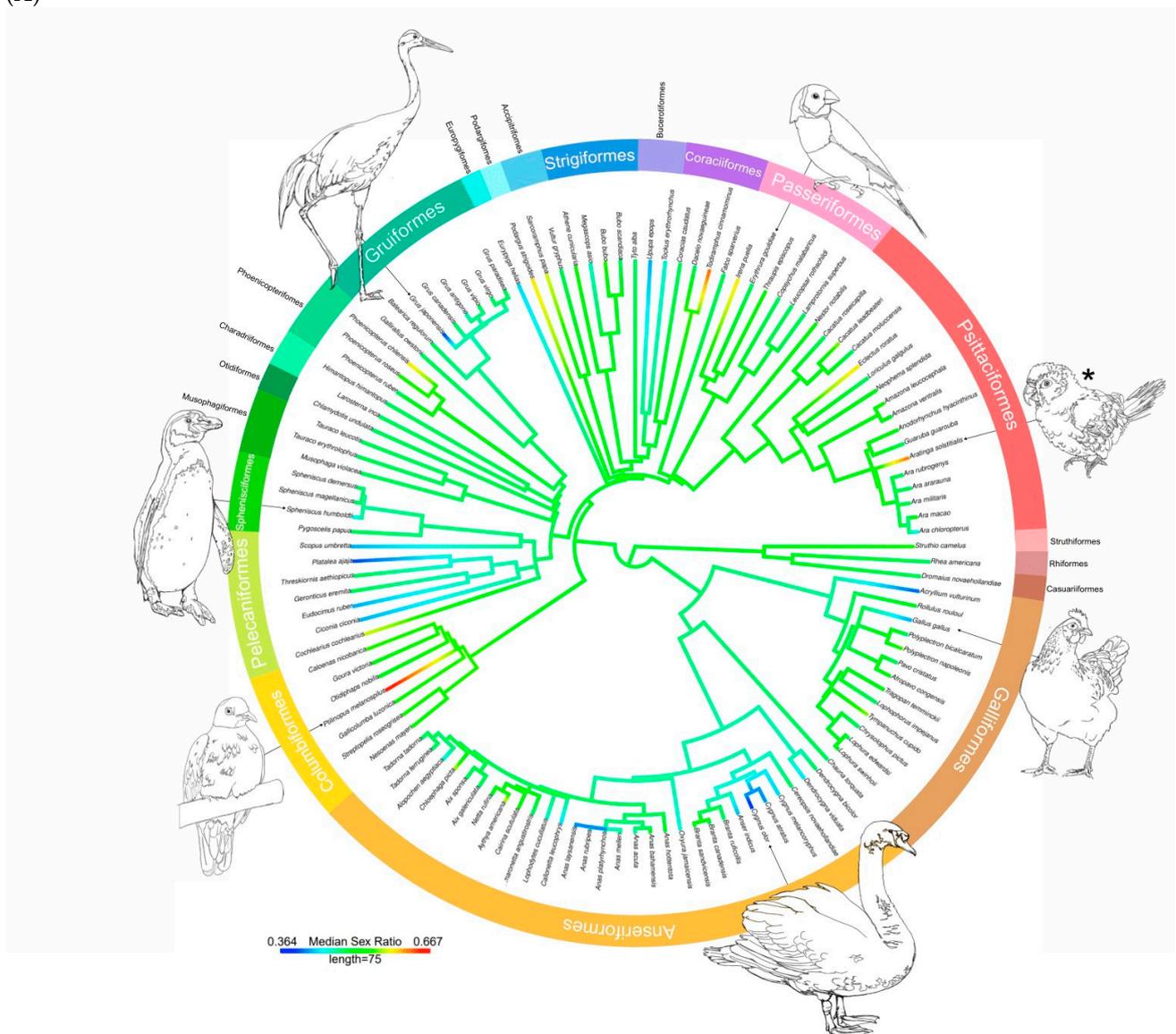
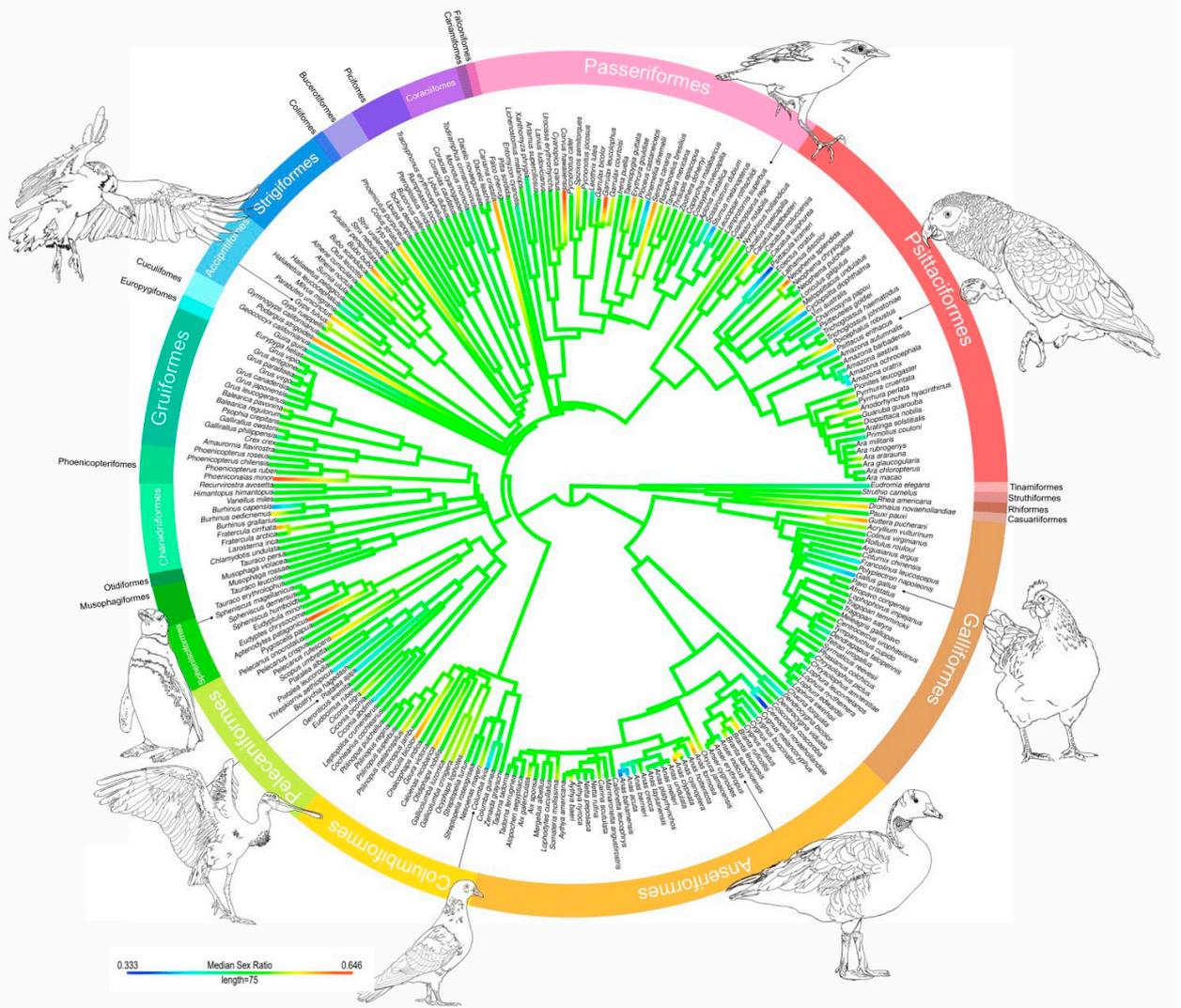


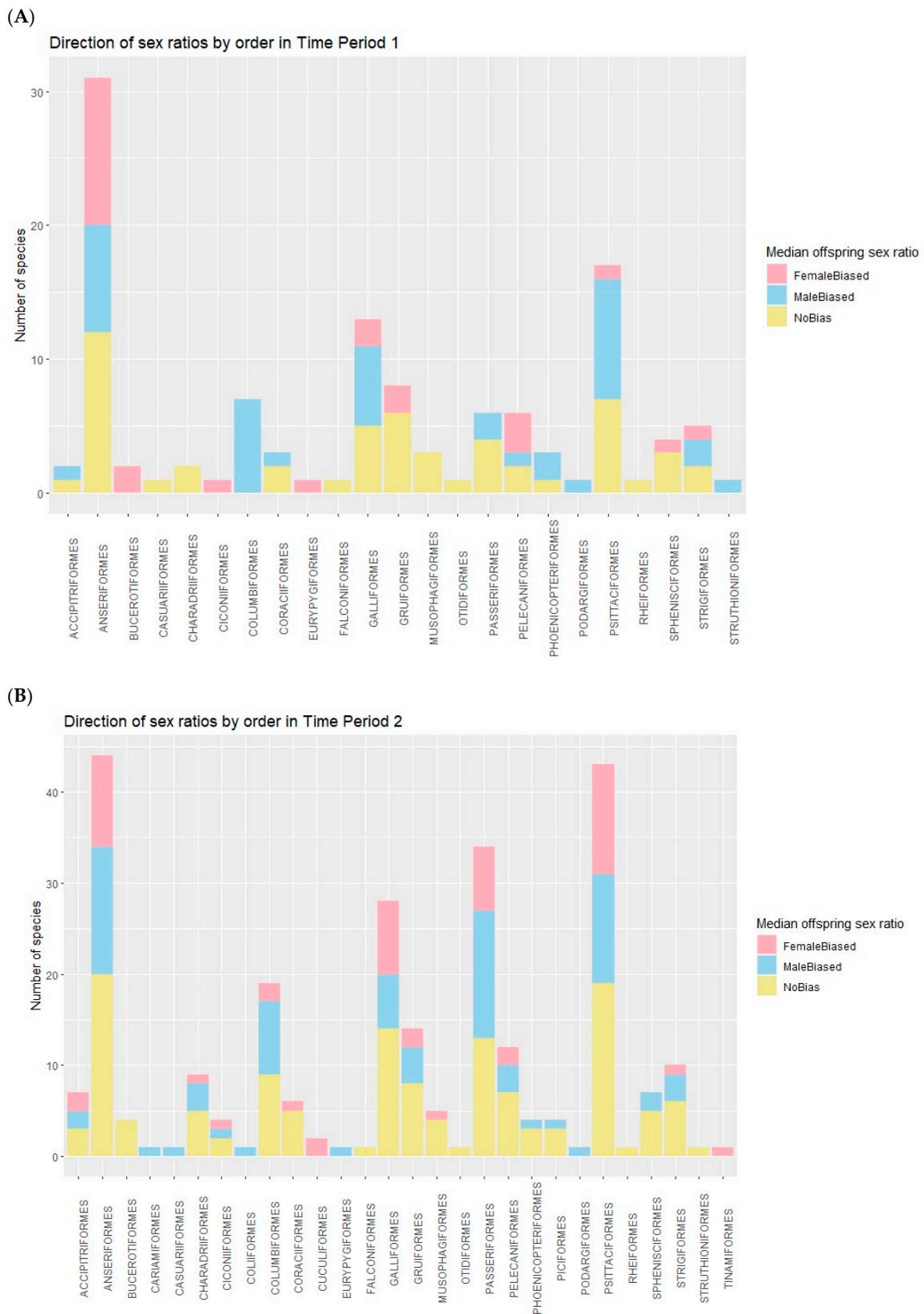
Figure 1. Cont.

(B)

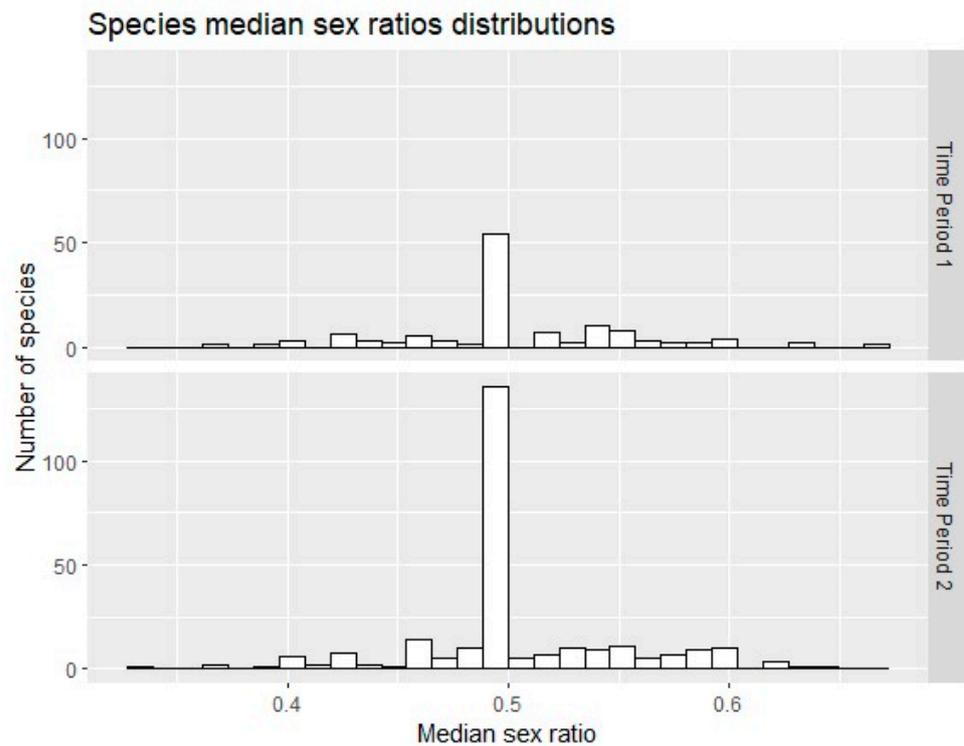


**Figure 1. (A,B)** Species median offspring sex ratios across phylogeny in Time Period 1 (A) and Time Period 2 (B). Phylogenetic data were obtained from Vertlife.org as 1000 randomly generated Ericson trees which were summarized into a single consensus tree. Trees which did not contain an edge were not included in the calculation of the consensus tree. Both the consensus tree and dendrogram were created using the package phytools [54] in R Studio version 4.3.1. Species are labeled with names used in [55] and may be synonyms of the IOC names used throughout the rest of this paper (Supplementary Table S1). Resultingly, certain taxons not recognized in (55) are not represented in the dendrogram. Warm colors represent a male-biased species median offspring sex ratio, while cool colors represent a female-biased species median offspring sex ratio. Green represents a species median offspring sex ratio of exactly 0.50. \* Only one species, the sun parakeet (*Aratinga solstitialis*), displayed a sex ratio skew, which met significance.

In total, 45% of the species analyzed had a median offspring sex ratio of 0.50 in Time Period 1, and 50.38% had the same in Time Period 2 (Figure 3). In Time Period 1, the lowest (most female-biased) species median sex ratio was the Laysan duck (*Anas laysanensis*) at 0.36, while the highest (most male-biased) was in the Black-napped fruit dove (*Ptilinopus melanospilus*) at 0.67. In Time Period 2, the lowest sex ratio was the Cape Barren goose (*Cereopsis novaehollandiae*) at 0.33, while the highest was the Northern Shoveler (*Spatula clypeata*) at 0.65.



**Figure 2. (A,B).** Direction of species median offspring sex ratios in Time Period 1 (A) and Time Period 2 (B) grouped by order. Male bias indicates a species median offspring sex ratio greater than 0.50, while female bias indicates a species median offspring sex ratio less than 0.50. No bias indicates a species median offspring sex ratio of exactly 0.50.



**Figure 3.** Species median offspring sex ratio distributions for Time Period 1 and Time Period 2. Sex ratios were calculated per dam as  $M/M+F$  for dams which had two or more sexed offspring. Median offspring sex ratios were only calculated for species which had 20 or more dams.

### 3.2. Significance Testing

The results of the Wilcoxon signed rank tests indicated that 8 species out of the 120 studied in Time Period 1 had significantly skewed species median offspring sex ratios. Three of these eight species were from the order Anseriformes, two species were from the order Psittaciformes, and there was one species each from the orders Galliformes, Gruiformes, and Sphenisciformes (Supplementary Table S2). Five species, or 4.17% of the species analyzed, were female-biased. Three species, or 2.5% of the species analyzed, were male-biased. In Time Period 2, the Wilcoxon signed ranks test reported that 23 species out of the 266 studied in Time Period 2 had significantly skewed species median offspring sex ratios. Eight species were from the order Anseriformes, two from the order Columbiformes, two from the order Passeriformes, five from the order Psittaciformes, two from the order Sphenisciformes, and one species each was from the orders Accipitriformes, Galliformes, and Pelecaniformes (Supplementary Table S2). Twelve species, or 4.5% of the species analyzed, were female-biased. Eleven species, or 4.14% of the species analyzed, were male-biased. When taking into account the over-representation of certain orders (3AB), significantly biased species median offspring sex ratios were evenly spread throughout the examined taxa in both time periods. A notable exception is the order Sphenisciformes. Despite forming only 3.33% of the population in Time Period 1 and 2.63% in Time Period 2, Sphenisciformes produced a species with a significant female-biased median offspring sex ratio in Time Period 1 and two species with significant male-biased median offspring sex ratios in Time Period 2. For comparison, the order Passeriformes made up 5% of the population in Time Period 1 and 12.78% of the population in Time Period 2 and produced two species with significant species median offspring sex ratios in Time Period 2, while producing none in Time Period 1.

After the Holm Bonferroni-adjusted alpha criterion was utilized, only one species in one time period displayed a significant species median offspring sex ratio. This was the sun parrot (*Aratinga solstitialis*) in Time Period 1 (1A). This species displayed a male-biased median offspring sex ratio (0.63) from a population of 40 dams. Interestingly, this species

displayed a female-biased species median offspring sex ratio of 0.33 in Time Period 2. However, the bias in Time Period 2 was not significant.

#### 4. Discussion

Our analysis was a largely exploratory effort to chart the offspring sex ratios of a large taxonomic group in zoological facilities and to identify if stable species-specific offspring sex ratio biases could be identified in a historical dataset. We analyzed a dataset of Avian acquisition events in zoological facilities, the size of which is truly rare in the field of zoo science. The majority of species analyzed displayed a median offspring sex ratio of exactly 50:50. As only one species in one time period displayed a significant median offspring sex ratio bias, we did not find evidence for stable species-specific offspring sex ratio biases.

To the authors' knowledge, this study is the first to examine sex ratios under human care across such a wide swath of phylogeny. Preliminary analysis of our descriptive statistics indicated a great degree of variance within closely related taxons. As an example, in Time Period 2, the family *Anatidae* contained both the most male-biased and the most female-biased species median offspring sex ratios in the time period (*Cereopsis novaehollandiae* and *Spatula clypeata*, respectively). While less extreme, the variation in the presence and direction of offspring sex ratio biases was prevalent across the phylogeny.

While dozens of species in both time periods displayed species median offspring sex ratios which differed from 50:50, virtually none differed significantly from parity. This result was surprising, as previous research has found sex ratio biases in several of the species analyzed. For example, a genetic analysis of Red-crowned cranes (*Grus japonensis*) chicks hatched over a 25-year time period at a breeding facility in Russia found a significant female bias [56]. We also found a female bias in the median offspring sex ratio of this species during both time periods; however, both proved to be non-significant.

To the author's knowledge, only one previous study exists which compares the sex ratios of multiple species of birds in human care [57]. This study analyzed 80 species of managed Psittaciformes and found 3 species with significant and male-biased offspring sex ratios. The species identified by [57] were the galah cockatoo (*Eolophus roseicapilla*), Senegal parrot (*Poicephalus senegalus*), and African grey parrot (*Psittacus erithacus*). The Senegal parrot was not present in either of the time periods analyzed in our dataset. However, the galah cockatoo was present in both and consistently displayed a median offspring sex ratio of exactly 0.50. The African grey was present only in Time Period 2, where it displayed a non-significant female-biased sex ratio. While the sun parrot was present in the [57] dataset, it displayed a slight male bias that did not reach significance even before the correction for multiple significance tests. Furthermore, 72% of the species analyzed in [57] displayed a male-biased offspring sex ratio. While we also found that the majority of Psittaciformes displayed a non-significant male bias in Time Period 1, this effect disappeared in Time Period 2. The large difference between the findings of [57] and our findings is especially surprising when considering that [57] used data from private genetic sexing companies. These kinds of companies are often utilized by zoos to sex their collection animals. As such, it is possible that our datasets contain many of the same individuals. However, there were numerous differences in our study designs, which may explain the differing results observed. Potentially the most relevant set of differences is that [57] did not separate into time periods, examined general sex ratios instead of offspring sex ratios, and did not control for the origin of the individual animal. That being said, the differences observed in Psittaciformes between the two time periods of our dataset are interesting in themselves. Future work investigating sex ratio biases could address what biological and environmental variables lead to variations in species median offspring sex ratios over time and condition.

The surprisingly low percentage of analyzed species which displayed a significant species median offspring sex ratio may be due to several important limitations in our study design. While epidemiological methods provide numerous benefits, in this case a sample size truly rare in the field of zoo-based animal welfare, they also present several limitations. One such limitation was an inability to control for the differences in sexing

procedures, which is important as many avian species are not sexually dimorphic or only become sexually dimorphic at maturation. As a result, sexing can require expensive and relatively invasive techniques that are applied conservatively. Indeed, roughly 40% of our dataset was composed of unsexed individuals. Unfortunately, this leaves open the possibility that external confounds affected our results. For example, if facilities waited until maturation to sex sexually dimorphic birds, sex-specific juvenile mortality could have impacted our list of species median offspring sex ratios. This is especially important to consider since sex-specific juvenile mortality is an important driver of sex ratio skew in wild bird populations [58–61]. The use of in-ovo sexing, a common management technique in which eggs are sexed and culled prior to hatching, likely impacted our data as well [26,62,63]. Future studies should consequently control for the methods with which facilities sex to their animals and the population management procedures employed.

Finally, the results of this study and future investigation into sex ratio biases within historical datasets could prove an important asset to the management of zoological populations for several reasons. From the perspective of zoo-based animal welfare science, promising scientific work has indicated a connection between the HPA axis and biased offspring sex ratios [4]. As sex ratio analysis is non-invasive, relatively cheap, and potentially scalable, it may hold potential as an epidemiological welfare indicator. From the perspective of conservation science, biased offspring sex ratios present a sizable danger to the long-term viability and conservation value of ex situ breeding populations [50]. Consequently, future work is needed to better understand the determinates of sex ratio biases in zoo-held species so as to better investigate the welfare of collection animals and maintain the health of professionally managed populations.

## 5. Conclusions

It is well understood that individuals of many species can adjust the sex ratio of offspring to obtain a fitness advantage based on numerous environmental and biological variables. Our study was an exploratory effort to investigate how the zoological environment may impact sex allocation strategies within the Avian class. We achieved this by evaluating whether stable species-specific sex ratio biases could be discerned in a large *n* dataset. We found only one species in one time period, the sun parakeet in Time Period 1, who displayed a significant species median offspring sex ratio. As a result, our investigation indicates that stable species-specific sex ratios may not be identifiable across time in similar datasets. Our study highlights new directions that future research into this topic could explore. In addition, we underscore the need to better understand and control for the role that species-specific biology, ecology, and management practices play in the sex ratio of zoo-housed avians. Finally, we highlight the importance of developing this measure from both a welfare and a conservation science perspective.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jzbg4040048/s1>, Table S1: List of Avian Synonyms; Table S2: Results from Statistical Analysis; Figure S1: Offspring Sex ratio Distributions.

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